SUSTAINABLE HARVESTING AND CONSERVATION OF THE EDIBLE NEST SWIFTLETS (*AERODRAMUS SPP.*) OF SARAWAK

by

LIM CHAN KOON

A thesis submitted to the University of Kent at Canterbury for the Degree of Doctor of Philosophy in Conservation Biology

Durrell Institute Of Conservation And Ecology (D.I.C.E.) 1999

ABSTRACT

Edible nest swiftlets belong to a group of small-sized cavernicolous swift from the family Apodidae. The swiftlets roost and nest in caves; building a cup-shaped nest that adheres to the cave wall. Depending on the species, the nest is mainly constructed using the salivary nest cement secreted from a pair of sublingual glands. Across their distribution range, several species are heavily exploited for the edible nests they produce, an esteemed Oriental culinary delicacy or commonly known as the "birds' nest soup". Over the past decades, annual nest production and population sizes across the edible nest swiftlets' range has fallen dramatically because of uncontrolled and unsustainable harvesting practices. As a consequence, the Italian Government proposed at the Ninth Conference of the Parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to list all species of swiftlets on Appendix II in 1994. This proposal was not accepted by all parties. Instead, Resolution Conf. 9.15, urging all producer States to encourage scientific research and to promote sustainable nest harvesting, was adopted. This current study was instituted in response to Resolution Conf. 9.15 and acted upon the recommendations of the 1996 CITES Technical Workshop on Conservation Priorities and Actions on Edible Bird's Nest in Surabaya, Indonesia.

In Sarawak, two species of swiftlets produce nests of commercial value. They are the White-nest Swiftlets (*Aerodramus fuciphagus*) and Black-nest Swiftlets (*Aerodramus maximus*). A 12-month comprehensive study of White-nest Swiftlets was carried out in two caves in middle Baram between 1997 and 1998 while sporadic investigations of the Black-nest Swiftlets were conducted at Bau and Bukit Sarang. Three main topics were studied. The first aspect of the study was breeding periodicity and reproductive performance. The annual breeding season, the number of breeding attempts, proportion of breeding, the rate of egg loss, the incubation and fledging period, the interval between clutches and the reproductive success were studied in detail. White-nest Swiftlets in middle Baram employ a multi-brooded reproductive strategy throughout a protracted breeding season of some nine months. Reproductive vigour gradually diminished towards the end of the breeding season. Two broods per year are the norm but some pairs are capable of producing a third clutch. In addition, comparative studies of the breeding periodicity of a non-commercial species, the White-bellied Swiftlets (*Collocalia esculenta*) and some cross-fostering experiments were carried out.

The second aspect of the study comprised the rate of nest building under natural conditions at different time of the year. The development and extension of the nest crest was measured *in situ*, without removing the nests from the cave. This enabled continuous observation on the changes of nest size covering a period of three complete bouts of breeding. Nest building was at its peak at the onset of the breeding season and the lowest activity was recorded during the heavy moulting period in May and June. Some marked nests were experimentally removed to emulate nest harvest conditions. Subsequent development of these nests allowed the impact of nest removal to be monitored and the dynamics of this process to be studied. Furthermore, the correlation of moult, nest building and breeding were examined.

The third aspect of this study concerned the seasonal variations and inter-specific differences in the chemical constituents of the salivary nest cement. The protein and carbohydrate composition of nests were analysed using High-performance Liquid Chromatography. Batches of *A. fuciphagus* nests constructed at different times of the year and nest cement of two other species, namely *A. maximus* and *C. esculenta*, were analysed. Seventeen amino acids were identified in the protein composition of nest samples of all three species. One sialic acid (*N*-acetylneuraminic acid), two hexosamines (glucosamine and galactosamine), three hexoses (galactose, mannose and glucose) and one deoxyhexose (fucose) comprised the carbohydrate composition. Results have shown that there were no significant seasonal variations in the chemical composition of the *A. fuciphagus* nest. On the other hand,

distinctive inter-specific differences were detected. Nest cement of *C. esculenta* has significantly lower sialic acid content but a significantly higher quantity of galactose. These differences were not observed between the nests of *A. fuciphagus* and *A. maximus*. Moreover, fucose was absent from the nests of *A. maximus* but occurred in high concentrations in nests of the other species. Since no differences were found in the chemical composition of nests constructed in different seasons, morphological appearance will be the decisive feature used in determining the quality of nest.

Finally, a sustainable management plan that was acceptable to the local communities and endorsed by the State authority was drawn up and implemented. The recommended harvesting scheme was based primarily on sound scientific data and observations but sensible social-economic factors were also taken into consideration. The management plan calls for a minimum of one full breeding bout to proceed undisturbed per year, which represents approximately half of the natural reproductive output. This undisturbed period should coincide with the second bout of breeding recorded in the natural breeding periodicity between December and March. This is because the breeding productivity of the swiftlets during this period is not seriously decreased and considerable numbers of young swiftlets can be produced from the same resources and investments. Under this scheme, it is possible to have two harvests of good quality nests before December followed by a third harvest after the nestlings have fledged. On top of that, it was recommended that all the small token nests constructed during the heavy moulting period to be removed, an action traditionally referred as "cave cleaning". This can be done twice but the last one should be carried out by late July so that the whole colony makes a clean start with better uniformity in the size of the nest during the following breeding season.

ACKNOWLEDGEMENTS

This successful outcome of this project arises from widespread support, enthusiasm, expectation I received from many affectionate people. First and foremost is the advocating and dedicated guidance from the Earl of Cranbrook, whom I deeply respect and to whom I am full of admiration. It has been a great pleasure to be able to explore the exciting world of swiftlets together with him. I am very grateful for his timeless patience and advice throughout the course of this project.

I would also like to thank my supervisor, Professor Ian Swingland of the Durrell Institute of Conservation and Ecology (D.I.C.E.) at University of Kent at Canterbury for his support and advice. I appreciate the cooperation from Dr. David James of the Biosciences Department for the use of his laboratory facilities. Cordial gratitude is also extended to the Director of Sarawak Forest Department, Mr. Cheong Ek Choon, and Head of the National Park and Wild Life Office, Mr. Sapuan Bin Ahmad, for their co-operation and permission in allowing me to embark on a study of two protected swiftlets species in Sarawak.

Significant scientific data collection and field observations would not have been possible without the full co-operation and *esprit de d'euipe* from the cave owners in middle Baram. Therefore, I would like to express my gratitude to the owner of Lubang Salai, Mr. Kebing Wan, and the respective co-owners, Mr. Lah Ding and Mr. Tuah Ding. Not forgetting also the contribution from Mr. David Labang who arranged for an introductory meeting and initial acquaintance in 1996.

I am also indebted to Laing Wan and Jacob Lah for their support, especially their logistic arrangements, that enabled my field work to be carried out smoothly. I would like to thank Usong Wan and Mulatua Hutabarat for their assistance and companionship throughout the duration of my field study at Lubang Salai. Likewise, it is hard to find sincere and nicer people than the Kayan-Kenyah communities at Kampung Long Laput and Kampung Sungai Dua.

In addition, I appreciate the invitation from Penghulu Bungan Arong for me to conduct a similar study in her caves, and am very grateful for her willingness to let out a small portion of Lubang Beruang for this purpose. This resulted in the establishment of a secondary sampling site — an added bonus for comparative study. Special thanks go to her sons, George Jalong Nawan, Jacob Lawai Nawan and Pall Nawan, who provided me with a lot of information on the historical background of their cave management.

I am also thankful to Balan Taja and David Erang Lian for their countless assistance every time I visited Lubang Beruang. This appreciation is extended to En. Ging Apoi, En. Lenggang Jau and their immediate family members for making my stay at Tuking very pleasant indeed.

Miles away from my field station, limitless support poured in from every corner for the single aim of saving the edible nest swiftlets of Sarawak. I am very grateful to Dr. Elizabeth Bennett for her helpful advice, usually over a wonderful meal, and for initiating a series of dialogue sessions between the community at Baram and groups of Forest Officers from Kuching. Special acknowledgement is extended to Mr. Braken Tisen (Assistant Director of National Parks and Wildlife Division), Mr. Mike Meredith, Mr. David Gill and many whose names are not mentioned here, but who played no less important role in making this dialogue a success.

Last but not least, I would like to thank all the sponsors that made this project possible. This programme was sponsored by the Tunku Abdul Rahman Sarawak Scholarship Foundation and Sarawak Foundation (U.K.). Field expenses were covered by a grant from the Wildlife Conservation Society in New York. I am also very grateful and wish to express my special thanks to Sir John Swire for his generous contributions for my accommodation during my stay in Canterbury, U.K., prior to my fieldwork in Sarawak.

Title Page i
Abstract ii
Acknowledgements iv
Table of Content vi
List of Tables xi
List of Figures xv
List of Plates xviii

CHAPTER 1. Introduction

1.1 GENERAL OVERVIEW. 1

1.2 CONFUSION IN SWIFTLET TAXONOMY. 2

1.3 CLASSIFICATION ADOPTED IN THIS STUDY. 4

1.4 UNIQUE CHARACTERS OF CAVE SWIFTLETS. 5
1.4.1 Echolocation. 5
1.4.2 Salivary Glands. 7

1.5 SWIFTLET DISTRIBUTION. 7

1.6 EDIBLE NEST SWIFTLETS. 9

1.7 EDIBLE NEST SWIFTLETS OF SARAWAK. 10
1.7.1 White-nest Swiftlet — *A. fuciphagus* (Thunberg, 1812). 11
1.7.2 Black-nest Swiftlet — *A. maximus* (Hume, 1878). 11

1.8 PROBLEMS IN SARAWAK. 11

1.9 OBJECTIVES OF STUDY. 12

1.10 THESIS ORGANISATION. 13

Chapter 2. Methods And Study Sites

2.1 SAMPLING LOCATIONS. 14
2.1.1 Lubang Salai. 14
2.1.2 Lubang Beruang. 16

2.2 BIOLOGICAL AND ECOLOGICAL STUDY. 17
2.2.1 History Of Nest Production. 17
2.2.2 Breeding Periodicity. 17
2.2.2.1 Proportion Breeding. 17
2.2.2.2 Hatching Success. 18
2.2.2.3 Fledging Success. 18
2.2.2.4 Reproductive Index (RI). 18
2.2.2.5 Incubation Period. 18
2.2.2.6 Fledging Period. 19
2.2.2.7 Nestling Growth Stages. 19

2.2.2.8 Inter-clutch Interval. 20
2.2.3 Moulting. 20
2.2.4 Nest Parameters. 20
2.2.5 Impact Of Nest Removal. 22
2.2.6 Weight-to-Measurement Ratio. 22
2.2.7 Population Census. 22
2.2.8 Behaviour Observation. 23

2.3 COMPARATIVE STUDY WITH *COLLOCALIA ESCULENTA*. 23
2.3.1 Breeding Periodicity. 23
2.3.2 Egg Transfer. 23

2.4 CHEMICAL ANALYSIS OF THE COMPOSITION OF NEST. 24
2.4.1 Nest Samples. 24
2.4.2 Carbohydrate Constituents. 24
2.4.2.1 Sialic Acids. 24
2.4.2.2 Amino And Neutral Sugars. 25
2.4.3 Protein Constituents. 26

Chapter 3. Social Relations And Human Exploitation

3.1 INTRODUCTION. 28

3.2 HISTORY OF THE EDIBLE NEST TRADE. 29
3.2.1 Origins Of Edible Bird Nest Industry. 29
3.2.2 Edible Bird Nest Trade In Sarawak. 30

3.3 SOCIAL AND ECONOMIC IMPORTANCE OF EDIBLE BIRD NESTS. 32
3.3.1 Source Of Income. 32
3.3.2 Value Of Nest And Demand. 33
3.3.3 Nest Production In Baram. 35

3.4 OWNERSHIP OF NEST-PRODUCING CAVES. 38

3.5 EXPLOITATION AND VARIOUS HARVESTING PRACTICES. 39
3.5.1 Legislation. 39
3.5.2 Typical Harvesting Practises In Sarawak. 40
3.5.2.1 Bau Region. 40
3.5.2.2 Niah Region. 43
3.5.2.3 Baram Region. 43
3.5.2.4 Kakus Region. 44

3.6 CONCLUSIONS. 45

Chapter 4. Breeding Periodicity

4.1 INTRODUCTION. 47

4.2 ANNUAL BREEDING SEASON AND BOUT PERIODICITY. 49

4.3 BREEDING SUCCESS. 58
4.3.1 Proportion Breeding At Various Periods. 58

4.3.2 Hatching Rate And Egg Loss. 59
4.3.3 Fledging Success. 61
4.3.4 Reproductive Index. 63
4.3.5 Percentage Success For Experimentally Removed Nests. 64

4.4 BREEDING AND BROODING. 65
4.4.1 Incubation Period. 65
4.4.2 Fledging Period. 66

4.5 INTER-CLUTCH INTERVAL. 69

4.6 CORRELATION OF MOULTING AND BREEDING. 75

4.7 BEHAVIOUR IN AND AROUND THE CAVE. 81
4.7.1 Foraging Patterns. 81
4.7.2 Roosting Habits And Nest Site Fidelity. 82
4.7.3 Multiple Nests On One Site. 84

4.8 CONCLUSIONS. 84

Chapter 5. Development Of Nest

5.1 INTRODUCTION. 87

5.2 PROGRESSIVE GROWTH OF NEST. 88
5.2.1 Parameters D. 89
5.2.2 Parameters R. 90
5.2.3 Parameters P. 98

5.3 COMPARATIVE RATE OF NEST BUILDING. 102

5.4 IMPACT OF NEST REMOVAL (HARVESTED NESTS). 103

5.5 EMPTY NESTS. 107

5.6 ABANDONED NESTS. 108

5.7 SEASONAL VARIATIONS OF SIZE AND WEIGHT OF NESTS. 109

5.10 CONCLUSIONS. 112

Chapter 6. Comparative Studies

6.1 INTRODUCTION. 113

6.2 COMPARATIVE STUDY OF *COLLOCALIA ESCULENTA*. 114
6.2.1 Annual Breeding Periodicity. 114
6.2.2 Incubation And Fledging Periods. 121

6.3 TRANSFER OF EGGS TO SURROGATE PARENTS. 121

6.4 CONCLUSIONS. 125

Chapter 7. Chemical Composition Of Nest

7.1 INTRODUCTION. 127

7.2 CHEMICAL CONSTITUENTS. 128
7.2.1 Carbohydrate. 129
7.2.1.1 Sialic acids. 129
7.2.1.2 Neutral and amino sugars. 132
7.2.2 Protein. 139

7.3 SEASONAL INTRA-SPECIES VARIATIONS. 146

7.4 INTER-SPECIES VARIATIONS. 147

7.5 CONCULSIONS. 149

Chapter 8. Sustainable Management

8.1 INTRODUCTION. 152

8.2 PROBLEMS AND NEEDS FOR SWIFTLETS CONSERVATION. 153
8.2.1 Declining Yield. 153
8.2.1.1 Over-harvesting. 153
8.2.1.2 Poaching. 154
8.2.1.3 Habitat Loss. 154
8.2.1.4 Potential Threat. 155
8.2.2 Current Population Size. 156
8.2.2.1 Primary Study Site At Lubang Salai. 156
8.2.2.2 Other Sites. 158

8.3 RECOMMENDED SUSTAINABLE HARVESTING STRATEGIES. 159

8.4 AN INTEGRATED APPROACH TO SWIFTLET CONSERVATION. 162
8.4.1 Participation Of Local Communities. 162
8.4.2 Establishment Of Nature Reserves. 162
8.4.3 Interactive Management — Swiftlets House Farming. 163

8.5 CONCLUSIONS. 164

REFERENCES. 166

PLATES. 182

APPENDIX 1. Systematic list of cave swiftlets of the genus *Hydrochous*, *Collocalia* and *Aerodramus*. 187

APPENDIX 2. The date of the lay of the first egg and the fledging of the last nestling for marked nests inside Lubang Salai from April 1997 to March 1998. 189

APPENDIX 3. The value of parameter P and R when the first egg was laid in each of the three breeding cycles from April 1997 to March 1998. 193

APPENDIX 4 Typical daily activities inside Lubang Salai during the brooding period of *A. fuciphagus* and the nature of a returning swiftlet locating its roosting site. 194

APPENDIX 5 The amount of released N-acetylneuraminic acid from hydrolysed edible nest samples quantified using high-performance liquid chromatography. 197

APPENDIX 6 Data for the 2-AA labelled monosaccharides from hydrolysed edible nest samples separated using GlycoSep R column. 198

APPENDIX 7 The amount of various amino acid from hydrolysed edible nest samples quantified using high-performance liquid chromatography. 202

List of Tables

Table 3.1 Comparison of the difference in the relative weight for the post-fledging nests of November 1992 and non-breeding nests at corresponding period of subsequent years. 37

Table 4.1 Comparative values of the proportion breeding recorded from three bouts of breeding between April 1997 and March 1998. 58

Table 4.2 Comparison of the breeding success during the first breeding bout. 58

Table 4.3 Comparison of the breeding success during the second breeding bout. 59

Table 4.4 Comparison of the breeding success in the third breeding bout during the moulting period. 59

Table 4.5 The percentage of hatching and egg loss for three observed breeding bouts between April 1997 and March 1998. 60

Table 4.6 The percentage of fledging success recorded from three bouts of breeding between April 1997 and March 1998. 61

Table 4.7 The number of double nestling broods and the percentage of sibling loss in each bout of breeding in Lubang Salai. 62

Table 4.8 The values of reproductive index (RI) of each bout of breeding for Lubang Salai and Lubang Beruang. 63

Table 4.9 Comparison of breeding successes for experimentally removed nests on 13 September 1997 in Lubang Salai. 65

Table 4.10 The incubation period (mean ± SE) of *Aerodramus fuciphagus* recorded from three breeding bouts observed at Lubang Salai. 65

Table 4.11 The fledging period (mean ± SE) of *Aerodramus fuciphagus* recorded from three breeding bouts observed in Lubang Salai. 67

Table 4.12 The comparison of fledging period (mean ± SE) for brood with single and brood with two nestling inside Lubang Salai. 67

Table 4.13 The time and frequency of feeding for nestlings in 27 marked nests inside Lubang Salai on 11 June 1997. 67

Table 4.14 Time and frequency of feeding observed on 8 October 1997 inside Lubang Salai. 68

Table 4.15 Interval from the previous brood or egg lost during the third breeding bout to the lay of subsequent clutch in the first breeding bout at Lubang Salai (mean ± SE). 69

Table 4.16 The interval from previous brood or egg lost during the first breeding bout to the lay of subsequent clutch in the second breeding bout at Lubang Salai (mean ± SE). 69

Table 4.17The appearance of the first egg in the first breeding bout for nests with successful breeding and those that lost their clutch in the third breeding bout. 70

Table 4.18 Marked nests in Lubang Salai that have a clutch laid during each bout of breeding between April 1997 and March 1998. 71

Table 4.19 Nests that have a second clutch within the first breeding bout after the first brood had fledged in Lubang Salai and Lubang Beruang. 71

Table 4.20 Nest with the lay of replacement egg during the first breeding bout in Lubang Salai. 72

Table 4.21Nest with the lay of replacement egg during the second breeding bout in Lubang Salai. 73

Table 4.22 Feather count for ten categories of primary feathers collected inside Lubang Salai between April 1997 and February 1998, including a collection in November 1998 for comparison. 76

Table 4.23 Three typical daily outward flights of swiftlet at each quarter from 0600 to 0700 hours at Lubang Salai. 81

Table 4.24 The distribution of roosting swiftlets outside and inside a nest at three sections inside Lubang Salai on 30 October 1997. 83

Table 5.1 Successive measurements of parameter D from nests marked inside Lubang Salai between April and August (n = 48). 89

Table 5.2 Measurements of parameter D from August to October in Lubang Salai (n = 45). 89

Table 5.3 Successive measurements of parameter D for nests marked in Lubang Beruang from May to August (n = 15). 90

Table 5.4 Successive measurements of parameter D from September to October for nests left unharvested inside Lubang Beruang (n = 14). 90

Table 5.5 Measurements for parameter R from marked nests in Lubang Salai between April and August 1997 (n = 50). 90

Table 5.6 Growth rate of parameter R from nests marked inside Lubang Salai between April and August 1997 (n = 50). 91

Table 5.7 Successive measurements of parameter R for nest marked in Lubang Beruang between May and August 1997 (n = 14). 91

Table 5.8 Growth rate of R for nests marked in Lubang Beruang between May and August 1997 (n = 14). 91

Table 5.9 Comparison of the mean value of R for nests with successful breeding (breeding nests); nests without any lay of a clutch or loss the content (empty) and harvested nests in Lubang Salai between April and August. 93

Table 5.10 Successive measurements of parameter R between August and December 1997 for marked nests left unharvested inside Lubang Salai (n = 49). 96

Table 5.11 Successive measurements of R-value between September and December for marked nests left unharvested at Lubang Beruang (n = 12). 96

Table 5.12 Comparison of the mean nest building rate for experimentally removed nests in Lubang Salai at different seasons. 98

Table 5.13 Successive measurements of parameter P for nests marked in Lubang Salai between April and August 1997 (n = 50). 98

Table 5.14 The growth rate of the parameter P for nests marked in Lubang Salai between April and August 1997 (n = 50). 99

Table 5.15 Successive measurements of parameter P for nests marked in Lubang Beruang between April and August 1997 (n = 15). 99

Table 5.16 The growth rate of parameter P for nests marked in Lubang Beruang between April and August 1997 (n = 15). 99

Table 5.17 Successive measurements of parameter P between August and December 1997 for nests left unharvested inside Lubang Salai (n = 54). 100

Table 5.18 Successive measurements of parameter P between August and December 1997 for marked nest in Lubang Beruang (n = 12). 100

Table 5.19 The growth rate of P for nests removed on 26 April 1997 in Lubang Salai (n = 14). 100

Table 5.20 The growth rate of the parameter P for nests removed on 13 September 1997 in Lubang Salai (n = 11). 101

Table 5.21 The comparative rate of nest building at different bout of breeding recorded in Lubang Salai. 102

Table 5.22 Comparison of the rate of nest building for successive generations of nests that underwent multiple harvest in Lubang Salai. 102

Table 5.23 Nests that were experimentally removed in Lubang Salai on April 1997 with the subsequent re-deposition and the lay of a clutch. 103

Table 5.24 Nests that were experimentally removed twice between April and September in Lubang Salai. 105

Table 5.25 Comparative data of nests harvested in Lubang Salai and Lubang Beruang on 13 September and 16 September respectively. 106

Table 5.26 The date of fledging until the lay of subsequent clutches for nests that were removed after the young had fledged. 106

Table 5.27 Nests of various categories that were removed twice between April and November in Lubang Salai. 107

Table 5.28 Percentage of nest that remained empty for each bout of breeding between April 1997 and March 1998. 107

Table 5.29 The date when the first egg was laid and the respective value of R and P for six marked nests that were empty in the April-July breeding bout. 108

Table 5.30 Seven nests that remained empty at Pasen Avut during the April-July breeding bout and the date of the subsequent clutch. 108

Table 5.31 The correlation of the mean weight and the P/R ratio for nests harvested from Lubang Salai at different seasons. 110

Table 5.32 The average weight of nest from three harvests in Lubang Salai categorised into various P/R ratio ranges and its percentage. 111

Table 6.1 The incubation and fledging period of *C. esculenta* from Lubang Salai recorded from beginning of June until November (mean ± SE). 121

Table 6.2 The outcome of the transfering *A. fuciphagus* eggs into *C. esculenta* nests in Lubang Salai. 122

Table 6.3 Experimental attempts and the outcome of the transferred *A. fuciphagus* eggs into *C. esculenta* nests in Lubang Ngawai. 123

Table 6.4 The experimentation on the removal of *C. esculenta* nest at various stages and their subsequent development in Lubang Salai on 9 August 1997. 125

Table 7.1 The concentration of *N*-acetylneuraminic acid from *A. fuciphagus* nests constructed at different months of the year in Lubang Salai. 129

Table 7.2 The concentration of *N*-acetylneuraminic acid for *A. maximus* and *C. esculenta* nests. 132

Table 7.3 The concentration of released amino and neutral sugars from hydrolysed edible nest samples produced by threes species of swiftlets. 137

Table 7.4 The concentration of amino and neutral sugars from *A. fuciphagus* nest constructed at different time of the year in Lubang Salai (mean ± SE). 138

Table 7.5 Inter-specific comparison of the concentrations of various monosaccharides from nest of three species of swiftlets (shown as the mean ± SE with the percentage in parenthesis). 138

Table 7.6 The amount of various amino acids from the hydrolysate of dried edible bird nest from three species of swiftlets. 140

Table 7.7 The concentration of various amino acids from *A. fuciphagus* nests constructed at different month of the year in Lubang Salai (mean ± SE). 141

Table 7.8 Inter-specific comparison of the concentration of various amino acids from nest of three species of swiftlets (shown as mean ± SE with the percentage of total in parenthesis). 145

Table 8.1 Population censuses of *A. fuciphagus* in Lubang Salai during April and May 1997. 157

Table 8.2 Total numbers of nests inside Lubang Salai including nests left for breeding and marked nests used in this study, and calculated numbers of breeding swiftlets based on two birds per nest. 157

Table 8.3 Estimated numbers of nests, and sexually productive individuals, of *A. fuciphagus* from major caves in middle Baram. 157

Table 8.4 Estimated numbers of nests, and sexually productive individuals, of *A. maximus* from caves around Bukit Sarang, Kakus. 158

List of Figures

Figure 1.1 World distribution of swiftlets (*Aerodramus spp. & Collocalia spp.*) and the ranges of White-nest Swiftlet (*A. fuciphagus*) and Black-nest Swiftlet (*A. maximus*). 8

Figure 2.1 Locations of Lubang Salai and Lubang Beruang. 15

Figure 2.2 Lateral and vertical view of a typical *A. fuciphagus* nest, showing all parameters (i.e. D, R, & P) applied in this study. 21

Figure 3.1 Annual production of nest from Lubang Salai between 1948 to 1998. 35

Figure 3.2 Annual nest production from Lubang Salai from 1992 to 1998. 36

Figure 3.3 The annual nest production from Lubang Beruang from 1991 to 1997. 37

Figure 4.1 Proportion breeding for *A. fuciphagus* at the marked nests in Lubang Salai and Lubang Beruang. 50

Figure 4.2 The number of eggs and nestlings at the marked nests in Lubang Salai between April 1997 and February 1998. 51

Figure 4.3 The number of eggs and nestlings at the marked nests in Pasen Avut (L. Beruang) between May 1997 and February 1998. 53

Figure 4.4 The number of eggs and nestlings at the marked nests in Pasen San (L. Beruang) between May 1997 and Frbruary 1998 54

Figure 4.5 Daily temperature outside and inside Lubang Salai with the respective relative humidity on 9 April 1997. 56

Figure 4.6 The correlation of moulting and breeding of *Aerodramus fuciphagus* in Lubang Salai. 78

Figure 5.1 The increment of parameter R for several nests with successful breeding between March and September 1997. 92

Figure 5.2 The increment of R-value for nests without any clutch laid from March to September. 94

Figure 5.3 Comparison of the average of R-value for nests with successful breeding, without any clutch laid and harvested nest between March and September 1997. 95

Figure 5.4 Pre-harvest and post-harvest profile of the increment of parameter R for several nests between March and September 1997. 97

Figure 6.1 Comparison of the proportion breeding for *C. esculenta* and *A. fuciphagus* at Lubang Salai. 115

Figure 6.2 Total number of eggs and nestlings of *C. esculenta* at Lubang Salai. 116

Figure 6.3 The proportion breeding of *C. esculenta* at Lubang Ngawai from June 1997 to February 1998. 117

Figure 6.4 Comparison of the proportion breeding for *C. esculenta* and *A. fuciphagus* at Lubang Beruang. 119

Figure 6.5 The total number of eggs and nestling of *C. esculenta* at Lubang Beruang. 120

Figure 7.1 Chromatogram of the DMB derivatives of neuraminic acids standard mixture. 130

Figure 7.2 Chromatogram of the DMB derivatives of neuraminic acid for *A. fuciphagus* nest constructed in April 1997 (marked nest S045). 130

Figure 7.3 Chromatogram of DMB derivatives of neuraminic acid for *A. maximus* nest. 130

Figure 7.4 Chromatogram of DMB derivatives of neuraminic acid for *A. fuciphagus* nest constructed in June during the heavy moulting period or "*melaie*". 131

Figure 7.5 Chromatogram of DMB derivatives of neuraminic acid for *A. fuciphagus* nest constructed in July (marked nest S045). 131

Figure 7.6 Chromatogram of DMB derivatives of neuraminic acid for replacement nest of *A. fuciphagus* constructed in August (marked nest S045). 131

Figure 7.7 Chromatogram of DMB derivatives of neuraminic acid for *C. esculenta* nest. 132

Figure 7.8 Chromatogram of 2-AA labelled monosaccharides from a standard solution. 133

Figure 7.9 Chromatogram of 2-AA labelled monosaccharides for *A. fuciphagus* nest constructed in April (marked nest S040). 134

Figure 7.10 Chromatogram of 2-AA labelled monosaccharides for *A. fuciphagus* nest constructed in June during the heavy moulting period (unmarked nest). 134

Figure 7.11 Chromatogram of 2-AA labelled monosaccharides for *A. fuciphagus* nest constructed in July (marked nest S040). 135

Figure 7.12 Chromatogram of 2-AA labelled monosaccharides for replacement nest of *A. fuciphagus* constructed in August (marked nest S040). 135

Figure 7.13 Chromatogram of 2-AA labelled monosaccharides for *A. maximus* nest. 136

Figure 7.14 Chromatogram of 2-AA labelled monosaccharides for *C. esculenta* nest. 136

Figure 7.15 Chromatogram of the PTC derivatives of amino acids for *A. fuciphagus* nest constructed in April 1997 (marked nest S058). 142

Figure 7.16 Chromatogram of the PTC derivatives of amino acids for *A. fuciphagus* nest constructed in June during the heavy moulting period (unmarked nest). 142

Figure 7.17 Chromatogram of the PTC derivatives of amino acids for *A. fuciphagus* nest constructed in July 1997 (marked nest S058). 143

Figure 7.18 Chromatogram of the PTC derivatives of amino acids for *A. fuciphagus* nest constructed in August 1997 (marked nest S058). 143

Figure 7.19 Chromatogram of the PTC derivatives of amino acids for *A. maximus* nest. 144

Figure 7.20 Chromatogram of the PTC derivatives of amino acids for *C. esculenta* nest. 144

Figure 8.1 The recommended sustainable harvesting schemes for *A. fuciphagus* in Sarawak. 160

List of Plates

Plate 1. White-nest Swiftlets (*Aerodramus fuciphagus*) nesting on near vertical surfaces of a narrow cavern in Lubang Tuking, middle Baram (1997). 182

Plate 2. Eggs and nestlings of *A. fuciphagus*; the naked pinkish ones are stage-1 nestlings of about 1 to 6 days old; to the right is a stage-2 nestling (L. Salai, 1997). 182

Plate 3. Two stage-2 *A. fuciphagus* nestlings of approximately 7 to 13 days old; note the minute feather sheath on the main feather tracks (L. Salai, 1997). 183

Plate 4. Stage-3 or porcupine-liked nestling of *A. fuciphagus* (≈ 14 – 20 days old); note the erupted feather sheaths; the nestling to the right is roughly a week older or stage-4 (L. Salai, 1997). 183

Plate 5. Two stage-4 nestling of *A. fuciphagus* between 21 – 27 days old (middle left); to the right are stage-5 nestling (≈ 28 – 35 days old) with well developed primary feathers but not over-shooting the tip of the rectrices (L. Salai, 1997). 184

Plate 6. Many stage-7 or near fledging nestling of *A. fuciphagus* (≈ 45 days old); their wings are fully grown and they spend most of the time hanging by the crest of the nest (L. Salai, 1997). 184

Plate 7. Nestling of *A. fuciphagus*, showing various stages of growth; the one to the extreme right is stage-6 nestling of 36 – 40 days old (L. Salai). 185

Plate 8. Multi-nest incident occurs exclusively after a successful breeding attempt; it is very likely that the pair responsible for the construction is the offspring(s) from the precusor nest (L. Salai, 1997). 185

Plate 9. Marked nest of *A. fuciphagus* used in this study; parametric measurements, i.e. D, R, & P, were obtained from these nests; the nest crest is beginning to form (L. Salai, 1997). 186

Plate 10. After a breeding attempt, deteriorated nest was restored, usually with addition of new salivary nest cement as clearly shown in this photograph; the brownish old nest has been in the cave for about five months (L. Beruang, 1997). 186

Chapter 1
Introduction

1.1 GENERAL OVERVIEW

The exponential growth of human populations and of technological advances have caused degradation of many world's ecosystems, while the majority of wild species that have some significant commercial value have been heavily exploited (Freese, 1997). Furthermore, misleading beliefs and myths as well as human greed have also brought about a flourishing trade in exotic wildlife and animal products, threatening the survival of many species throughout the world (Sankaran, 1995; Little, 1996). Some good examples are the lucrative trade of ivory (Milner-Gulland & Beddington, 1993), rhinoceros horn (t'Sas-Rolfes, 1995), tiger penises and tiger bones (Mills & Jackson, 1994). Edible nest swiftlets from the genus *Aerodramus* — a unique and intriguing group of small-sized cavernicolous bird from the family Apodidae, are now adding to this list of critically threatened and endangered species.

Besides the astonishing biology of these birds, another remarkable aspect of the edible nest swiftlets that deserves attention is its long standing association with mankind, and his ensuing acts that have caused the decline of this group. The discovery of this natural product and its subsequent introduction to China towards the end of the Ming Dynasty around 1368 – 1644 AD marked the beginning of an intricate association between swiftlets and humans (Medway, 1963; Lau & Melville, 1994). The edible nest swiftlets are heavily exploited because of the edible nest they produce. The commonly known "birds' nest soup", an esteemed Oriental culinary delicacy and highly treasured Chinese traditional medicine, is consumed for its reputed recuperative properties. Such is the brilliance of the edible birds' nest soup that it has continued to enthral gastronomists for almost four centuries and the commodity today commands a multi-million dollar industry in South East Asia (Er *et al.*, 1995). These nests are believed to reinforce body fluids, nourish blood and moisten the respiratory tract and skin; they are believed to replenish the vital energy of life, build up health and aid metabolism, digestion and absorption (Lau & Melville, 1994; Mainka & Mills, 1995). This list also includes further unsubstantiated claims such as prolonging life, resisting ageing, treatment of pulmonary diseases, cancers and as an aphrodisiac.

Throughout the range, over-collecting is undoubtedly the main reason that has caused wild swiftlet populations to diminish sharply, and for local extinction to occur in some areas (Er *et al.*, 1995; Good, 1993; Tompkins, 1997). In Sarawak, a 48% decline in the Black-nest Swiftlet population was recorded at Niah between 1935 and 1987, while the White-nest

Swiftlet population at Baram was reduced by 43% over a 17 years period (Good & Wong, 1989). At Gomantong in Sabah, Malaysia, the nest yield of Black-nest Swiftlet decreased from 12,000 kg in the turn of the century to 5,000 kg in 1985, representing 58% decline. The fate of White-nest Swiftlet in Sabah suffered even a greater impact, losing 84% of the population from 1924 to 1985 (Francis, 1987b). Similarly, a decline of 33% was recorded at Songkhla Lake in Thailand and a 41% reduction in nest harvests of White-nest Swiftlet in Myanmar between 1951 to 1956 and 1978 to 1982 (Lau & Melville, 1994).

In response to widespread concern in 1994, the Italian Government presented a proposal at the Ninth Conference of the Parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) at Fort Lauderdale, United States of America, to list all species of swiftlets on Appendix II. However, exporting countries and representatives of the birds' nest industry reacted by proposing a review of current trade management to assess whether a CITES listing was justified, instead of an outright listing (Broad, 1995). In concession, Resolution Conf. 9.15 was adopted, which calls for a technical workshop to be held for the purpose of reviewing current management practices in the range states and to recommend necessary research in order to formulate management strategies that will enhance conservation of the species, while ensuring that use of and trade in the wild resource is sustainable (Anon., 1994). Subsequently in 1996, a CITES Technical Workshop on Conservation Priorities and Actions on Edible Bird's Nest was held in Surabaya, Indonesia. The outcome of the workshop falls short of a listing in CITES Appendix II, but has, nevertheless, prompted international action for management research and leaving the region to ensure that the trade is carried out on a sustainable basis instead (Anon., 1996).

Acting upon the recommendations of the CITES Surabaya Workshop 1996, the Sarawak Government has incorporated conservation of edible nest swiftlets into its comprehensive Wildlife Master Plan. This plan outlines the regulations for the protection and conservation of wildlife in general and in particular calls upon sustainable management strategies for the edible nest swiftlet throughout the state. An effective and sustainable management plan of the edible bird nest requires sound biological and ecological data. Unfortunately, few data are available, especially information on their breeding cycle (Cranbrook, 1984; Cranbrook *et al.*, 1996), although Sarawak has been known as one of the major producers, as well as a centre for processing edible bird nests.

1.2 CONFUSION IN SWIFTLET TAXONOMY

The term "swiftlet" is generally applied to a group of small-sized swifts from the family Apodidae in the Order Apodiformes (which also comprises the Treeswifts). Precise

species limits in certain genera remain unresolved. This is nowhere more apparent than in the genus *Collocalia*, which constitutes one of the most difficult of all groups of birds. Principal revisers of this genus also acknowledged this fact, admitting that their results are purely tentative and liable to modification (Peters, 1940). Lack (1964) placed the swiftlets in the subfamily Chaeturinae. However, Brooke (1970a) noted that no known characters above the generic level, with the exception of foot structure, separated *Chaetura* and *Apus*. Therefore, Chantler and Driessens (1995) rejected the division of subfamilies based on these genera. Current thinking tends to place the swiftlets in the subfamily Apodinae, within which they have been classed as the tribe Collocaliini (Brooke, 1972; Becking, 1985; Chantler & Driessens, 1995).

At generic level, there are disputes to which genus the edible nest swiftlets should be placed, that is, whether in the genus *Collocalia* Gray 1840 or in the genus *Aerodramus* Oberholser 1906. Salomonsen (1983) stated that the classification of the swiftlets presents one of the most difficult problems in avian systematics, while Cranbrook (1984) cautioned that there is much confusion over the validity of many described subspecies because the morphological differences among them are restricted to slight colour variations and sizes.

Oberholser (1906) divided *Collocalia* Gray on micro-anatomical features, choosing *innominata* Hume as type of a new subgenus *Aerodramus* that was characterised by the presence of tarsal feathering. Brooke (1970b) split the genus *Collocalia* into three subgenera, namely *Hydrochous*, a monotypic genus comprising the Giant Swiftlet (*H. gigas*), *Collocalia*, which include the glossy and non-echolocating species, and *Aerodramus* consisting of the non-glossy, grey species with the ability to echolocate. The same author (Brooke, 1972) later drew together evidence indicating that these differences justify a separation at generic level. Although his classification produces a division that is not compatible with Oberholser's scheme, Brooke adopted *Aerodramus* Oberholser as the valid generic name of the grey-brown group, limiting *Collocalia* to the group of small, glossy-plumaged swiftlets.

This division was re-affirmed by Medway and Pye (1977) based on the echolocation ability of the genus *Aerodramus* Oberholser. Developments in molecular studies now provide new opportunities for recognising phyletic affinities. Electrophoresis assays of nine enzyme systems from samples of *Collocalia esculenta*, *Aerodramus fuciphagus* and *Apus affinis* involving nineteen loci showed that there is a lesser intergeneric difference between *Collocalia* and *Apus* as compared to the genetic distance between *Collocalia* and *Aerodramus* (Lim, 1993). A phylogeny of the swifts based on cytochrome *b* mtDNA produced anomalous clustering among examples of *Aerodramus* species, but also emphasised the phylogenetic distance between sampled representatives of *Collocalia* and *Aerodramus*, indicating that these genera are not sister taxa and, thus supporting the generic split (Lee *et al.*, 1996).

Nevertheless, some authors have preferred to retain all swiftlets in the genus *Collocalia*. Sibley and Monroe (1990) regrouped all swiftlets in the genus *Collocalia* Gray but retained the monotypic genus *Hydrochous* Brooke based on evidence of the DNA-DNA hybridisation studies. Sseveral subspecies within *C. fuciphaga* were recognised. The subspecies *C. f. inexpectata* is restricted to the Andaman and Nicobar Islands, *C. f. fuciphaga* is found in Java and Lesser Sunda Islands, and the subspecies *C. f. vestita* was designated for the birds in Vietnam, southern Malay Peninsula and Sumatra. In addition, *C. germani* is restricted to birds from the coastal lowlands of northern Malay Peninsula including the Mergui Archipelago, north of Borneo and south-western Palawan islands group in the Philippines.

Chantler and Driessens (1995) recognised eight races of *C. fuciphaga* with *C. germani* treated as a race. The race from Andaman and Nicobar Islands remains the same as *C. f. inexpectata*, while *C. f. fuciphaga* is restricted to birds from Java Island. Birds from the Lesser Sunda Islands are recognised as *C. f. micans* and those from Flores (known from only one specimen) are designated as *C. f. dammermani*. Different from Sibley and Monroe's (1990) classification, the race *C. f. vestita* is strictly for the birds from Sumatra and Borneo while *C. f. perplexa* is confined to the Maratua Archipelago. The race *C. f. germani* is specifically meant for birds from Hainan Island, along the coast of Vietnam and Cambodia, Mergui Archipelago in Myanmar and Thailand south into the Malay Peninsula. Any group of birds clustering in the Malay Peninsula south of the distribution range of *germani* race is recognised as *C. f. amechana*. The black-nest builder is accepted as *C. maxima* with three races, namely *C. m. maxima*, *C. m. lowi* and *C. m. tichelmani*. On the other hand in a more generalised manner, Inskipp *et al.* (1996) recognised two species of white-nest builder. These are *C. fuciphaga* and *C. germani*. However, three races of *C. fuciphaga* were recognised, namely *C. f. inexpectata*, *C. f. perplexa* and *C. f. vestita*, but the distribution of each form was lacking.

The classification adopted in the proposed listing in Appendix II follows Sibley and Monroe (1990). The four species of swiftlets recognised by CITES as the producer of edible bird nest are *Collocalia fuciphaga* (Gmelin) 1789, *Collocalia germani* Oustalet 1878, *Collocalia maxima* Hume 1878, and *Collocalia unicolor* (Jerdon) 1840 (Lau & Melville, 1994; Er *et al.*, 1995). The first two species are the "white-nest" builders while the latter two species are generally taken as the "black-nest" builders. *Collocalia unicolor* occurs only in Indian sub-continent and is outside the scope of this study while taxonomy of *C. maxima* is less problematic and generally accepted without much confusion.

1.3 CLASSIFICATION ADOPTED IN THIS STUDY

The classification adopted in this thesis follows Cranbrook *et al.* (1996). In addition, many authors have now recognised the weight of the differences and adopted Brooke's (1972)

usage of *Aerodramus* (Medway & Pye, 1977; Langham, 1980; Tarburton, 1986a, 1986b; Francis, 1987b; Good, 1993; Leh, 1993; Cranbrook *et al.*, 1996). In all, 26 species of swiftlets are recognised in the world with many localised or endemic species and only four wide-ranging species (Appendix 1). Distinctions at the generic level are based on the morphological characters as well as behaviour and the ability to echolocate (Medway & Pye, 1977). The genus *Collocalia* is reserved for swiftlets with a glossy plumage, generally green or bluish-green gloss, and unable to echolocate. Species that have a non-glossy, dark greyish-brown plumage and the ability to echolocate are placed under the genus *Aerodramus*. The genus *Hydrochous* is monophyletic with a single representative, the Giant Swiftlet, with a dark-brownish plumage and disorientated in darkness.

1.4 UNIQUE CHARACTERS OF CAVE SWIFTLETS

1.4.1 Echolocation

Animals use a combination of senses and techniques in finding their way around the environment. Vision, olfactory perception and touch are few elementary senses found in the animal kingdom. Other less commonly encountered mechanisms include echolocation (Kellogg, 1958; Barrett-Lennard *et al.*, 1996) and electro-magnetic pulses or electroreception (Hopkins & Bass, 1981; Young, 1981; Landsman, 1993). Echolocation or sonar is a way of finding objects using sound to locate objects by their echoes. The direction and temporal difference between the emission and the returning echo can allow where and how far any objects are. Among bats, it can be more complicated, involving frequency sweep pulses and Doppler shifts (Sales & Pye, 1974).

It is known that certain species of cave swiftlets possess an ability to echolocate, enabling them to orientate and navigate in total darkness. No other bird except the Oilbird of South America (*Steatornis caripensis*) has this capability (Medway, 1959, 1966, 1967; Fullard *et al.*, 1993; Chantler & Driessens, 1995; Cranbrook *et al.*, 1996). Field observations have shown that species from the genus *Aerodramus* can utter this echolocation call but not the genus *Collocalia* (Medway, 1966; Chantler & Driessens, 1995). The ability to echolocate has influenced, in many ways, their evolutionary direction and the adaptation to their habitat. Is has enabled them to penetrate into the darkness of caves to roost and nest where they are relatively safe from predators or sheltered from outside weather conditions (Francis, 1987b). In addition, it allows them to forage far away from their roosting cave, returning after sunset, making full use of the last remaining light of twilight and perhaps crepuscular flights of insects (Medway, 1962c).

The function of acoustic orientation by echolocation among swiftlets was initially postulated by Griffin (1958). This discovery was then confirmed by Novick (1959) who demonstrated that this call is essential for oriented flight in darkness by *A. unicolor*, a swiftlet found in Sri Lanka. Similar calls were heard from *A. maximus* by Medway (1959). This echolocating tone, a double click, differs from avian song or any other vocalisation produced by swiftlets. The mechanism of click production is assumed to be syringeal because the echolocating call and other vocalisation can not be uttered simultaneously. The syrinx is an enlargement at the lower end of the trachea, containing a pair of semilunar tympaniform membranes with muscles that alter the tension to produce a sound (Young, 1981; Gill, 1990). Experiment has shown that muscles on the side of the syrinx cause it to close suddenly as a burst of air comes out. As the syrinx closes, it emits the first part of the click. The second, louder half is produced when the syrinx reopens (Suthers & Hector, 1982).

Sonic analysis has demonstrated that the component clicks are of short duration (mean 2 to 5 msecs), comprising a broad band of mixed frequencies peaking within the range audible to human ears (Medway, 1959). Therefore, the echolocating calls of swiftlets can be heard as a series of clicks in rapid succession culminating in a staccato rattle. The frequency range of the calls is between 1 to 16 kHz (Fullard *et al.*, 1993), with most of the energy focussed between 2 – 5 kHz (Francis, 1987b). Although calls from different individuals fall within this frequency range, they exhibit a slight difference in the distribution of frequency peaks. For example, *A. sawtelli* emits distinct single pulses with peak frequencies within the range of 6 – 8 kHz (Fullard *et al.*, 1993) while those of *A. fuciphagus* falls within 1.5 – 4.5 kHz with a repetition rate of 9 – 10 pulses per second (Medway, 1967).

Unlike the emission produce by most microchiropteran bats, the swiftlets' echolocation is of a lower frequency sound that is not sensitive enough to detect small objects like insects (Medway, 1959; 1967). Swiftlets appear to use this low-resolution echolocation for target discrimination only. The unstructured, click-like quality of swiftlets' echolocation lacks the manipulation of the frequency configuration within each call found among bats (Fullard *et al.*, 1993). This suggests that frequency structure is not an important element in these calls and swiftlets use only temporal information to determine features about their targets (Pye, 1980). The sensitivity of swiftlets' echolocating call remains debatable. Smyth and Roberts (1983) concluded that *A. spodiopygius* is only able to detect obstacles between 10 – 20 mm in diameter while Griffin and Thomson (1982) showed that it could resolve objects as small as 6 mm in diameter.

Observations near the entrance of caves confirmed that swiftlets flying out of a cave stop clicking went they get close to the entrance where it is bright enough to see. In contrast, the echolocating calls are uttered and can be heard as soon as the swiftlets approach the entrance. Medway (1959) proposed that the use is not obligatory because the call in dimly

lighted areas is not continuous but periodic. Furthermore, there is no ultrasonic component (i.e 20 – 160 kHz) in the echolocating calls, as proven in *A. maximus* and *A. salanganus*, or any vocalisation of the *C. esculenta* in Peninsular Malaysia (Cranbrook & Medway, 1965). Young swiftlets do not utter the rattle call until shortly before fledging (Medway, 1959; Harrison, 1966).

1.4.2 Salivary Glands

The nest cement is manufactured and secreted from a pair of sublingual glands located beneath the tongue that become hypertrophied during the nest-building period (Johnston, 1958; Medway, 1962a). Both male and females have a pair of lobed glands, one on each side of the midventral line. Each gland tapers anteriorly to short ducts opening into the floor of the buccal cavity. Histological cross section revealed that the lobes are divided into numerous alveoli, each lined with a single layer of columnar epithelium cells on the basement of infolded connective tissues. The secretion of the sublingual glands performs no known digestive function, but is used in nest construction (Medway, 1962a).

Cyclic variations in the size of the glands, which imply different stages of activity, in two species of swiftlets collected in a Siamese cave was suspected to be correlated with different breeding seasons (Marshall & Folley, 1956). The salivary gland is enlarged and becomes active during the nest building season. At other times of the year, it degenerates into a rudimentary inactive stage. In addition, it was postulated that there might be a direct endocrinological relationship between the phase of reproductive activity and the state of the sublingual glands (Johnston, 1958). However, in a study of *A. maximus* in Sarawak, Medway (1962a) concluded that there is no correlation found between the reproductive state of individual birds and activity in the sublingual glands. Surprisingly, it was noted that when in breeding condition, females had totally inactive glands, while the opposite was true in all males. The salivary gland is enlarged and becomes active during the nest building season; at other times, it can degenerate into diminished inactive state.

1.5 SWIFTLET DISTRIBUTION

The general distribution of the three genera of swiftlets (Figure 1.1) extends from the Seychelles Islands in the western Indian Ocean through southern continental Asia, the Indo-Australia archipelago, the Philippines, northern Australia, to the west and south-west Pacific (Medway, 1966). In more detail, the limits of the swiftlets' world range lies to the west on the Seychelles Island (4° 30′ S, 55° 33′ E) in the Indian Ocean, and to the east on the Marquesas

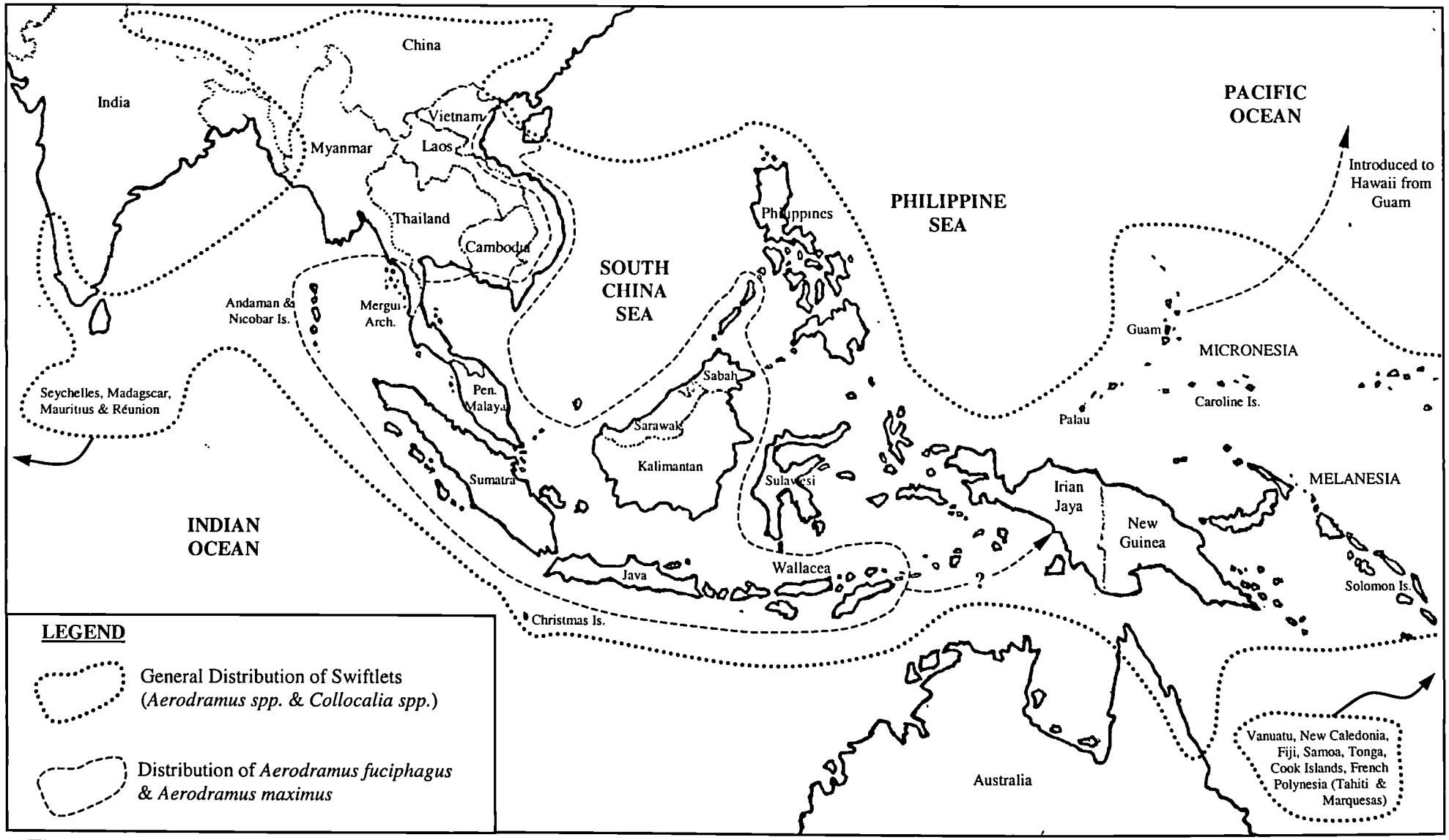

Figure 1.1 World distribution of swiftlets (*Aerodramus spp. & Collocalia spp.*) and the ranges of White-nest Swiftlet (*A. fuciphagus*) and Black-nest Swiftlet (*A. maximus*) based on latest reference in Appendix 1.

Islands (10° S, 140° E) in the Pacific. Northwards they extend to 33° N in Himachal Pradesh, India, and 32° N in Szechwan, China, and southwards to about 20° S on Mauritius in the Indian Ocean, and in Queensland, Australia, and about 22° 30′ S on New Caledonia in the south-western Pacific (Cranbrook, 1984). A comprehensive distribution list for each species of edible nest swiftlets in the world is given by Chantler and Driessens (1995) and Er *et al.* (1995)

The distribution of edible nest swiftlets (Figure 1.1) includes the Andaman and Nicobar islands (Sankaran, 1995), Hainan Island in China (Fan & He, 1996), Vietnam (Nguyen Quang, 1990; 1994), the coast and islands of Thailand (Medway, 1963; De Groot, 1983; Valli & Summers, 1990), Peninsular Malaysia (Langham, 1980), Singapore (Kang & Lee, 1991; Kang *et al.*, 1991), Indonesian archipelago from Sumatra, Java and the Lesser Sunda Islands (Medway, 1963; Pakpahan & Soehartono, 1994; Raharjo *et al.*, 1996; Soehartono & Mardiastuti, 1996; Mardiastuti & Mranata, 1996), Palawan Islands in the Philippines (Corpuz & Leon, 1996), the island of Borneo including Sarawak (Medway, 1957; 1960; 1962b; 1962c; Good, 1993; Leh, 1993) and Sabah (Burder, 1961; Orolfo, 1961; Francis, 1987b).

1.6 EDIBLE NEST SWIFTLETS

Throughout their ranges, nests from the two species are heavily harvested and contribute to the bulk of the world supply of edible nests (Medway, 1969). The nests produced by *A. fuciphagus* are the most highly prized because they are made up entirely of pure hardened salivary nest cement (Plate 1). These nests need little cleaning and are often sold in their original cup-shaped form in the market. The second important species is *A. maximus*, which also construct a self supporting cup-shaped nest, but many feathers are included between the salivary laminae, which makes the nests look black and fluffy. Nests from this species need elaborate and extensive cleaning. They are first soaked in cold water until the nest cement is softened. The feathers are then picked out one by one. Finally, the cleaned salivary strands are then rearranged and reconstructed, or moulded into chips of various shapes; usually being either oval or diamond-shaped.

Nests from another species, the Indian Swiftlet (*A. unicolor*) found in the Western Ghats and rocky islets of the Malabar coast in south-western India and in Sri Lanka, were collected for export to China during the British colonial rule (Ali & Ripley, 1983). This species builds nest with a mixture of grass, moss or feathers, which necessitates processing before sale. However, the trade of this species faded out at the turn of this century, as a result of over-exploitation of the colonies and the disproportionate risks and organisation involved in collecting the nests (Sankaran, 1995; 1998).

Owing to a shortage supply of nests from *A. fuciphagus* and *A. maximus*, there are now reports that the trade in nests of *A. unicolor* has recommenced in the Western Ghats and in Sri Lanka (Gunawardena, 1997; Sankaran, 1998). Elsewhere, in Peninsular Malaysia (Wells, per. comm.) and Sarawak, there appears to be a growing market demand for nests of *Collocalia esculenta*, which has a copious salivary content only at the base, but is otherwise entirely made of intricately woven mossy matrix. Driven by a lucrative monetary reward, nests of this species are being collected for sale because it is worthwhile to do so now.

Medway (1963, 1966) also refers to claims that the Pygmy Swiftlet (*Collocalia troglodytes*), a Philippines endemic, produces an edible nest. Nevertheless, this assertion has never been confirmed (Dickinson, 1989). The nest of this species has been described as bracket-shaped nest of fibrous vegetable material held together by strands of firm nest cement. As Medway (1966) had suggested, it is possible that during periods of high demand, it is worth extracting the small proportion of saliva from the nest. Lau and Melville (1994) stated that similar case appeared to be happening also to another species, the Mossy-nest Swiftlet (*A. salanganus*), although seems highly improbable.

1.7 EDIBLE NEST SWIFTLETS OF SARAWAK

Five species of swiftlets are present in Sarawak, of which, only two are known to produce nest of commercial value. These are *Aerodramus fuciphagus* (Thunberg, 1812) and *Aerodramus maximus* (Hume, 1878). They are locally known as the White-nest Swiftlet and the Black-nest Swiftlet respectively. In this study, the acceptance of the generic name, *Aerodramus*, is based on the fact that these swiftlets are able to echolocate and the type of nest they build (Medway, 1966). A third species, the White-bellied Swiftlet (*Collocalia esculenta*), has the potential to be exploited if the current stocks of the other two species run out.

In Sarawak, the distribution of the *A. fuciphagus* is more restricted or localised. This species is said to have occurred at Satang and Lakei island off the Sarawak delta, Tanjung Dato at the western tip of the state, the upper Suai River and numerous caves around Long Laput in the middle Baram District (Medway, 1957; Smythies, 1960; Leh, 1993). Duckworth and Kelsh (1988) reported sighting swiftlets over the estuary of Sungai Similajau, but unfortunately, the species concerned was not confirmed. During the course of this study, several colonies of this species were discovered around Bintulu Division, which presumably have migrated or spread from the Similajau National Park area.

By contrast, *A. maximus* is widespread throughout the state, inhabiting caves in gigantic limestone outcrops around Bau District, Serian District, the Klingkang range, Niah, Kakus and Mulu (Medway, 1957, 1962b, 1962c; Leh, 1993). These represent the major

mountain ranges bordering Kalimantan in Indonesia. In recent years, many new caves were discovered around Batu Tuju and Bukit Siman in the upper Baram District and Merapok in Lawas District with substantial colonies of this black-nest builder.

1.7.1 White-nest Swiftlet — *A. fuciphagus* (Thunberg, 1812)

The plumage is dark blackish brown in general appearance. The upperparts are uniformly blackish brown, invariably perceptibly paler over the base of the tail. They build a cup-shaped nest, entirely made of laminated concentric layers of salivary secretion with no plant material. Occasionally, a few fluffy down feathers are struck between these laminae. Therefore, the nest has a whitish, semi-translucent appearance. This species lays two eggs per clutch. The morphometric measurements were given by Cranbrook (1984) as: wing-length 112 - 121 mm; tail 48 - 56 mm; and weight 15 - 18 g.

Two subspecies are known to be present in Sarawak. The subspecies *A. fuciphagus germani* colonises caves on coastal areas or islands off the Sarawak delta. They have a brownish grey band with dark shafts across the rump. The other subspecies, *A. f. vestitus*, lacking a whitish rump but with a uniform plumage on the back and upperparts. The distribution range of this subspecies is very restricted in the middle Baram where they roost in caves between 03° 38′ N to 03° 47′ N and 114° 25′ E to 114° 32′ E.

1.7.2 Black-nest Swiftlet — *A. maximus* (Hume, 1878)

The plumage is dark blackish brown on the upperparts, while the underparts are brownish grey with dark feather shafts. This species is much larger and heavier than the previous species, and easily distinguished by the nest they build. The nest is also cup-shaped, but many are feathers incorporated among the salivary laminae. This gives the nest a blackish appearance and fluffy texture. This species lay a single egg per clutch. Size moderate to large with wing-length 128 - 136 mm; tail 52 - 58 mm; weight 28 g (Cranbrook, 1984).

1.8 PROBLEMS IN SARAWAK

Traditionally, nest harvesting is often restricted to certain seasons. For instance, the Bidayuh people in Sarawak used to collect nests twice a year at an interval of three months, thus enabling the birds to produce at least one brood per year (Medway, 1958). Cultural and religious beliefs sometimes affect the timing or duration of the harvest too (Francis, 1987b). It was only in the past few decades that harvesting practices became excessive and

uncontrollable. Consequently, species that had apparently withstood exploitation successfully for over one or two centuries began to decline rapidly (Good, 1993; Sankaran, 1998). At the present time, because of the escalating price fuelled by an ever-increasing demand, most colonies of edible nest swiftlets across their ranges are repeatedly stripped of nests regardless of whether or not there are eggs or nestlings in them. Medway (1966) believed that a regime of rigorous and repeated nest collection at that time did not significantly reduce the size of breeding population, but it is apparent now that present populations cannot withstand the magnitude of exploitation and indiscriminate nest harvesting (Tompkins, 1997; Sankaran, 1998).

In Sarawak, the Niah Caves are the main producer of the edible nest beside some smaller caves in Baram District, Kakus and Bau. Over the past five decades, annual nest production has fallen dramatically because of a sharp decline in the swiftlet populations (Good & Wong, 1989; Good, 1993). Despite the decline, and concern for their future, essential biological data such as the breeding periodicity, nests building phase, laying, incubating and fledging were still sparse. There was no secure knowledge of the timing of the breeding cycle in Niah or Baram District (Cranbrook, 1984). Moreover, it is doubtful whether sustainable harvesting is being practised by the local communities, owing to a lack of knowledge of the breeding cycle as well as the breaking down of traditional control.

1.9 OBJECTIVES OF STUDY

The objectives of this study were to elucidate in detail the biology and ecology of the edible nest swiftlets in Sarawak. Medway (1962b, c) indicated that there are possible geographical and seasonal variations in breeding cycle within Sarawak. Elsewhere. regional and seasonal variations has also been reported in Vietnam (Nguyen Quang, 1990, 1994) and in Singapore (Kang & Lee, 1991; Kang *et al.*, 1991). Impact of nest harvesting upon a productive colony or population was studied in detail. A better knowledge of time lapse between removal of nest, its subsequent replacement and the lay of successive clutch is crucial in maintaining a sustained productive colony. Finally, a sustainable harvesting strategy based on sound scientific data, and concurrently acceptable to the local communities, who were entrusted with the responsibility of managing the nest producing caves, was drawn up and implemented.

In addition, despite the widely acclaimed medicinal and therapeutic properties of edible bird's nests, there is a paucity of scientific research on the chemical properties of the nest (Lau & Melville, 1994). Whether or not such properties exist in edible bird nest is still open for debate. Likewise, there is no information on the cyclic or seasonal variations of the composition or the biochemical properties of the nests (Cranbrook *et al.*, 1996). Taking a step

ahead, the second aspect of this study was designed to test for the seasonal, intra- and interspecific as well as the geographical variations of the nest chemical constituents. Various amino acids in the protein composition, and three sub-types of monosaccharides, namely sialic acid, neutral and amino sugars, of the carbohydrate component in the glycoprotein molecules were quantitatively investigated in detail on selected samples using high performance liquid chromatography. Rapid identification of the correlation between time of harvest and the nests' chemical constitutes is beneficial and abets in refining the management plan by helping to identify the best time to harvest.

1.10 THESIS ORGANISATION

The first chapter of this thesis presents a general overview of the unique characters of cave swiftlets and the edible nests they produced as well as the concern of a decline in the wild swiftlet populations. Problems on nest exploitation in Sarawak and the objectives of this study are outlined. The descriptions of study sites and methods used in this study are given in Chapter 2, which is divided into two parts. The first part describes all the methods used to collect biological and ecological data. The second part gives detailed procedures of the chemical analysis of the composition of nest materials. Chapter 3 demonstrates the intriguing relationship between edible nest swiftlets and human. The social and economic importance of edible nests, including various harvesting practices employed in four separated regions, is discussed. Chapter 4 describes the breeding periodicity, reproductive performances, and the correlation between moult and breeding of edible nest swiftlets in Sarawak, while Chapter 5 outlines the development of nest building activities. A comparative study of the While-bellied Swiftlets is presented in Chapter 6. This includes some egg transfer and cross-fostering experiments. The questions on seasonal and inter-specific variations of the chemical constituents of nest materials are discussed in Chapter 7. The carbohydrate and protein compositions of nests from three species of swiftlets were analysed. Finally, problems and the needs for swiftlet conservation in Sarawak are discussed in Chapter 8. A sustainable plan for the management of edible nest swiftlets is presented as conclusion of this thesis.

Chapter 2
Methods And Study Sites

2.1 SAMPLING LOCATIONS

Two sampling sites among the numerous caves scattered in the middle Baram were used throughout this study from April 1997 to March 1998. These caves are situated in the outcrops of Melinau Limestone Formation (Wilford, 1964). The land on both sides of the Baram River and its tributaries, extending several hundred metres from the bank, had long been cleared and farmed. Beyond that is the Telan Usan Protected Forest to the right of Baram River, and the vegetation on the other side of the river comprises of selectively logged-over forest, abandoned farmland or locally referred as "temudak", medium sized orchards and emerging oil palm plantation.

The primary sampling site was Lubang Salai (3° 39′ 5″ N, 114° 24′ 57″ E), which is about 1.6 km north-west of the Liang tributary of the Baram. The secondary site is Lubang Beruang (3° 41′ 34″ N, 114° 28′ 2″ E), located near Sungai Kejin-Tugang. Both are accessible by boat and jungle trial. Both White-nest Swiftlet (*Aerodramus fuciphagus*) and the White-bellied Swiftlets (*Collocalia esculenta*) inhabit Lubang Salai and Lubang Beruang. A third cave, Lubang Ngawai, situated about 15 meters away from Lubang Salai is inhabited only by *C. esculenta*. This site was used for egg-transfer experiments and the comparative study of the breeding periodicity.

One site with Black-nest Swiftlet (*Aerodramus maximus*) at Bau, at the south-western part of Kuching Division, was used for a short monitoring period. This small cave is known by the local as Lubang Poyang in between May and June 1997. Unfortunately, this site had to be abandoned owing to repeated poaching and ownership disputes. Subsequently from June to August 1998, another site at Bukit Sarang (02° 38′ 53″ N, 113° 02′ 57 ″ E), near to Sungai Mayeng at Tatau, was selected for the Black-nest Swiftlet study. Similarly, this study also failed owing to poaching and a weakness in the management of the caves.

2.1.1 Lubang Salai

Lubang Salai (Figure 2.1) can be reached by boat from Kampung Long Laput (03° 44′ 23″ N, 114° 26′ 06″ E), followed by 30 minute walk from the riverbank. Kampung Long Laput is an Orang Ulu longhouse with more than one hundred families or "bilik" and is located in the middle Baram basin. This village is linked overland to Miri, a moderate yet modern township,

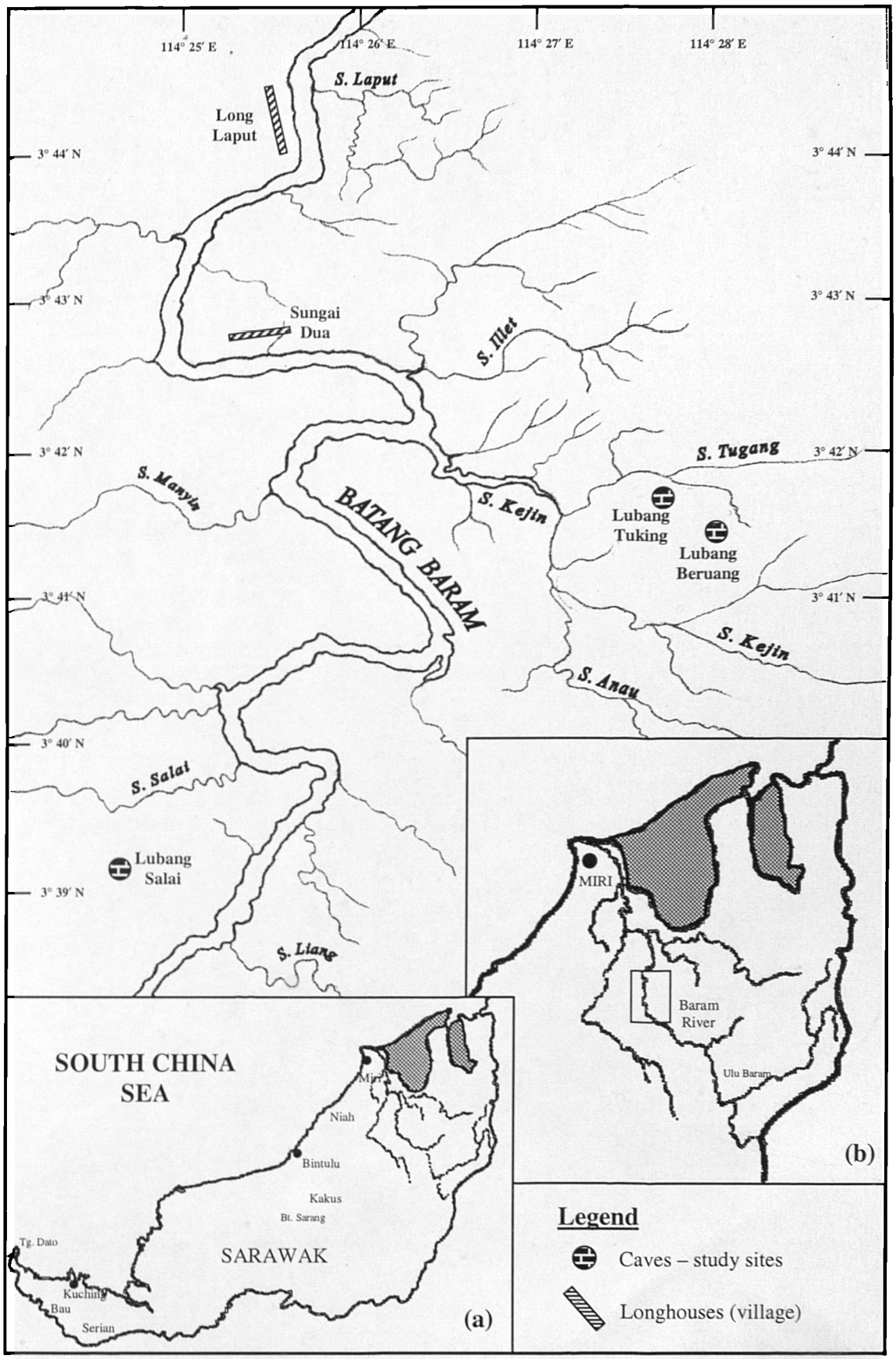

Figure 2.1 Locations of Lubang Salai and Lubang Beruang. Inserted maps showing: (a) the state of Sarawak and Baram River and main tributaries; (b) relative position of study sites in middle Baram.

by a route combining sealed trunk road and logging track toward the interior, a 2½ – 3½ hours journey depending on weather. This area is also serviced by daily express boats, plying to and fro between the mouth Baram River (i.e. Kuala Baram) and Long Lama town. The journey up the winding Baram River takes no less than six hours.

Lubang Salai is a very unusual limestone cave sandwiched between thin layers of shale situated in undulating ground with the entrance located at the side of a hill (Banks, 1935). It is the only edible swiftlet cave located on the true left-hand bank of the river. Lubang Salai consists of a single chamber about 9 meters (30 feet) across and 4.5 meters (15 feet) high. The only entrance is approximately 2 by 3 meters across at ground level, entered by a passage extending downwards at a 45° inclination. The upper half of the chamber is hemispherical with irregular wall that is most suitable for roosting and nesting. This is where all the nests are found. The wall itself is relatively dry, although a thin film of water occasionally covers certain portions of the cave, especially after successive rainy days.

Like most swiftlet-producing caves in this region, Lubang Salai is zealously guarded with fencing and armed guards posted in a guardhouse nearby. Outsiders and even other villagers are strictly prohibited from visiting this area without prior consultation with the owners who have inherited traditional rights over the harvesting of the swiftlets' nest.

In this cave, seventy-five nests were marked on 7 April 1997. These were used mainly for continuous observation, and for the collection of all the parametric measurements and breeding data. Prior to the marking, these nests were last harvested on 12 March 1997 and were partially rebuilt at the time of the marking. All these marked nests were left unharvested for a whole full year until March 1998. Hence, this sample allowed the monitoring of the annual breeding periodicity of *A. fuciphagus* under natural conditions. After the first breeding cycle, eleven more nests were built between the formally marked nests in August 1997, and these were subsequently marked.

The marked nests here were visited two to three times weekly between April 1997 and March 1998. Inspections were done in the morning around 1000 to 1200 hours when most swiftlets were out foraging, except for the incubating birds which remained during breeding period. During the egg-laying phase, routine checks were carried out daily. In addition, several sporadic visits were carried out in June 1998, November 1998 and January 1999 for general observations and to cross-check data gathered previously.

2.1.2 Lubang Beruang

Lubang Beruang is located in the catchment area of Kejin-Tugang (Figure 2.1). This cave is situated on hilly terrain 1 km east of Lubang Tuking, another cave in the Kejin valley with a huge colony of White-nest Swiftlets. There is a jungle trail connecting these two caves.

Depending on the level of the Kejin River, this location is accessible by a 30 – 45 minutes boat ride from Kampung Sungai Dua (03° 43′ 42″ N, 114° 25′ 02″ E).

The only entrance to Lubang Beruang is about 2.5 meters directly below ground level. The main chamber is of moderate width with several narrow ceilings of various heights, ranging between 6 to 20 meters high. The confined cavern in the main chamber, a narrow and elongated formation, is known as Pasen San. Roughly 30 meters directly opposite the entrance, the chamber branches into two low tunnels that expand out at the end. To the right is Pasen Avut and Pasen Lawai is to the left.

Fifteen nests were marked in Pasen Avut of Lubang Beruang on 7 May 1997. In addition, forty more nests at the innermost end of Pasen San were selected for general observation without any measurement being taken. The nests here were last harvested on 14 April 1997. All marked nests were visited regularly on a weekly basis from May 1997 until March 1998.

2.2 BIOLOGICAL AND ECOLOGICAL STUDY

2.2.1 History Of Nest Production

Data on nest yields from Lubang Salai and Lubang Beruang were compiled from the harvesting records kept by the respective owners for the period between 1991 and 1997. These data were summed to give an annual production as well as the total numbers at each harvest. The smallest value was chosen as the standard relative scale. Because not all harvesting dates correspond from year to year, data were also grouped into three 4-month's period, e.g. January to April, May to August, and September to December for comparative purposes.

2.2.2 Breeding Periodicity

Before permission was granted for the study to be conducted in the selected sampling sites, the owners specifically requested that (a) the swiftlets were not subjected to any handling (e.g. catching with mist net, and (b) routine checks and other observations inside the cave were carried out with minimum disturbance.

2.2.2.1 Proportion breeding

An effective management plan for edible nest swiftlets requires the knowledge of the timing of the breeding period and the number of breeding attempts or cycles. Since annual breeding periodicity is reflected by the onset of each breeding cycle, which corresponds with

the number of eggs present, it could be deduced that the proportion breeding indirectly represents and reflects the timing of each bout of breeding. In this study, the assessment of the proportion breeding at each sampling period was carried out based on the formula listed below:-

$$\text{Percentage breeding} = \frac{\text{Number of nests with egg (either 1 or 2 eggs)}}{\text{Total number of nest marked/examined}} \times 100\%$$

2.2.2.2 Hatching Success

Hatching success is the assessment of egg loss during incubation. This value was based on the number of eggs hatched divided by the total number of eggs laid among all the marked nests in each bout of breeding.

2.2.2.3 Fledging Success

The fledging success was calculated based on the number of nestling that survived until they fledged divided by the total number of eggs hatched in any one sample. The number of fledgings that survived on their first maiden flight outside the cave and return to roost could not be determined. The percentage of nestling loss was calculated from the numbers of nestlings disappear divided by the total number of nestlings produced. In addition, only nests with two nestlings were used to determine the proportion of sibling loss possibly because of siblicide, and hence, nestling loss from single brood was not consider as sibling loss. This was calculated as the number of nest with loss of one chick divided by the total number of double nestling brood.

2.2.2.4 Reproductive Index (RI)

The reproductive index is expressed as the mean number of nestlings raised per adult pair per brood (Lee & Kang, 1994). In this study, this value was calculated from the total number of nestlings that survived until fledging divided by the number of adult pairs that produced a clutch in each bout of breeding.

2.2.2.5 Incubation Period

The incubation period was calculated from the day the first egg was noticed to the day it was last seen. For *A. fuciphagus* that lays two eggs per clutch, the first egg was marked in pencil and the duration of incubation was calculated according. In cases when the first egg was

laid outside the inspection routine, the incubation period was determined from the day when the second egg was laid to when the second nestling hatched (Moreau & Moreau, 1940; Skutch, 1945; Medway, 1962b).

2.2.2.6 Fledging Period

The fledging period was calculated according to Moreau & Moreau (1940) and Medway (1962b). For *A. fuciphagus*, when both nestlings survived to fly, this period was taken from the hatch of the second egg to the departure of the second nestling. When only one nestling survived, it was assumed that this was the first to hatch and the fledging period was calculated accordingly.

2.2.2.7 Nestling Growth Stages

The growth rate of nestlings can be calculated by weighing the nestling at regular intervals, but this requires the removal of the nestling from the nest, which could be traumatic. The growth rate of swiftlet young has been studied in *A. maximus* and *A. fuciphagus* (Lee & Kang, 1994), and *C. esculenta* (Tompkins, 1997). In order to reduce disturbance to the nestlings, weighing was not carried out in the course of this study. However, to give a general idea of the nestlings' growth, they were categorised into seven stages by appearance as listed below and Plate 2 to 7.

Stage 1 — newly hatched; naked and pinkish colour (≈ 1 – 6 days old).

Stage 2 — small feather sheaths visible on main feather track, but not yet erupted (≈ 7 – 13 days old).

Stage 3 — feather sheaths erupted from skin; porcupine-liked; exposed skin; eyes still closed (≈ 14 - 20 days old).

Stage 4 — overall plumage coverage but primary feathers have not developed yet; eyes barely opened (≈ 21 - 27 days old).

Stage 5 — Body entirely covered with well-developed down feather; primary feathers semi-developed, not over-shooting the tip of the rectrices (≈ 28 – 35 days old).

Stage 6 — Almost all primary feathers have developed, about half of adult length; primary feathers over-shooting the tip of the rectrices (≈ 36 – 40 days old).

Stage 7 — fully grown, near fledging; attained complete plumage (≈ 45 days old).

2.2.2.8 Inter-clutch Interval

When a successful breeding was accomplished, regardless of the number of nestlings fledged, the inter-clutch interval was taken as the day the last nestling was seen until the day an egg was first noticed in the subsequent clutch in the same nest. Failure in breeding occurred in two ways. One results from the loss of egg or eggs during incubation, and the other factor is the loss of young before fledging. When this occurs during incubation, the interval of egg lost to the replacement clutch was calculated from the day the lost egg was last seen to the day when a replacement egg was laid. On the other hand, if brooding was terminated prematurely as a consequence of the loss of nestlings, the interval of subsequent clutch was calculated starting from the day when the last nestling, if two originally, was last seen until the subsequent egg was laid.

2.2.3 Moulting

In order to maintain a minimum disturbance to the colonies, moulting stages were determined by an indirect scheme of feather count. In this study, it involved the collection of fresh primary feathers found lying on the ground inside Lubang Salai on a weekly basis for one year. However, this method reflects only the general moulting cycle of the whole colony within this cave and not of individual birds.

Prior to the first collection at the end of April 1997, the ground inside Lubang Salai was cleared of all fallen feathers. Thereafter, all fallen feathers were collected, categorised into PF-1 to PF-10, in accordance to the successive numbering of primary feathers, and counted. The identification and separation of each feather categories was aided by a reference set of primary feathers taken from a swiftlet sacrificed for this purpose. The fallen feathers collected every week comprised feathers from both the left- and right wing. Therefore, to avoid duplication and for comparison purposes, only the value from the side with the highest count in each category was taken into consideration.

2.2.4 Nest Parameters

The swiftlet nest is typically a cup-shaped structure constructed entirely of nest-cement or salivary secretion. Most nests adhere independently to the cave wall but some are joined at the base. Because of the irregularity of the limestone formation on the wall, the shape of the nest also varies, ranging from a shallow crescentic bowl to a perfect quarter of hollow-sphere. Occasionally, a few nests are constructed with a narrow base and a very elongated nest crest. The dimensions of nests measured were according to the methods of Nguyen Quang (1996)

with modifications. A thin copper wire was used to trace the outline of each dimensions and measured along a ruler with an accuracy limit of 1.0 mm. Figure 2.2 illustrates the main parameters used for the progressive measurement in this study.

Parameter "D" is the measurement of the length at the base of a nest or locally termed as the "nest's foot". Medway (1966) referred this as the "hinge" of the nest. In the cave, this parameter was measured as the distance between both edges of the nest crest at the nearest point adhered to the cave wall.

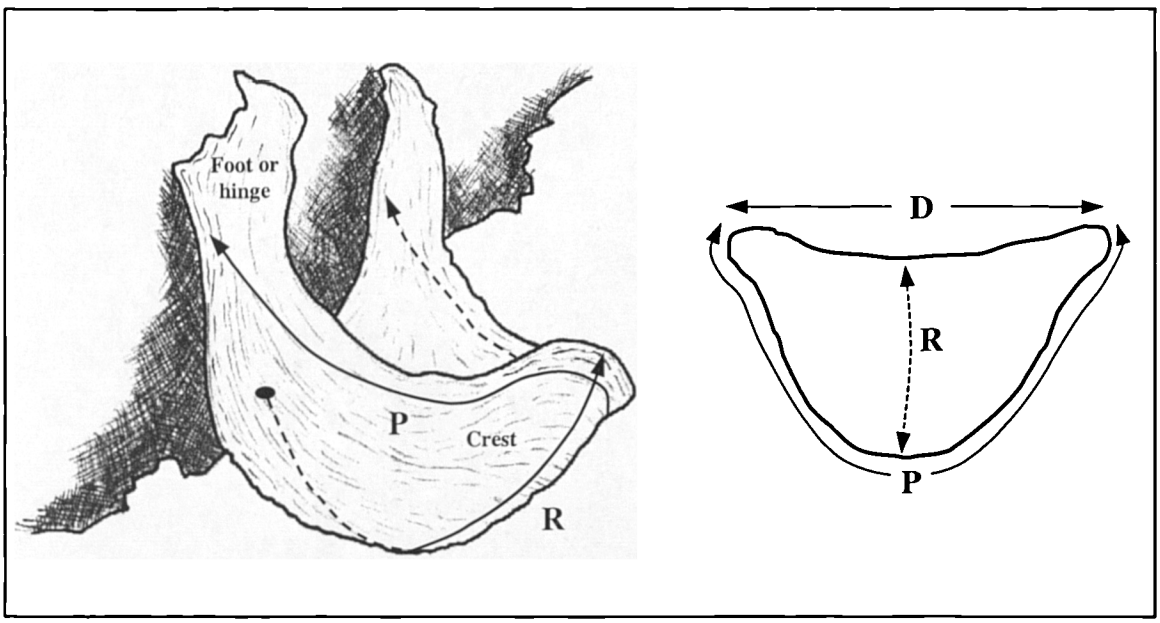

Figure 2.2 Lateral (left-hand diagram) and vertical (right-hand diagram) view of a typical *A. fuciphagus* nest, showing all parameters (i.e D, R, & P) applied in this study.

Parameter "R" was measured from the middle of the base, along the curvature of the nest towards its crest, and perpendicular to the base in a two-dimensional profile. Another parameter measured was "r", which is the perpendicular length from the middle of the base to the nest crest. However, it was discovered that there were several drawbacks in measuring the parameter "r". The first difficulty is that it was impossible to measure this distance accurately without damaging the egg once it was laid. Secondly, if the eggs have hatched, this caused too much disturbance and interference to the nestling.

Parameter "P" was measured from the uppermost part of the nest crest that is in contact with either the wall or the nest's leg. This represents the measurement for the actual elongation of the outer circumscription of the nest crest, ignoring any extension or enlargement at the base. Therefore, it was one of a few reliable measurements applied in this study where more information could be obtained and derived from it.

2.2.5 Impact Of Nest Removal

Thirteen of the seventy-five initially marked nests were deliberately removed at Lubang Salai on 26 April 1997, and the sites monitored for post-harvest developments. This nest removal served as an experimental treatment of a nest harvest in April. The interval from nest removal to the first deposition of nesting saliva was noted and the lay of a subsequent clutch was recorded. Another eleven marked nests were removed at Lubang Salai on 13 September 1997. Eight of these served as a second experimental treatment of a nest in September. The subsequent deposition until further lay of a clutch was calculated and compared with the treatment in April. In addition, three nests were at sites where a previous nest was removed on 26 April, and served as third experimental treatment for multiple nest harvest. These acted as controlled parallel of commercial harvesting.

At Lubang Beruang, three of the fifteen marked nests were removed on 7 May 1997. On 16 September 1997, seven more were removed from the same sites. The same observations as those adopted at Lubang Salai were employed. In addition, harvesting and the subsequent development of other unmarked nests inside Lubang Salai and Lubang Beruang were closely monitored. The ratio of empty nests to nests with egg(s) was determined at regular intervals after each harvest.

2.2.6 Weight-to-Measurement Ratio

Only nests from Lubang Salai were used to determine weight-to-measurement ratios. Nests from three harvests in July, September, and December 1997 were measured. After these harvests, samples of nests were selected randomly, measured for the parameters P and R, and weighed. Weights were taken using Pesola Scale of ranges 10 g and 30 g (with an accuracy limit of 0.2 g and 0.5 g respectively). The relationship between the average weight for nests harvested at various time of the year was analysed using a one-way ANOVA. In addition, standard curves for the weight of nest with respect to the parameters P and R were also produced.

2.2.7 Population Census

Population census of the swiftlet colony was carried out only at Lubang Salai in April and May 1997. For every census, emerging birds were counted between 0600 – 0700 hours. In the first and last quarter of the hour, individual birds could be counted singly. When the emerging flock was huge, the birds were then counted in blocks of 5-individuals and 10-individuals.

In addition, the number of breeding pairs within Lubang Salai was estimated by the total count of nests in each harvest, and multiplied by two to give the number of individuals. The total count comprised of harvested nests, nests that were left inside the cave for breeding and all marked nests used in this study.

2.2.8 Behaviour Observation

Behavioural observation inside Lubang Salai was carried out in total darkness with the aid of a night scope equipped with an infrared illuminator. A secluded position in the cave, roughly 2.5 meters away from the nearest marked nest, was selected from which to make observations. Once this position was taken up, body movement and noise was limited to the minimum. Throughout the study period, two intensive monitoring periods were undertaken done from 0900 – 1745 without relief on 11 June 1997 and 8 October 1997. Other shorter periods of monitoring were carried on 8 September 1997, 20 October 1997, 30 October 1997, 20 January 1998 and 22 January 1998. No observation was carried out at night because it was prohibited by the owners.

2.3 COMPARATIVE STUDY WITH *COLLOCALIA ESCULENTA*

2.3.1 Breeding Periodicity

Sixteen nests of *C. esculenta* inside Lubang Salai and fifteen inside Lubang Ngawai, another small cave nearby, were marked. These nests were examined weekly and the absence or presence of any egg was recorded. The incubation and fledging period was calculated based on the same methodology as those of *A. fuciphagus* described under section 2.2.2.5 and section 2.2.2.6 respectively.

At Lubang Beruang, about 300 nests were examined regularly. All these nests had been destroyed in April by the owners before the start of any observation. This colony together with those inside Lubang Salai and Lubang Ngawai were used to determine the onset of the breeding season and to investigate the annual breeding periodicity of this species. The proportion breeding at each month was calculated as in section 2.2.2.1.

2.3.2 Egg Transfer

A small number of nests in Lubang Salai were selected and set aside for the egg-transfer experiments in May, September and November 1997. This exercise involved the transfer of *A. fuciphagus* eggs from other unmarked nests, usually during or shortly before the

harvesting period, into *C. esculenta* nests. This experiment could only be carried out on limited number of nests owing to the fact that *A. fuciphagus* eggs were very difficult to come by as the timing of such transfer was very critical. When large number of *A. fuciphagus* eggs were available, there was a limited number of *C. esculenta* containing eggs with the appropriate age for substitution. After hatching, the latter species acted as the surrogate parent for the *A. fuciphagus* chicks. Several treatments were employed, some with one of the *C. esculenta* egg removed and the other one damaged by puncture of pin-sized hole; others involved the removal of both *C. esculenta* eggs.

2.4 CHEMICAL ANALYSIS OF THE COMPOSITION OF NEST

2.4.1 Nest Samples

Nest samples for *A. fuciphagus* were collected from Lubang Salai between April and August 1997. Nest samples were collected in April, July and August 1997 from the same nesting site, which were presumably constructed by the same pair of swiftlets while samples collected in June were from different nesting sites. Nest samples of *A. maximus* were obtained from Bau in September 1997. Freshly collected nests were air-dried for one day and immediately transferred into a sealed plastic bag with silica gel for further drying. In addition, three nest samples from *C. esculenta* were also collected from Lubang Salai. Only the copious salivary portions from *C. esculenta* nest was gathered while the mossy cup-shaped structure was discarded. After the nests were removed from the cave, they were cleaned from any debris without wetting the nests. Only the portions lacking any feathers were selected to avoid the inclusion of any unwanted feathers.

These thoroughly dried nest samples were crushed before hydrolysis. This was carried out in the laboratory in the department of Bioscience. The hydrolysed samples were analysed using a High-performance Liquid Chromatography (HPLC) apparatus in the Welcome Trust Protein Facilities in the university.

2.4.2 Carbohydrate Constituents

2.4.2.1 Sialic Acids

Hydrolysis of edible bird nest for sialic acid determination was carried out according to Varki & Diaz (1984) with modifications. 200 – 400 μg of bird nest sample was placed in a 1.0 ml polypropylene vial (Supelco; 2-7269) with screw cap (Supelco; 2-7413) and 10 mm septa

(Supelco; 2-7277). 100 μl of 2 M acetic acid (pH 2.2) was added and the vial capped. Hydrolysis was carried out at 80 °C for 2 hours.

The sample was cooled after hydrolysis to room temperature. Labelling of released sialic acids was carried out with fluorescent DMB (1,2-diamino-4,5-methylenedioxybenzene) dye provided by Signal™ DMB Sialic Acid Labelling Kit (OSG Cat. No. K-407). 5 μl of the hydrolysate and 20 μl of freshly prepared DMB labelling reagent were transferred into a clean reaction vial. The vial was capped and the content mixed by vortex and incubated for 3 hours at 50 °C in the dark. The labelling reaction was terminated by adding 0.5 ml water to each reaction vial and mix thoroughly. An aliquot of 50 μl was then injected into the HPLC.

Separation of labelled sialic acids was carried out at ambient temperature using a reversed phase GlycoSep™ R HPLC column (OSG Cat. No. I-4727). The mobile phase used was a mixture of acetonitrile-methanol-water (9:7:84, v/v) at a flow rate of 0.9 ml/min. Detection was done using fluorescence detector at excitation wavelength of 373 nm and emission wavelength of 448 nm. The turn around time was approximately 15 minutes. A standard solution was prepared from a standard reference panel (OSG Cat. No. RP-2503). The quantification of released sialic acids and establishment of calibration curves was according to Hara *et al.* (1989). A series of standard solutions of individual neuraminic acids (10 nmole – 4 μmole) was prepared, and each were subjected to the same procedure without hydrolysis. The peak heights in the chromatogram were used for the quantification of the individual neuraminic acids.

2.4.2.2 Amino And Neutral Sugars

Hydrolysis of edible bird nest for monosaccharides analysis was carried out according to Honda *et al.* (1983) with modifications as listed in the protocols from the Signal™ 2AA Monosaccharide Analysis Kit (Oxford Glycosystems Catalogue No: K-409). 200 – 400 μg of crushed nest sample was placed in a 1.0 ml screw-cap polypropylene vial (Supelco; 2-7269). 400 μl of 6N HCl was pipetted into each vial and subsequently sealed using polypropylene cap (Supelco; 2-7413) with a 10 mm septa (Supelco; 2-7277). Hydrolysis was carried out by incubating the capped vials at 100 °C for 4 hours. After hydrolysis, the vials were cooled. 200 μl of the hydrolysate was transferred into a 15 ml tubes and vacuum dried to remove hydrochloric acid. Residual traces of acid were removed by re-dissolving the dried sample in 100 μl water and dried again. After drying, the samples were stored at – 20 °C until analysis.

The released monosaccharides were labelled using 2-AA fluorescent tag (2-aminobenzoic acid) by reductive amination using the Oxford Glycosystems Signal™ 2-AA glycan labelling kit. The hydrolysate were redissolved in 1% fresh sodium acetate (0.1 – 0.2

ml) and an aliquot (20 – 100 µl) was transferred to a screw-cap freeze vial. 5 µl of 2-AA labelling reagent was then added and heated at 65 °C in an oven for 2 hours. The mixture was vortexed 30 minutes after the start of the incubation to encourage complete dissolution of the samples. The samples were removed after the incubation and allowed to cool to room temperature.

The excess 2-AA fluorescent dye was removed from the labelled samples using the Signal™ cleanup cartridges. Each cleanup cartridge was first washed with 1 ml of water, followed by 5 ml of 30% acetic acid, and subsequently washed with 1 ml of acetonitrile after the former had completely drained. The labelled sample was spotted onto the centre of the disc while it was still wet with acetonitrile and set aside for 15 minutes for the glycan to absorb onto the disc. Then the disc was washed thrice with 1 ml of acetonitrile allowing each to drain before the next aliquot was applied. The cartage was placed over a collection vessel and elution of the glycans was accomplished by three aliquots of 0.5 ml water. The collected sample was evaporated to dryness and redissolved in 0.5 ml of water. 50 µl of this was then injected into the HPLC.

The 2-AA labelled monosaccharides were analysed by fluorescent reversed phase on GlycoSep™ R column (OSG Cat. No. I-4727). All separation were carried out at ambient temperature using a flow rate of 0.7 ml/min with solvent A (0.25% 1-butylamine, 0.5% phosphoric acid, 1% tetrahydrofuran in water) and solvent B (50:50 methanol to water). The elution sequence was isocratic with 75% A and 25% B for 30 minutes, followed by 60% A (40% B) for 1 minute, and 100% B (0% A) at 31 min for the remaining 5 minutes and finally equilibrated for 15 minute to initial conditions, i.e.75% A and 25% B. Detection was performed by fluorescence detector with excitation wavelength at 230 nm and emission wavelength at 425 nm. Standard solutions were made of known amount of glucosamine, galactosamine, galactose and fucose with internal standard (mannose or glucose). All derivatization and separation conditions were the same.

2.4.3 Protein Constituents

Hydrolysis of bird nest chips was carried out according to Strydom and Cohen (1994) with modifications. 1.5 – 2.5 mg of crushed nest sample was transferred to a 1 ml polypropylene screw top vial (Supelco; 2-7269) together with 1.25 nmole of norleucine as internal standard. 300 µl of 6N HCl was then pipetted into each vial. The vial was sealed using polypropylene yellow holed cap (Supelco; 2-7413) with a 10 mm septa (Supelco; 2-7277). The cap was turned until the septum touched the top of the vial and it was further tightened by another ¼ turn to secure the cap. Each hydrolysis vials was purged for 20 seconds from a nitrogen source at 3 – 5 psi. Hydrolysis was carried out at 110 °C for 24 hours in batches of six

samples. After hydrolysis, the vials were removed and cooled. 200 μl of the hydrolysate was transferred into 15-ml tubes and dried in vacuum without centrifugation. Immediately after that, each sample was dissolved in 0.25 ml of 0.025% K_3EDTA that was prepared fresh daily and refrigerated in –20 °C until analysis.

For precolumn derivation, 20 μl of sample was transferred to a small vial and dried using a Speed-Vac. 15 μl of coupling reagent [methanol:DIEA:phenylisothiocyanate (5% in heptane) 7:2:] was added. The mixture was then incubated at 25°C for 20 minute. After incubation, the mixture was dried and re-suspended in 0.5 ml of extraction buffer. 100 – 200 μl of the resultant PTC-amino acids were separated in a Perkim Elmer Brownlee Spheri-5 PTC column (220 x 2.1 mm) at 25°C with a flow rate of 0.3 ml/min using Solvent A and Solvent B. Solvent A was 50mM sodium acetate, pH 5.4. Solvent B was 70% acetonitrile in 32mM sodium acetate pH 6.1. Elution gradient conditions were initially equilibrate at 95% A, linear gradient segment to 82% A at 4 min, 68% A at 10 min, 38% A in 20 min and 100% B in 25 min. The column was equilibrated to initial 95% A at 31 min. Detection was done by absorbance at 254 nm. The amino acids were quantified using calibration curves calculated from three standard runs (i.e. 400 pmol, 800 pmol and 1600 pmol) at the beginning of each set of samples.

Chapter 3

Social Relations And Human Exploitation

3.1 INTRODUCTION

Many popular articles have been published on the edible bird nest trade and the life-style of those involved, from the highly skilled nest collectors to the wealthy middlemen that sustained this industry (De Groot, 1983; Broad, 1987, 1995; Valli & Summers, 1990; Kang & Lee, 1993; Klatchko, 1994; Sim, 1994; Eu, 1996). However, the history of when this natural product was first harvested as food remains shrouded with mystery. The beginning of this fascinating industry can most likely be linked to the expansion of the Chinese maritime trade to the South Seas under the T'ang dynasty which dated as far back as A.D. 618 – 907 (Harrisson, 1959). From that era on, the relationship between man and edible nest swiftlets has blossomed, and this commodity has since gained a very highly esteemed reputation and appreciation many centuries later. Today, edible bird nests have acquired an undisputed status as a well-known oriental gastronomic delicacy and gourmet cuisine fit for royalty and the social elite, and worth their weight in silver to Chinese epicures (Price, 1996). However, its prestige has also resulted in the devastation of edible nest swiftlets, so much so that wild population have witnessed a drastic decline and local extinction across their ranges over the years.

Much of our present knowledge on this intriguing relationship between various indigenous communities and edible nest swiftlets is due to the early work of Lord Medway, and later the Earl of Cranbrook, in Sarawak in the early 1960s (Medway, 1960, 1961a, 1961b, 1962b, 1962c, 1963, 1969; Cranbrook, 1984). The different traditional tools used for collecting nests and the associated cultures and customs for each ethnic group were discussed in detail (Medway, 1957, 1958). The delicate balance between nest exploitation and "conservation" was very much respected in the olden days while efforts were clearly vested to allow at least a season of young to fledge every year. Under these circumstances, the author expressed confidence in his belief that the productive populations could sustain repeated nest collections practised in those days (Medway, 1966).

Thirty years has passed since the first report on the edible bird nest by Medway (1960) was published in Sarawak. The edible bird nest industry in Sarawak has seen tremendous changes over the years, as have the living standards and lifestyles of various ethnic groups of nest collectors. The most important change is the breakdown of traditional harvesting practices, as well as the culture and alliance between the older conservative generations and the cash-hungry youngsters. The consequences and implications are not to the advantage of the swiftlets,

but have severely undermined any sustainable management schemes and threatened the long-term survival of the species.

Therefore, this study aimed to review the present human relationship between swiftlets in a hope that this inquiry would be able to identify the cause and consequence of current weaknesses. Subsequently, these findings could be considered along side results from sound scientific study of the breeding biology, to help draft recommendations for the sustainable management of edible nest swiftlets. It is of crucial importance that the recommended plan is feasible, practical and most important of all, acceptable to the local communities or guardians of the swiftlets whom would exercise it willingly.

In this chapter, the origin and history of edible nest industry is described, while detailed descriptions of the trade of edible nest in Sarawak are given in section 3.2.2. Section 3.3 presents the social and economic importance of this industry to the local communities. The value of edible nests and the productions of white nests in middle Baram are discussed. Two types of ownership of nest-producing caves are described in section 3.4. The legislation regulating the time and number of harvest in Sarawak is outlined in section 3.5.1, while the following sections give descriptions of various harvesting practices employed in four regions in Sarawak, namely Bau, Niah, middle Baram and Kakus district.

3.2 HISTORY OF THE EDIBLE NEST TRADE

3.2.1 Origins Of Edible Bird Nest Industry

The earliest history of the edible nest trade has been traced back and found in the official annals of the Ming dynasty (1368 – 1644). The western world came to know this natural product by the early seventeenth century and by then it has already become a valuable commodity (Medway, 1963). It is likely that the swiftlet colonies in limestone caves alone the coast of Vietnam (Nguyen Quang, 1990, 1993, 1994, 1996) and several granite caves in Hainan Island (Fan & He, 1996) were the birth place of the bird nest trade because of the geographical proximity to China. Legend had it that the swallow-like birds responsible for producing these nests feed on a certain mollusc, the froth and foam of sea water, whereby the indigestible filamentous tendons on the back of this shellfish are regurgitated and mixed with saliva to construct the edible nests. Coupled with the prowess and endurance of the swiftlets' flight, it contributes to the common belief, especially among the Chinese, that these translucent filaments possess tonic, therapeutic, medicinal and even aphrodisiac, properties. The restricted range of *A. fuciphagus* and its confinement to seas caves in northern part of its range must have given rise to the sentiment of all these legends and myths.

In the reign of the T'ang (618 – 907) and Sung (960 – 1279) dynasties, there was a flourishing sea trade in the South China Sea. By the twelfth century, China's trade with countries around this region and the Indian Ocean was well established and reached their height in the beginning of fifteenth century (Chêng, 1969). Therefore, the discovery of tools for scraping edible nests off the cave wall among T'ang and Sung ceramics in Mongoloid burials at Niah suggests that Chinese traders were there in search of these valuable commodities (Harrisson, 1959; Chêng, 1969). Nevertheless, it is widely believed that the renowned Ming dynasty eunuch, Admiral Cheng Ho, was responsible for the introduction of foreign nests to the Imperial Court of China, because his seven magnificent voyages to the South Seas touched all major edible nest producing regions (Valli & Summers, 1990; Price, 1996). Unfortunately, no written documentation of this milestone has been found and perhaps is still waiting to be discovered. There was also no mention of this commodity by western sources earlier than late sixteenth century. By mid seventeenth century, edible nests were a prized substance. In the nineteenth century, it was a major commodity traded between China and numerous states in the South China Sea (Medway, 1963).

In India, edible bird's nest became a regularly traded commodity by early 1800s where contracts were auctioned annually (Sankaran, 1995). The earliest reference to the trade in swiftlet nests appears to be from the late 17th and 18th century, when Malay and Burmese procured considerable quantities of nests from the Andaman. However, the locations of swiftlet caves were known to the Great Andamanese, although the exact date or how long they have been collecting the nest is uncertain. Between 1869 and 1888, the British took over the governance of Nicobar Islands and one of the products exported by the settlement authorities was edible swiftlet nest (Sankaran, 1998).

3.2.2 Edible Bird Nest Trade In Sarawak

Like many other regions in South-east Asia, the historical origin of birds' nest industry in Sarawak remains obscure and can only be traced back to the late eighteenth century. There were no written records of swiftlet nest exploitation earlier than 1840. Although Harrisson (1959) suspected this commerce could to be dated far back to the T'ang dynasty, genealogical accounts from the cave owners at Niah, more or less consistently suggested that the caves were discovered by their forefathers shortly before 1800 (Medway, 1963). Edible nests have been harvested and traded, at least at Niah Cave, while Sarawak was still under the sovereignty of the Sultanate of Brunei (Cranbrook, 1984).

Similar accounts were also recorded among the Kayan communities at Baram. Edible nests were commercially exploited at least two to three generations back. It is believed that the caves in the Middle Baram regions were discovered by an early primordial indigenous tribe that

is referred to as the Tring of the Murut subgroup (Hose & McDougall, 1912). Nobody then knew anything about edible bird's nests and the white nests attached to cave wall were thought to be rock fungus. Later the Kayan tribe came and drove away or assimilated the Tring into their tribe and deprived them of their possessions, including the cave ownership (Hose, 1926). Spenser St. John, the personal secretary of Rajah James Brooke, made an excursion into the upper Baram territories in April 1851 and noted that caves occupied by edible nests swiftlets were prized assets of the Kayan community and considered as family wealth of the aristocrats (St. John, 1862). Upon the death of the owner, these caves were treated as hereditary assets and divided among the children.

Exploitation of edible nests around the caves at Gumbang near Bau had been carried out before 1848 when Hugh Low briefly mentioned bird's nest collecting activities and equipment from that district (Low, 1848; Cranbrook, 1984). Harvesting of edible bird nests was also witnessed at Sirih caves in Samarahan and Gunung Rambung caves in the upper Sungai Sarawak Kiri in 1850 (St. John, 1862). Although no description was given of the swiftlets that built these nests, it was clear from the lower quality nest produced that the species involved was *A. maximus*. All these narratives and anecdotes from mid nineteenth century affirm that the edible nest industry in Sarawak has survived the test of time and is at least 150 years old.

As well-known swiftlet caves are currently being plundered of the valuable nests, resulting in the diminishing of nest yield, people are searching harder and harder for unexplored caves with a desire to discover new and unmolested colonies of swiftlets. For example, the recently discovered caves in Batu Asi, Batu Tujoh and Bukit Siman in the Ulu Baram, and unconfirmed report of edible swiftlets nests from Gunung Buda, have been exploited. For *A. maximus*, several major caves, notably Niah Great Cave and limestone caves in Ulu Kakus, still has substantial population of swiftlets with feasible but declining nest yields. Some smaller nest producing areas include caves at the Batu Tujoh in the Ulu Baram, Jambusan and Meraja caves in Bau and Lubang Batu in the limestone mountain of Selabor around Tebakang. The numerous limestone caves along Kuching-Serian Road especially at Km-20 (Padawan), Km-28 (Siburan), Km-33 (Beratok) and Km-38 (Tapah) (Wilford, 1964), must have exhausted the production by now, or at most yielding a negligible quantity of nests.

In Sarawak, the caves in the middle Baram are the main source of white-nests. Only four major producing caves remain, namely Lubang Sepayang, Lubang Tuking (including L. Beruang), Lubang Salai and Lubang Mering Jau Sing in the Malui area. Other big caves with lesser nest yields include Lubang Anau, Lubang Materae and Lubang Payung. Currently, the caves around Long Laput in the middle Baram still have some healthy and viable populations of *A. fuciphagus*. On the extreme western tip of the state bordering the Indonesian Kalimantan, another small colony of *A. fuciphagus* is found inside a small sandstone cave within the Tanjung Dato National Park. The entrance to this cave has been gated, and therefore this colony

should be safe and secure, although it is assumed relatively small according to local sources. The colony at Satang Besar Island mentioned by Leh (1993) has apparently gone. One inspection of this cave in 1997 failed to locate any swiftlets in the vicinity. Similar investigation is needed to confirm the existence of the *A. fuciphagus* colony at Lakei island.

3.3 SOCIAL AND ECONOMIC IMPORTANCE OF EDIBLE BIRD NESTS

3.3.1 Source Of Income

Revenue from sales of edible nests contributed 4.2% of the total exports from Sarawak in 1871 (St. John, 1879). While the importance of the trade has since declined, it nevertheless contributes a substantial source of income for various groups of people. From 1888 to 1894, the duty on edible nests ranked anywhere from fourth to sixth largest source of revenue to the Rajah Brooke's government, but duty from this source has declined steadily in relative importance in the early 1930's, with the advent of other commodities (Banks, 1935). In Sarawak, the total value of exports of edible bird-nests in 1995 was valued at RM[1] 26 million (Bennett *et al.*, 1996), with many beneficiaries. Individuals, families or communities who have rights to those caves benefit directly from the sales of the nests. The collectors and cave guards earn wages or a percentage of the harvested nests. Intermediate middlemen, edible nest entrepreneurs and processors, and finally the exporters or wholesalers, usually the ethnic Chinese traders, profit indirectly from the downstream activities of birds' nest related businesses. In Sarawak, the entire edible nest industry is very well organised and nests from Indonesia Kalimantan are known to be sent here for processing (Sim, 1994). This enterprise has withstood the test of time for more than a century but unfortunately, it appears not to be self-sustaining of late.

Niah Cave used to be the main producing cave of black nests, yielding 18,500 kg or approximately 70% of the total state production in 1931 (Cranbrook, 1984). Hose (1927) commented that the trade in black nests at Niah alone amounted in a year to over three and a half million nests or about fifty tons. Although its production has dropped dramatically from the all time highest, Niah Cave remains an important source of black nest production. Currently, its nest production stands at about 300 – 400 kg of nests from each harvest on official record. There are reasons to suspect that more nests have been smuggled out from the cave without declaration to the forest officer in charge, or during the off-harvesting period. Elsewhere, the production from Berkuyat caves in Ulu Kakus was reported to be in the range of 800 – 900 kg per harvest, although there is reasonable doubt this figure is a little exaggerated.

[1] Ringgit Malaysia; 1 RM ≈ £ 0.24

Caves around Batu Tujoh at Ulu Baram yield over 100 kg of black nests annually and this is expected to increase as more caves are being explored. Reliable informants claimed that black nest yields from caves between the Tutoh and Limbang Rivers can be as high as 40 kg. A huge portion are suspected to be poached nest from Mulu. For the white-nest produced by *A. fuciphagus*, the total production from middle Baram is estimated to be between 80 to 120 kg per harvest.

Processing of raw black nests is a major downstream enterprise that requires extensive labour. The whole of this multi-million dollar business in Sarawak is carried out in the kitchen of residential houses or sundry shops, which otherwise seem perceptively ordinary at first glance. Examples of such places are the rows of shophouses at Siniawan and Jambusan bazaar, as well as few residential households in Siburan, Beratok town and even in Kuching City. Inside these disguised and distractible processing mills are pails of water soaked with raw nests and rows of women, usually numbering a dozen, engrossed in cleaning the nests. One end of the workplace is packed with neat rows of processed nests drying under homemade desiccators. The task of removing feathers of all sizes is simple but tedious. It takes a person eight hours to separate about 150 g of raw nests of *A. maximus*, and the daily wages for this job is about RM 5 to RM 15 depending on the skill of the workers (Sim, 1994).

3.3.2 Value Of Nest And Demand

Since the beginning of the birds' nest industry, this commodity has experienced a progressively rising price, showing how competitive this trade can be. The price for the black nests produced by *A. maximus* was $1.82/kati[2] in 1960 and this increased to $8.36/kati in 1973. This is equivalent to an annual inflation rate of 27.7%. For the white nests built by *A. fuciphagus*, the market price was $7.56/kati in 1933 but had risen to $74.06/kati in 1965 (Cranbrook, 1984), giving an equivalent annual inflation rate of 27.5%. In words, the price of white-nest has increased by 880% in three decades! Lau and Melville (1994) concluded that this incremental trend does not reflect inflationary increase but attributed it to the fact that supply never catches up with market demand.

In 1997, the price of unprocessed black nests ranged between RM 400 to RM 1,800 per kg, depending on the quality of the nests and amount of feathers incorporated. Nests harvested at the end of the year, generally in October or November, contain fewer feathers and have higher proportions of saliva, so usually fetching the highest price. In contrast, nests collected between June and August are the lowest of grade. The white nests from Baram could command from RM 5,000 to 6,800 per kg. The price at the end of the marketing chain, usually in major

[2] Old Chinese measuring system still widely used in the bird nest industry; 1 kati = 16 tahil ≈ 0.6 kg. The symbol $ denotes local currency.

towns with nest cleaning and processing facilities, might double or even treble. If larger and whiter nests are carefully selected, they can fetch for as high as RM7,000 per kg. On one occasion, a reliable source reported that specially selected nests from one cave in Baram secured a selling price of an extraordinary RM12,000 per kg. Nevertheless, nests of such high quality are hard to come by and only small quantities of 100 to 200 g changes hands in each transaction. Comparatively, the retail price of Indonesian white nests (i.e. mostly from swiftlet farming) in Hong Kong was from RM 5,180 to RM 7,728 per kg while that of the processed black nests was from RM 1,036 to RM 2,800 per kg (Pakpahan & Soehartono, 1994).

The huge difference between the price of black nests and white nests is because of the cleaning and processing required by the former before it can be marketed. The process of removing all large and tiny feathers incorporated in black nests is time consuming and labour intensive, which adds to the cost. Furthermore, there is a considerable loss of weight between the collecting raw nests and producing the final product. The proportion recovered is between 45% to 52% where one kilogram of fresh nest could yield 450 to 520 g of cleaned materials, depending on the season when the nests were built and quality of the nests (local trader, per. comm.). Cranbrook (1984) reported the average loss on conversion amounted to 88%, i.e. 1 kg of raw nests reduced to 120 g of marketable materials. One possibility for the different recovery rates is because of the slight variation in weight before cleaning or simply the processing technique has been refined and is now more efficient. I have observed in many occasions that not a single minute amount of edible material is wasted during the numerous processing stages. Extreme care and multiple filtration procedures are applied throughout the whole process. The cleaned nests are in the form of disintegrated edible salivary strains that are subsequently reconstructed into chips of various shapes and air-dried before packing. When fully dried each chip weighs roughly 3 to 4 g.

In the 1950s, the local production of edible nests in Sarawak was mainly to satisfy internal demand. The market value of this commodity reached its highest during the past few decades. Cranbrook (1984) attributed this tremendous increment to the influence of international market, especially Hong Kong. The consumptive power of Hong Kong has tremendous impact on the edible nest sector. In addition, this demand has fluctuated as people of Hong Kong tend to react to economic uncertainty and setback by reducing patronage of luxury restaurants or by cutting down on costly delicacies (Lau & Melville, 1994). Hong Kong is the largest consumer of edible nests in the world. Between 1980 and 1989, Hong Kong imported about 81,000 to 160,000 kg of edible nests with a value of HK $ 40 million to HK $ 300 million (Kang & Lee, 1991). Only small portions of these nests are redistributed to other countries such as the United States, Canada, Japan and Taiwan. In 1989, an estimated 25 million nests were consumed in Hong Kong alone (Good, 1993). Beside the increasing demand, locally or internationally, the consequences of declining yields could not be ruled out as the

main driving force behind increasing prices. However, the stabilising of the market price in Sarawak around middle of 1980's did not necessary reflect a steady supply of edible-nest. Instead, it seems more probably to have arises as a result of elimination of intense competition, through better control and regulation of local market price on the merchants' part after the formation of the Bird Nest Import and Export Association in 1985.

3.3.3 Nest Production In Baram

There is no properly kept record of edible nest yield from any of the cave owners in Baram before 1990. However, records of nest auctions, a trading system carried out between 1933 and 1969 by the administration to safeguard the interest of the owners from unjust exploitation, were kept in the Baram District Office's files (Cranbrook, 1984). The typical decline in nest production for Lubang Salai over the past 50 years, from 1948 to 1998, is shown in Figure 3.1. The average weight per harvest from this particular cave was reduced by 64% from 1948 to 1998. The fact that the swiftlet colony still survives after 50 years of exploitation may be attributed to part efforts by the owners. There were claims that some nests in certain portions of the cave were left for raising the young. Between 1948 and 1959, nests were harvested twice annually in 1948, 1949 and 1953 while three to four times in other years

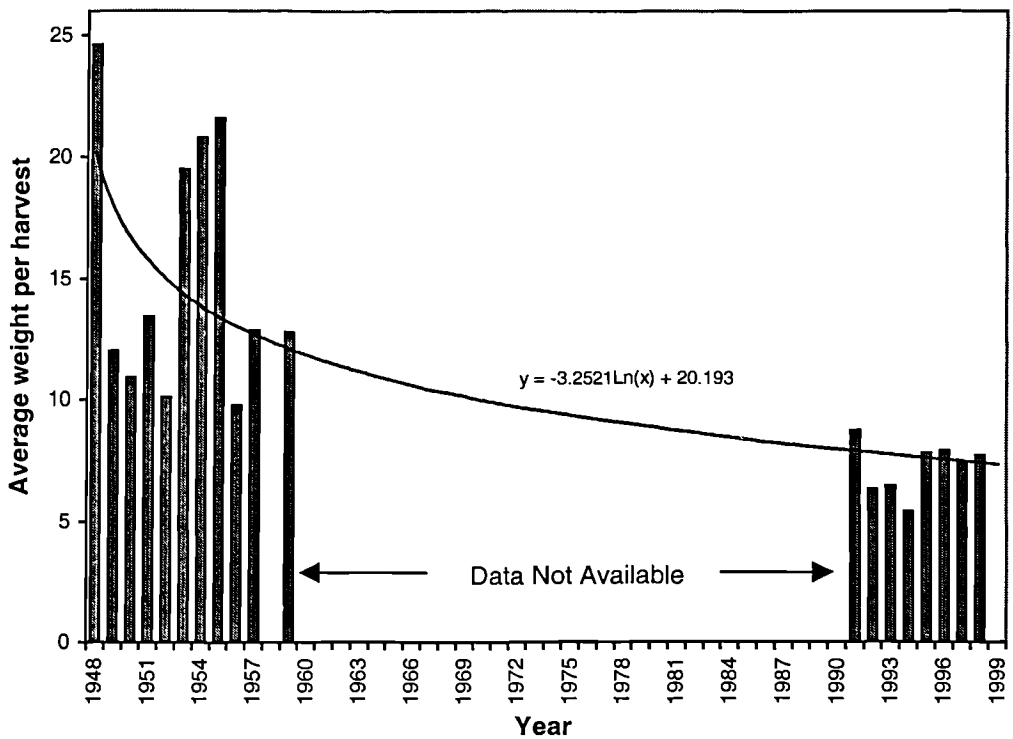

Figure 3.1 Annual production of nest from Lubang Salai between 1948 to 1998 (data from 1948 to 1959 are from Medway, 1962c).

(Medway, 1962c). Apparently, the most significant factor that helped to maintain the declining population in check appeared to be the longer interval between harvests practised in the past that might allow some nestlings to fledged and to replenish the breeding stock.

Between 1990 and 1998, the relative increment in edible nest production observed from Lubang Salai was directly due to an increased harvesting frequency (Figure 3.2). The owners claimed that the number of nests harvested had increased since 1996, but no convincing records were available to verify this claim. Another claim that could not be confirmed was that the physical structure of the nests had become thinner over the years. There is a possibility that the vitality of the sublingual glands' diminishes because of old age. Studies have shown that reproductive vigour decreases with age in *Parus major* (Perrins & McCleery, 1985) and *P. caeruleus* (Dhondt, 1989), hence suggesting this could be true for the swiftlets if no young birds are recruited into the aging colony.

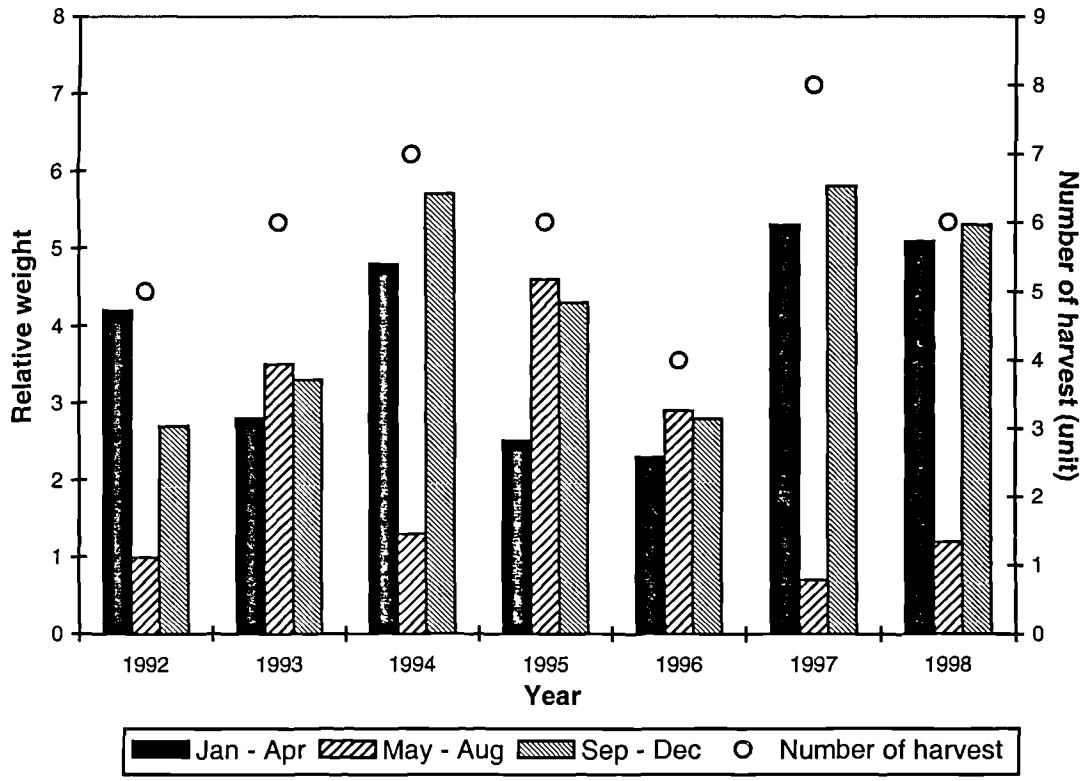

Figure 3.2 Annual nest production from Lubang Salai from 1992 to 1998 (data showing relative production only with the actual value not being revealed).

In 1992 when most nests in Lubang Salai were left for breeding, the total weight of nests harvested after the young had fledged was roughly 25% heavier as compared to the pre-breeding harvest from the same period (Table 3.1). This arises because not post-fledging nests contain extraneous dirt left behind by the nestling, but are also generally larger. Even though these post-fledging nests are somewhat dirty and of unappealing appearance, they are worth more than half the price of the cleaner pre-breeding nests. Therefore, if the whole colony of

swiftlets in the cave is left for breeding, the owner would suffers about 40% reduction in revenue due to the lower quality of the post-fledging nests, but extrneous dirts contribute roughly 25% increase in total weight. This would partially compensates for the financial losses. In addition, the owner would secure a batch of young swiftlets, the most important entity for maintaining and increasing the productivity of the swiftlet colony in long run.

Table 3.1 Comparison of the difference in the relative weight for the post-fledging nests of November 1992 and non-breeding nests at corresponding period of subsequent years.

Date	Category	Weight (mean)	Difference from post-fledging nests of Nov 1992 (unit)
24 November 1992	post-fledging nests	10.8	—
17 October 1993	non-breeding	8.9	- 1.9
19 November 1994	non-breeding	9.4	- 1.4
11 December 1995	non-breeding	8.0	- 2.8
12 July 1996	post-fledging nest	11.5	+ 0.7
14 November 1996	non-breeding	8.0	- 2.8
1 November 1997	non-breeding	8.9	- 1.9

The production from Lubang Beruang seemed to increase from 1992 to 1994 (Figure 3.3). However, it was impossible to evaluate the validity of this observed increment by just the total weight alone, because nests with more moisture content are heavier. Furthermore, lower

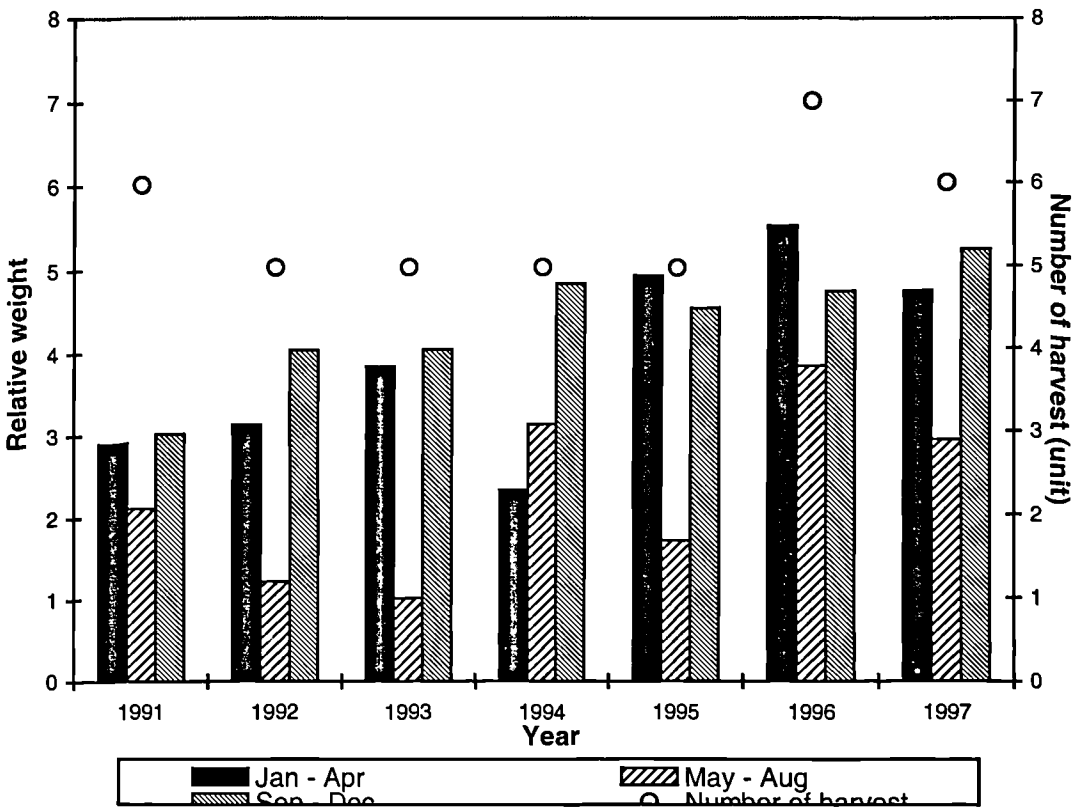

Figure 3.3 The annual nest production from Lubang Beruang from 1991 to 1997 (data showing relative production only with the actual value not being revealed).

production could simply arise because more nests were left behind in the cave for breeding in some years, a practice not uncommon at Lubang Beruang. Therefore, it was recommended that a thorough nest count should be done after each harvest to obtain the exact number of nests in the cave.

3.4 OWNERSHIP OF NEST-PRODUCING CAVES

In the Laws of Sarawak, the Wild Life Protection (Edible Birds' Nest) Rules, 1998, Section 8(1), states that the issue of any licence under these Rules shall not confer upon the licensee any rights or interests to or over any caves or any land upon which collection of edible bird's nests is permitted under the licence. Therefore, in this context, the "ownership of the cave" is defined through customary rights over particular cave or caves, and by being given the rights or license by the government to collect edible-nest within. If no valid license is issued, then such customary ownership is recognised and valid among the respective community only.

Generally, there are two types of cave ownership. One is communal and the other is personal or family-owned. A good example of communal ownership is the numerous caves scattered in the limestone outcrop in Bau. There are many black-nest yielding caves within the vicinity of Gunung Jambusan, namely Lubang Jambusan, Lubang Tupak and Lubang Tingang (Wilford, 1964). The villages surrounding these caves, comprising the Bidayuh ethnic group, have shared rights to these caves. Another example of a communally owned cave is Lubang Batu located in the limestone massive of Selabor about 15 km from Tebakang village. The Bidayuh communities around Tebakang shared the customary rights to this cave.

At Niah, the type of ownership is personal except for some, which are owned by consortia, syndicates or nominees. The majority of owners are descended from the original Penan families, now integrated with Malay society (Medway, 1957). Because of the complex topography on large limestone outcrops, the owners recognised separate features such as tunnels, grottoes or even distinctive sections of large caves among the ramifying cave system. Each portion was designated with a name, known locally as "*lubang*" or "*pasen*". Certain larger ones are further subdivided. For instance, Lubang Dat has ten subdivisions while Lubang Tulang has eleven (Cranbrook, 1984). In Bintulu Division, several individuals and families of the Punan Bah ethnic group have undisputed customary rights to many black-nest producing caves in this division. These include caves at Bukit Sarang near Sungai Mayeng Sarang and many impressive caves scattered along a 16-km long Miocene limestone massive at the headwater of Kakus River (Wilford, 1964).

There are hundreds of known or named caves, large and small, accessed with difficulty or ease, in the limestone hills of the Baram. They are found from Kuala Temala, 114° 28′ E, 3°

48′ N, up river to Bukit Salai, 114° 25′ E, 3° 39′ N (Smythies, 1960). In 1978, the registrar of licences in Baram District Office listed 201 named caves (Cranbrook, 1984). Customary rights of these caves belong to the Kayan ethnic group living in several villages around Long Laput area in the middle Baram. All the caves here are individually or family owned. Management and guarding is much simpler for personal or family-owned caves, especially when it involves only a single cave. Sometimes the parties concerned own more than one cave in different block of the limestone outcrops, but nowadays only few are still inhabited by *A. fuciphagus*. In the case of very large caves, several closely related families usually shared the rights with each family controlling a portion inside the cave and could only collect the nests found within their section.

3.5 EXPLOITATION AND VARIOUS HARVESTING PRACTICES

3.5.1 Legislation

The existence of edible nest caves in Sarawak territory was undoubtedly known to James Brooke, the first Rajah of Sarawak. Before then, nest harvesting had been in practice, at least at Niah, while Brunei rule still prevailed. Nevertheless, the first central intervention was in 1876, during the reign of Rajah Charles Brooke where a five percent export duty of natural produce was imposed, which resulted in the setting of the taxation for edible nests of 15 cents per kati (Cranbrook, 1984). In addition, ownership of cave rights clearly preoccupied the Brooke administration over the subsequent years. The Edible Birds' Nests Ordinance, 1940, proclaimed and clarified the legality of any ownership rights. In addition, it also entrusted the Curator of the Sarawak Museum with the responsibility to rule or govern the collection and auction of nests.

In the post war colonial administration, this Ordinance was revised and incorporated in the new edition of the Laws of Sarawak as the Edible Birds' Nests Title (Collection and Auction) Rules, 1948. This specified the number of harvest permitted per year and, for the first time, the obligatory presence of a government representative to inspect the cave prior to any harvest. A Native Officer or Up-river Agent or some other Government Officers appointed by the District Officer in that behalf had to be present during every collection of nests in a prescribed place to ensure that collection was conducted in an orderly manner, without waste, and only nests of considerable size are collected.

Over the years, another substitute legislation was introduced and this could be cited as the Miscellaneous Licences (Edible Birds' Nests) Regulations, 1963. This regulation further reasserted the role of the Curator of the Sarawak Museum. Until 1996, the Sarawak Museum was empowered to examine the rights and claims to the birds' nest caves and issued a licence to

the rightful owners (Leh, 1993). Nevertheless, the Minister of Public Health and Environment (formerly the Ministry of Environment and Tourism) would determine the timing of each collecting season, acting upon the advice of the Sarawak Museum as well as the National Parks and Wildlife Office after the caves were inspected.

Because both species of edible nest swiftlets, *A. fuciphagus* and *A. maximus*, are listed as protected animals under the Wild Life Protection Ordinance, 1990, permits were required to collect and trade of the edible birds' nest (Basir, *et al.*, 1996). This has been amended, and powers to licence the bird-nests and trade are placed under Section 29(2) of the Wild Life Protection Ordinance, 1998. Under this, regulating and licensing fall within the full jurisdiction of the Forest Department.

3.5.2 Typical Harvesting Practises In Sarawak

Following the Edible Birds' Nests Title (Collection and Auction) Rules, 1948, only two collections were permitted at Niah and not more than three in any other prescribed place, without permission in writing from the District Officer in any one year. The revised Miscellaneous Licences (Edible Birds' Nests) Regulations, 1963, stated that nest harvesting shall not be carried out except at such times and places as authorised by the person granting the licence, that is the Curator of the Sarawak Museum. For the past few decades, there have been two official harvesting seasons every year. The first one is in May and another collection is allowed in November. A 30 days harvesting period is allowed in most parts of Sarawak except in Baram where the permitted duration is limited to 14 days (Leh, 1993). All these regulations have since been superseded by a new set of Rules in 1998. Under section 6 (3) of the Wild Life Protection (Edible Birds' Nests) Rules, 1998, authority is vested upon the Controller to determine the date and number of harvests allowed, as specified in the terms and conditions in the license.

3.5.2.1 Bau Region

The study of *A. maximus* at Lubang Poyang was abandoned in May 1997 owing to frequent poaching that interfered with data collection. The three months' observation and discussion with the local community, nevertheless, unveiled much useful information. Firstly, villagers here claimed to share equal rights to any communal caves around the village and they are represented by a Cave Committee. This committee works side by side with the Village Committee, but makes final decision on matters related to harvesting of nests, such as the date and number of harvest in a year.

Surveys and interviewing with local inhabitants revealed that harvesting was carried out at an average interval of 40 days at nest-yielding caves around Bau. Traditionally, the timing of each harvest is fixed after most nests contain eggs. The reason behind this unusual practice lies with the perception that it would be harmful to female swiftlets if they were prevented from laying by premature removal of the nests prior to egg laying.

Generally, there are two main harvesting seasons in a year, one early of the year and another at the end. In any year, the first harvest is sometimes carried out at the end of February, and from then onwards at an interval of 40 days until the month of May when all harvesting activities cease. This is presumably at the beginning of the moulting period, as supported verbally by the villagers. The second harvesting season commences in early September where all the small token nests built during the moulting period are scraped off, anticipating a good nest-building season to follow. The following harvest is usually in November. The community at Kampung Skiat Baru claimed that there is a three months break where all harvesting activities ceased from November to February, to allow some nestlings to be raised until fledging. However, this does not guarantee any successful breeding of the swiftlets owing to uncontrollable poaching activities. In theory, the cycle is completed or resumed with the subsequent harvest after the young have fledged at the end of February.

Participation by the community and teamwork during harvesting is rather interesting. Each family who wishes to retain their share of the collected nests is obliged to send an adult man, usually the head of the family, to join in the task of nest harvesting. Any agile person possessing the skill to do the actual climbing and collecting would get additional pay for his labour. Nest harvest used to take several days years goneby, because there were just too many nests to collect. Now, it takes one whole day at the most. Each participant brings their own rations for the day and they start early in the morning, taking advantage of the extra hours to work the entire cave. The collected nests would be tied into stacks of 80 pieces each known locally as a "*bubuk*". Only a few trust-worthy persons are given the responsibility of handling and bringing these stacks out from the cave. To prevent any nests from being stolen during transportation, the name of each "*bubuk*" carrier and the consignment carried is thoroughly recorded. This shows the profound degree of mutual distrust among the group. After each harvest, the nests are sold immediately to middlemen from Jambusan town, or from Bau town in the case of the villagers from Kampung Skiat Baru. Revenue from the sale is divided equally among those who participated. The balance, usually about RM 50 to RM 100, is deposited in the Village Committee's bank account and used for development of community projects. Unfortunately, personal gains outweigh communal interest because this sum represents a mere 0.6% to 1.3% of the total sale value.

The market price paid by the middlemen varies from season to season, which depends very much on the physical state and the feathers-to-saliva ratio of the nests. Nests of the lowest

grade sell for RM 30 per tahil. These nests are usually built during the moulting period, distinguishable by the small size and many feathers that are incorporated. Top quality nests are produced between October to February, and they can sell easily for RM 40 to 45 per tahil. The dependency of the community on edible nests is undeniable. For example, the current population of Kampung Skiat Baru stands at 112 families. On an average, 60 to 80 men would participate in any harvesting party. Therefore, 54% to 71% of the entire community benefited from this natural resource.

There are only three caves with a substantial amount of nests near Kampung Skiat Baru that can be guarded effectively, namely Lubang Merasuk, Lubang Tupap and Lubang Bak. The villagers claimed that the production from Lubang Merasuk had declined by 10% from the previous year. Lubang Tupap suffered a 75% decline from a formal output of 1 pikul[3] 60 katis (≈ 100 kg) in 1981 to only 40 katis (≈ 25 kg) in 1996. This decline appear to continue as the total nest yield from this cave in 1997 was reported to be 14 katis 14 tahil (≈ 9 kg). The villagers here blamed the rapid decline over the years on the effluent from pig and poultry farms that contaminated Sungai Jambusan, which flows through the entire length of the cave systems.

In addition, it was said that two caves were tendered out by the District Office but the validity of this claim could not be verified. The first cave subjected to this unusual treatment was Lubang Meraja near Kampung Krokong, which was alleged to be tendered out in 1995 to a Chinese trader from Sibu. It was reported he discontinued the tender in 1997 and the same tender was later taken by a local from the village. The second tender was alleged to occur in 1996. The cave involved was Lubang Staat (or/and Lubang Tubis) near to Kampung Sekubang to the left branch of Sungai Sarawak. The amount of nest yield was said to be 100 katis (60 kg) and 16 katis (10 kg) from Meraja and Lubang Staat, respectively.

Concerning the conservation of *A. maximus* in Bau, the critical issue lies more with the disunity among the villagers, especially between the older generation and the youngsters, rather than any lack of knowledge of the breeding biology of the swiftlets. The village elders favour the idea of allowing the swiftlets to raise at least one brood every year, while the younger generation strongly oppose it and want to harvest as many times as possible even if it is illegal. Therefore, a successful conservation program for *A. maximus* in Bau can only be achieved by first solving the social-economic problems and disunity among the community, followed by recommendations for management guidelines based on sound scientific research.

Based on information gathered through discussion with numerous people, *A. maximus* from Bau area appeared to exhibit the same breeding pattern as that of *A. fuciphagus* in middle Baram. This presumption is supported by the fact that nest collecting begins in September,

[3] Traditional Chinese measuring system. 1 pikul = 100 katis; 1 kati = 16 tahil; 1 tahil ≈ 38 g.

which suggests that there is a good nest-building period. Secondly, nests constructed between October and February were said to be of the finest quality. Thirdly, it was reported that if nests constructed after the harvest in February were not disturbed, eggs and young could be found in any month between April and July.

3.5.2.2 Niah Region

A total ban on nest harvesting was imposed at Niah Great Cave, a major producer of black nests, from 1989 to 1991 in order to allow the swiftlet population to recover. Owing to the continual and rapid decline in the number of swiftlet despite the ban, another four years ban was imposed in 1993 but this was lifted in 1997. Previously, a 30- to 60-days collecting period was allowed but now the cave is opened to licensees three times a year for a short harvesting period of only a month (Then, 1997).

Generally, there is no proper management or harvesting practices throughout the black-nest producing areas. At Niah, the rightful licensees have leased or contracted out their caves or nest-yielding portions for a quick sum of money and spare themselves the troubles of overseeing guarding and nest harvest. Such practices have been in existence for years. Many of these are then sub-leased out, sometimes with several changes of hand, creating an irreversible confusion and chaotic state of management. Since enforcement is impossible in this massive cave with a floor area of about 24 acres (10 ha.), the contractors are largely responsible for harvesting the nest in an unsustainable and profit-driven manner.

3.5.2.3 Baram Region

The limestone caves scattered throughout the middle Baram region are the only remaining major white-nest producing area, and the last remaining viable *A. fuciphagus* population, in Sarawak. One significant difference between Baram and Bau is the ownership of caves, which are not shared among the community, but exclusively owned by individuals or families. Naturally, the cave owners at Baram express a more concerned attitude and greater interest in sustainable management. The Kayan ethnic group, who have customary rights over the white-nest caves in the middle Baram, are better organised and efficient in guarding their caves. However, there is room for improvement in management, because harvesting practice here is no doubt unsustainable too.

Generally, nest harvesting is carried out all year round at an interval of 60 to 65 days. Altogether, there are six harvests in a year: January, March, May, July, September and November. Apparently, the Kayan at Baram share the same concern as the Bidayuh community at Bau, whereby they believe it is harmful to the female swiftlets if nests are collected before

the eggs are laid. Good quality nests are produced between September and March while lower quality ones are obtained during the moulting period, known as "*melaie*" in Kayan dialect. During the moulting period between April and July, the cave is usually cleaned of any small nests several times until post-moulting nests are deposited in early August. At Lubang Salai, the 60-days harvesting interval was adopted after a reshuffle in the management committee in 1995. Between 1991 and 1997, nestlings from only two breeding seasons were allowed to fledge. The first one from June 1992 to November 1992, while the other between February and July 1996. Since then, the owners claimed that the yield has increased, but the nests have become thinner.

The caves in Baram are small when compared to the black-nest yielding caves such as Niah and those in Bau. Therefore, nest harvesting could be done swiftly within a day in a more relaxed atmosphere. Although the caves are not communally owned, nest harvesting always involves people from the community. In the past, nest harvesting was a major event that lasted several days and involved the whole village. Now, it could be done with a handful of people but a party of 10 to 30 persons is not uncommon. There is no shortage of food and alcoholic drinks, which are provided free by the owners after the task has been accomplished. In contrast to Bau, intricate networks of bamboo scaffolding are not used. Modern aluminium ladders and long bamboo poles are used as substitute. In Lubang Sepayang, electric wire runs the entire length of the cave, which is lit up with many bulbs and florescent lighting to facilitate harvesting. The traditional step-cut log ladder described in Medway (1957), each measuring about 8 meters in length is still in use at Lubang Beruang. Another intriguing method employed is a tripod erected using tree trunks of moderate length. Each each leg would be manned by one adult or two teenagers, while one nest harvester would climb to the top with the aid of an aluminium ladder. His relative position to the nesting sites could be shifted around, like a moving three-legged creature, by altering the legs of the tripod one at a time.

3.5.2.4 Kakus Region

There are two major edible nest-producing areas in the upper Tatau River. The most notable one is Berkuyat region in Ulu Kakus, while the other is near the tributaries of Sungai Tatau and Sungai Mayeng. The swiftlet caves upriver of Sungai Mayeng Sarang are located within two blocks of limestone outcrops (Bukit Sarang and Bukit Lebik) that are surrounded by peat swamp forest. The total production from the Bukit Sarang area is about 30 to 40 kg of nest produced by *A. maximus*. Several noble-class (*maran*) individuals of the Punan Bah community from Rumah Bilong have customary rights over the harvesting of swiftlets' nest in these caves. Other petty cave owners include members of the Berketan ethnic group, who have rights to lesser part of the caves.

The state of development at Berkuyat in Ulu Kakus is in a shocking condition. Caves around this area are alleged to be taken over, with partial consent, and more likely forcefully, from the rightful Punan licensees by several groups of debt collectors. Fighting and the involvement of gangsters are frequent, while nest harvesting is alleged to happen every month. Elsewhere, the caves around Bukit Sarang are harvested monthly, also by the licensees. In the latter case, the owners claimed that they have no other alternatives but to harvest the nests before they are stolen. They stressed that they were compelled to do so by the prevailing and uncontrollable poaching activities. Although this was later proven to be true, equally important is the need to acquire cash to settle their accumulating debts.

In spite of the fact that the timing of every harvest is the same at Bukit Sarang, the management of the caves differs in terms of profit sharing and wages for the workers. There are three different approaches. The first one places a lot of weight on the dependency on nest yield. The cave guards cum collectors are compelled to collect as many nests as they could find because their income is based on the quantities of nest harvested. The more frequent they harvest, the more earnings they would receive. After each harvest, the nests are divided evenly among the owner and his workers, all having equal share but the owners reserve the right to buy their employees' share at a lower price. In this kind of arrangement, the cave guards are responsible for their own necessities, such as food and living quarters, during the guarding period at the interval between harvests.

In the second approach, the cave owner would provide accommodation to the cave guards and oversee their weekly rations and basic requirements. All expenses are then deducted from the profit from the sale of nests and the balance is divided equally among both parties. The third approach is rather unusual and it is to the advantage of the cave guards or workers. Proceeding from sales of nests is divided into three portions and the owner receives 1/3 of the net profit while the remainder 2/3 goes to the cave guards. The logic behind this kind of settlement is that more workers are usually employed, and therefore it is reasonable to set apart a larger allotment for them. In this instance, the owner is spared of the hassle of providing food or personal needs to the workers.

3.6 CONCLUSIONS

The history of edible birds' nest trade is shrouded with mystery and myth because there were no proper records or any traceable writing earlier than late sixteenth century in the official annals of the Ming dynasty. In Sarawak, the earliest mention of edible nest trade in any European writings was in 1840 but it is believed this trade had long been in existence. Therefore, it could be concluded that the edible nest industry is at least 150 years old. Although

it has lost its former importance, ranking between the fourth and sixth largest source of revenue in duty to the Brooke government as far back as 1888, it nevertheless still represents a substantial source of income for various groups of people, especially those who were given the rights to harvest these nests. There is always a possibility of bringing this industry back to its former position of importance if the current populations of *A. fuciphagus* and *A. maximus* are managed properly on a sustainable basis.

Of all the nest-yielding caves in Sarawak, those in middle Baram are in a better condition because they are easily guarded and sustainable management practices have been adopted in the past one or two years. The Kayan community there is now more aware of the need to conserve the swiftlets and additional efforts were made to allow at least a season of young nestlings to fledge every year. The major challenge now is the plight of the black-nest producing caves that are unfortunately community owned. The circumstances in Niah Great Cave are hopeless, as poaching is widespread and uncontrollable. The *A. maximus* populations in Bau stands a chance of recovery if the local community could be united and put more efforts in conservation. The prospect of the black-nest caves in Ulu Kakus, Bukit Sarang and several more in the upper Baram provide what could be the last hope for conserving this species in Sarawak because they are mostly individually or family owned. Furthermore, these caves are located in remote and less accessible part of the state.

What is more important is the fact that international market for edible swiftlets nests amount to several hundred tons every year and it appears that demand still far exceeds supply. Although the practice of "farming" the swiftlets in specially constructed buildings has been practised widely in Indonesia, such lucrative enterprise is absent in Sarawak. This technique ought to be introduced as an integrated community-based project that operates concurrently with efforts in sustainably managing and conserving the wild edible nest swiftlets' populations. With the value of nests ranging between RM 400 to RM 6,800 per kg in local market, this renewable natural resource could contribute substantially to local economic development. Therefore, the edible birds' nest industry has the potential to grow into small or moderate sized commercial enterprise that is localised and self-sustaining.

Chapter 4
Breeding Periodicity

4.1 INTRODUCTION

In an attempt to stem the loss of biodiversity, sustainability has been hailed the new paradigm of conservation (Salwasser, 1990). The sustainable management of edible nest swiftlets differs from many other form of wildlife resource utilisation, in the sense that the nest is the harvested product, without any fatal harm done to the adult swiftlets. In order to maintain the population size of a colony of animal in a stable condition, equilibrium has to be reached between the reproduction and mortality rate (Callaghan *et al.*, 1997). Any inclination toward the latter causes the decline of the population, and *vice versa*. The first indicator of ineffective management of swiftlets will be reflected in the long-term reduction of nest production. The overall breeding periodicity of the swiftlet and the onset of each period of breeding are two important elements, which must be thoroughly understood, in order to achieve effective management.

Over the past few decades, nest yields recorded from natural cave sites throughout the edible nest producing regions have declined dramatically (Cranbrook, 1984; Francis, 1987b; Good & Wong, 1989; Leh, 1993; Lau & Melville, 1994; Tompkins, 1997). This is mainly attributed to the unsustainable and uncontrollable harvesting regimes that were being practised. Partly to blame is the lack of accurate and sound scientific knowledge of the breeding periodicity of the edible nest swiftlets (Cranbrook, 1984; Kang *at al.*, 1991; Cranbrook *et al.*, 1996). Consequently, intervals between each harvest have been too short to permit any successful fledging, and hence, no new additional recruitment into the population as a whole. If these effects are prolonged over the years, no young swiftlets are produced to replace and supplement the dying older population.

The biology of three species of swiftlets in Southeast Asia, namely the Black-nest Swiftlet (*A. maximus*), the Mossy-nest Swiftlet (*A. salanganus*) and the White-bellied Swiftlet (*Collocalia esculenta*), were studied by Medway (1962b, 1969). However, many of the observations were carried out during sporadic visits associated with the Sarawak Museum's archaeological research programme at Niah. In addition, little is known regarding the annual periodicity or the incubation and fledging period of *A. fuciphagus*. Langham's (1980) study on this species could be considered a more comprehensive, but the study period only lasted seven months, and failed to clearly define a breeding season. Furthermore, the colony was not located in natural caves but situated at the back of a shophouse in George Town, Penang.

Similarly, another colony of *A. fuciphagus*, occupying man-made tunnels in old fortifications on Sentosa Island, Singapore, was studied for a short six month period from March to August 1984 (Kang *et al.*, 1991). This study concentrated more on the energetic and growth of nestlings, and the influence of nest harvesting upon nest construction, rather than on investigating the onset of the breeding season. Another study on the reproductive strategies and behaviour of *A. fuciphagus* and *A. maximus* using the same colony in Singapore employing clutch manipulation experiments was carried out between April and June 1984 (Kang & Lee, 1991; Lee & Kang, 1994). Both these studies also failed to establish the natural annual breeding periodicity of *A. fuciphagus*.

In Vietnam, the breeding season of *A. fuciphagus* was established for the populations at Da Nang and Khanh Hoa (Nguyen Quang, 1994, 1996). There were some observed differences and seasonal variations in the onset of breeding, with northern populations in Da Nang beginning and ending nest building earlier than the southern population in Khanh Hoa. General climatic factors have been shown to influence the onset of the breeding season of different swiftlet colonies in Vietnam. This further reaffirms the suggestion by Medway (1962b, 1962c) that there were possible geographical and seasonal variations in the breeding cycle, even within Sarawak.

In Sarawak, despite the decline in edible swiftlet populations, and concern for their future, essential biological data such as the breeding periodicity, nest-building phase, laying, incubating and fledging are still sparse. There is no good information of the timing of the breeding cycle across its distribution ranges in general or in Sarawak in particular, especially at Niah or Baram District (Cranbrook, 1984).

Therefore, this study was designed specifically to elucidate in detail the breeding biology of the edible nest swiftlets in Sarawak. A 12-month study was carried out from April 1997 until March 1998, under natural condition, at several colonies of *A. fuciphagus* in middle Baram. All the marked nests were constantly monitored and routinely checked at regular intervals for eleven full months, the first ever attempt of comprehensive and conclusive long-running observations for either this, or any other species, of swiftlet. The reproductive capability and the breeding success of *A. fuciphagus* were determined. This included the number of breeding attempts every year, the onset of each season, the proportion breeding at various periods, the hatching and fledging rate.

In this chapter, I present an overview of the annual breeding season of *A. fuciphagus*, including the number of breeding bouts, in Section 4.2. The reproductive performance, which includes the proportion of breeding birds at each breeding bout, egg loss, hatching and fledging success, are discussed in Section 4.3. The incubation and fledging period of *A. fuciphagus* are presented in Section 4.4. The inter-clutch interval and possible cues regulating the onset of breeding are discussed in Section 4.5. Section 4.6 explains the correlation between moult and

breeding. Finally, the behaviour of *A. fuciphagus* in and around the cave is presented in Section 4.7.

4.2 ANNUAL BREEDING SEASON AND BOUT PERIODICITY

The annual breeding season of *A. fuciphagus* is a protracted event lasting at least nine months from August to March, with three bouts of breeding. The timing of each bout varied slightly among the colonies in Lubang Salai and Lubang Beruang. For comparison, the proportion breeding for three sampling sites is shown in Figure 4.1. The breeding bout that marked the beginning of the breeding season occurred in late August or early September, and ended in early December. This was followed by a second bout of breeding starting from the middle of December that lasted until March the following year. The third bout of breeding commenced in April, but not all sexually mature adult pairs produced a clutch. These three bouts of breeding generally overlapped at both limits. Each bout of breeding was recognised as the first, second, and third breeding bout, respectively.

As the nests used in this study were marked in March 1997 after one harvest, the subsequent breeding observed was the third breeding bout when the annual breeding season was approaching its end in July. At Lubang Salai, the egg-laying phase within this third bout of breeding stretched over six weeks from middle of April until the end of May with little synchronisation (Figure 4.2). In addition, the highest proportion breeding recorded during this period was only 30% of the entire marked sample (Figure 4.1), implying that about two-thirds of the nests did not have a clutch.

Breeding asynchrony was even clearer in Lubang Salai during the first breeding bout. Eggs were found among the marked nests from early August until the end of December (Figure 4.2), indicating a prolonged egg-laying phase. At any month, less than half of the marked nests contained at least one egg. The highest proportion breeding was recorded in the middle of September, which amounted to roughly 50% of the entire marked colony (Figure 4.1). During the second breeding bout, the proportion breeding continued to increase starting from early December and reached its peak in early February, although the maximum value recorded was only slightly over 50%. For any pair that bred early in the first breeding bout, the subsequent clutch was produced in December, at a time when many of the other nests still contained near-fledging nestlings (Appendix 2 & Figure 4.2).

The general breeding pattern exhibited in the second breeding bout was also not synchronised. Hence, eggs were present throughout the year, and overall breeding was less than 50% (Figure 4.1) despite the fact that the marked nests were left undisturbed inside the cave since last April, and had accomplished two previous breeding attempts. Hence, the breeding pattern of *A. fuciphagus* at Lubang Salai is never in perfect synchronisation. After one bout of

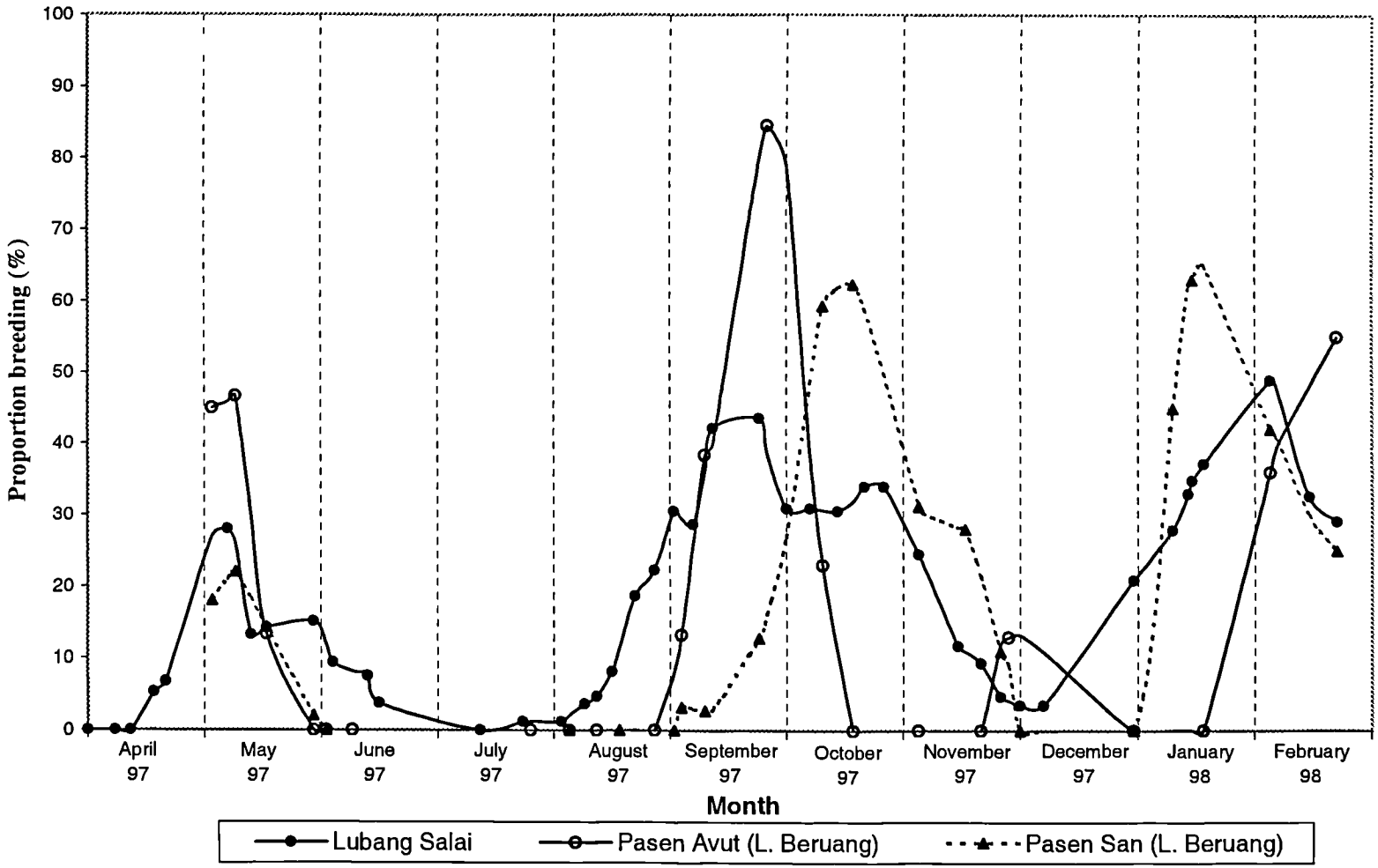

Figure 4.1 Proportion breeding for *A. fuciphagus* at the marked nests in Lubang Salai and Lubang Beruang.

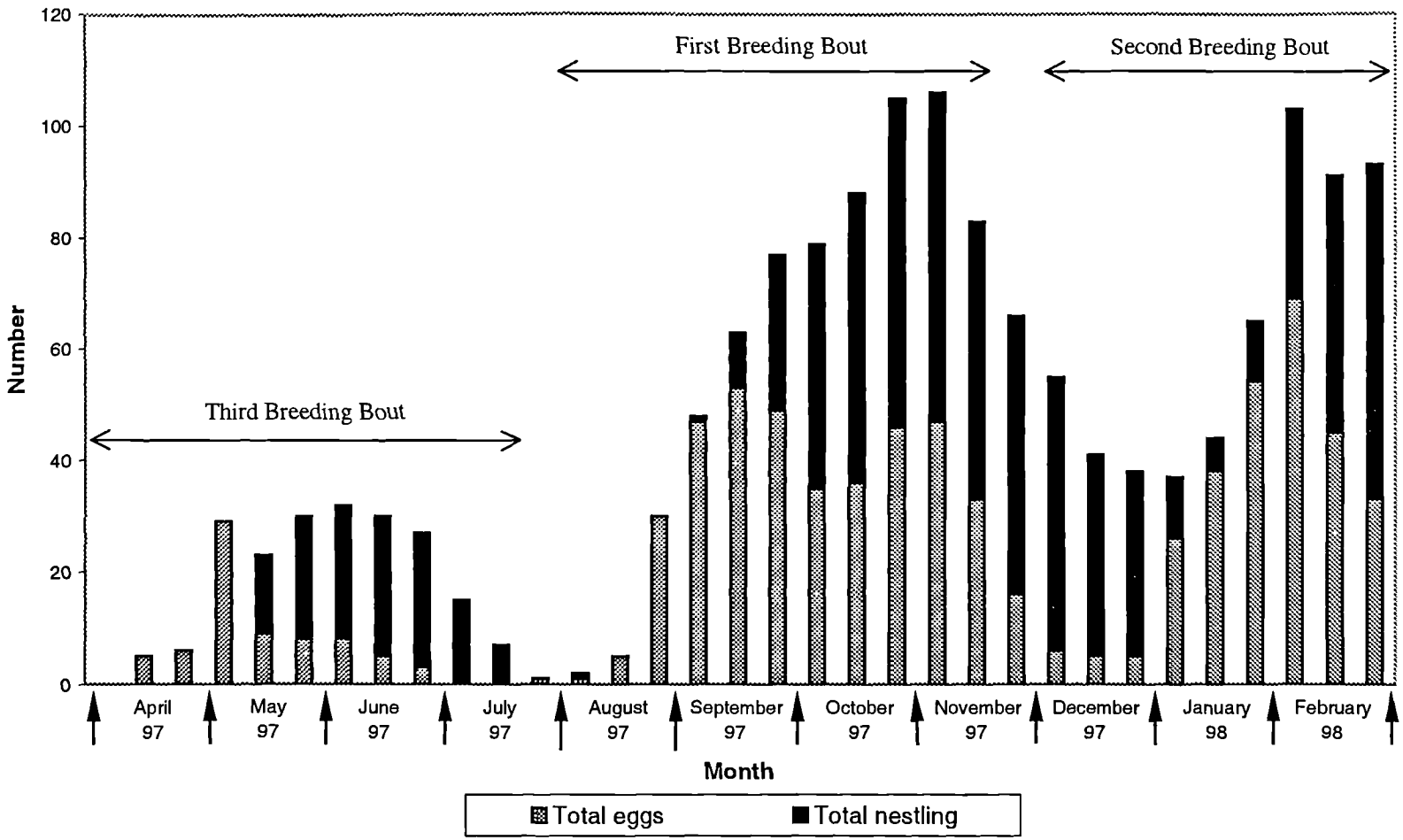

Figure 4.2 The number of eggs and nestlings at the marked nests in Lubang Salai between Arpil 1997 and February 1998.

breeding, some nests would definitely drop off the cave wall naturally, perhaps caused by a combination of wetness on the cave wall and the deterioration of the nesting materials. For example, in Lubang Salai, 12 of the marked nests, or 32% that contained a clutch during the third breeding bout, fell off by themselves after the young had fledged. Then, in the subsequent breeding bout, any pair with the nests still intact will lay their first egg approximately a month earlier than those that lost their nests. Such delay is the first contributing factor towards asynchronization, and the effects are staggered and become more apparent over several bouts of breeding. The asynchrony in breeding at Lubang Salai was further evidenced by some off-season breeding between June and August.

Results from Lubang Beruang showed a closer synchronisation in breeding. During the first breeding bout, a clear and distinctive egg-laying phase was exhibited at Pasen Avut that occurred within a short 4-week period from mid-September to mid-October (Figure 4.3). Ninety per cent of the eggs produced in this bout of breeding were laid by early October (Figure 4.1). The egg-laying phase at Pasen San, on the other hand, stretched from mid-September to late November (Figure 4.4), but nevertheless exhibited a maximum 70% of breeding by late October (Figure 4.1), but still suggesting a more concentrated egg-laying phase pointing to a closer breeding synchrony than at Lubang Salai.

The second breeding bout at Lubang Beruang also began a few weeks later than at Lubang Salai. The egg-laying phase lasted four weeks in February at Pasen Avut, while this was extended from January to February at Pasen San (Figure 4.1). Both figures illustrate three distinctive peaks, one each in May and October, and another in late January. However, the peaks shown in Figure 4.1 are narrower, representing a short egg-laying phase. All nests at Pasen San were empty, without any nestlings or eggs between July and August (Figure 4.4) showing evidence of good synchronisation in breeding.

One possible explanation for the observed difference at these two colonies is that Lubang Beruang did not encounter any problems from falling nests. None of the marked nests fell off between April and December, apart from three nests that were experimentally removed. Medway (1962b) came to the same conclusion that unseasonably early fall of certain nests might contribute to asynchrony in breeding. Generally, the nesting sites inside Lubang Beruang were noticeably drier without any film of water covering the surfaces even during the wettest months of the year. In contrast, many of the nesting sites in Lubang Salai were wet and damp, especially after a prolonged downpour.

The protracted breeding season, incorporating several bouts of breeding observed at Baram for *A. fuciphagus*, is in good agreement with observations made by Medway (1962b) for *A. maximus* at Niah, although the latter study did not clearly define each bout of breeding or resolve the number of breeding attempts. However, the breeding season of *A. maximus* lasted eight month, beginning in September and ending in April. Within these limits, there was little

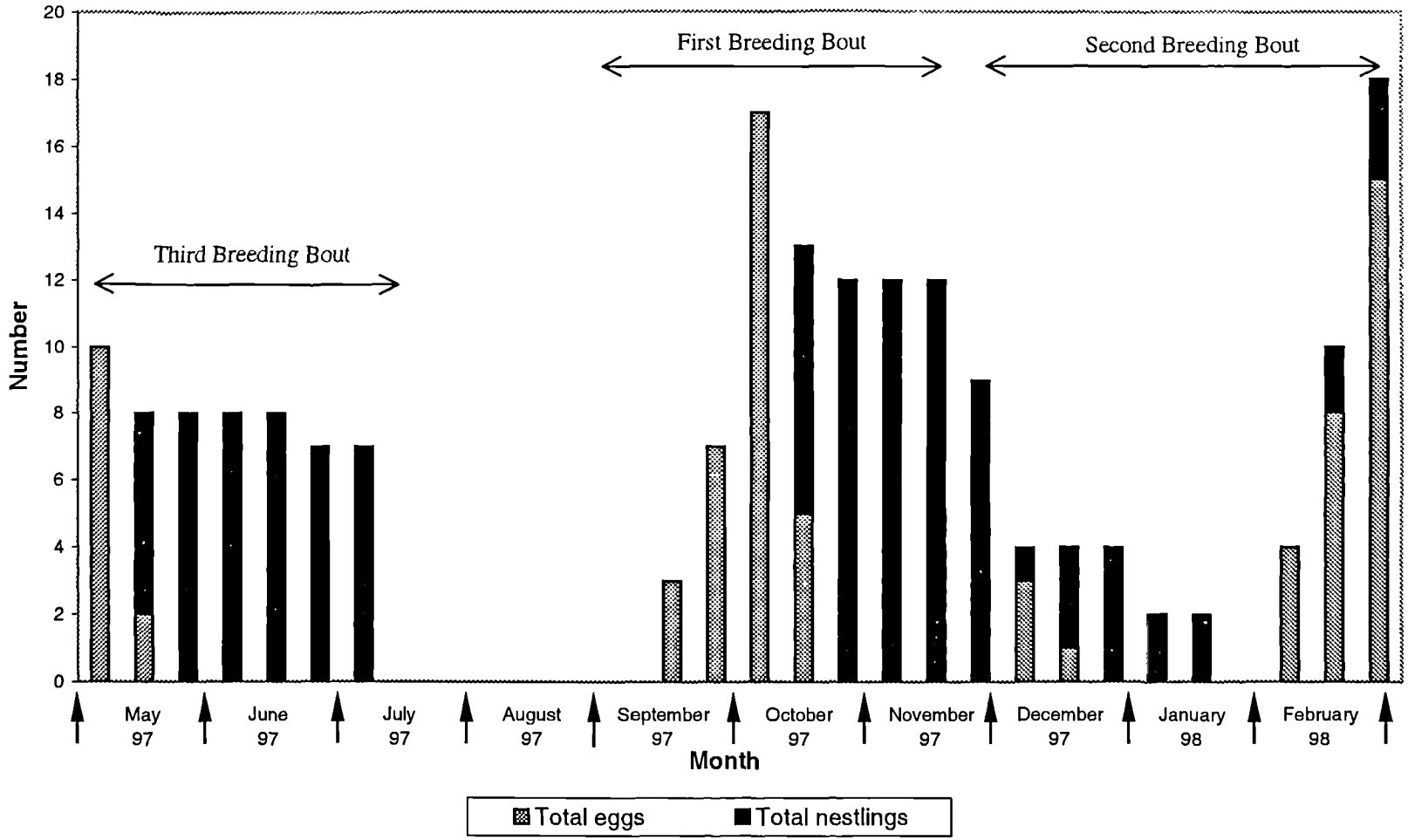

Figure 4.3 The number of eggs and nestlings at the marked nests in Pasen Avut (L. Beruang) between May 1997 and February 1998.

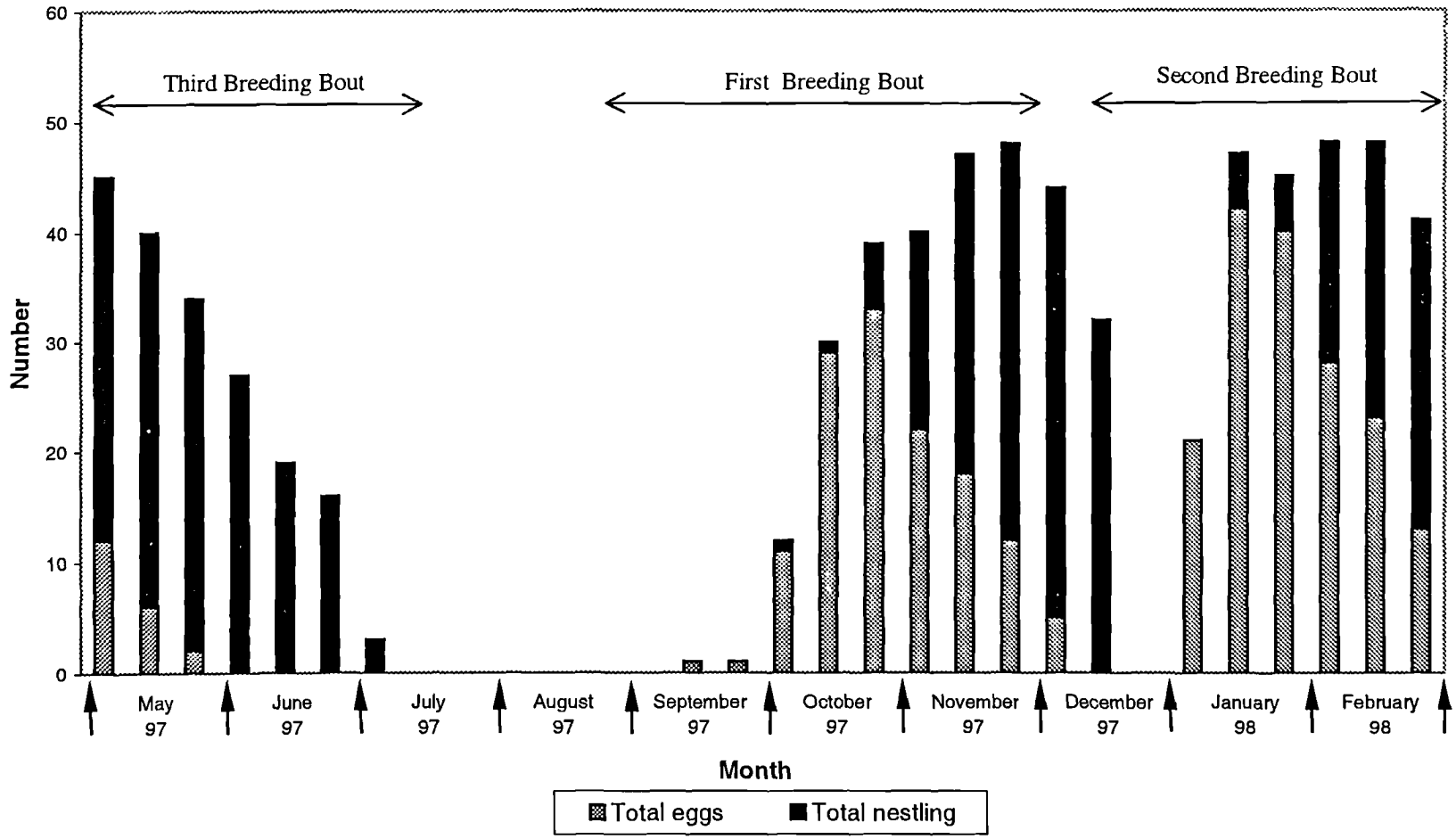

Figure 4.4 The number of eggs and nestlings at the marked nests in Pasen San (L. Beruang) between May 1997 and February 1998.

synchronisation of breeding either within or between groups of nests. In the first week of February 1958, the colony of *A. maximus* at Niah was reported to contain eggs and nestlings at all stages of growth from newly hatched to almost flying, while reproductive activity had declined in April (Medway, 1962b). Comparing with the breeding pattern of *A. fuciphagus* in Baram, this corresponds with the second breeding bout and the decline in number of nests with eggs in April. At Lubang Salai, 47% and 22% of the marked nests contained eggs and nestlings of various growth stages respectively in the first week of February 1998.

The observations made at Niah in August also matched those recorded in Baram. Four hundred nests examined were empty and in most cases were rotten and broken, or fallen from the cave (Medway, 1962b). It was noted that in July, 98% of *A. maximus* nests were empty while 86% of the nestlings was at near fledging stage. Comparable representation was also manifested by *A. fuciphagus* during the first breeding bout in Lubang Salai where all the nestlings were about to fledge by July (Figure 4.2). Similarly in November 1957 and 1959, 94% and 92% of the *A. maximus* nests examined at the undisturbed sites were empty where most of the nestlings had already fledged (Medway, 1962b).

One colony of *A. fuciphagus* in Penang also begins egg lying in August with two distinctive peaks. The first extends from October to the beginning of December, and the second occurs in February, followed by a rapid decline in March to almost no laying in April (Langham, 1980). These two periods correspond with the first and second breeding bouts observed in this study.

It has long been recognised that birds have short breeding seasons at higher latitudes and longer ones at low latitudes or the tropics (Wyndham, 1986). The less marked tropical climates permits a longer breeding season than those in the temperate zone, and a nesting period of six to ten months or even throughout the year, is not uncommon (Gill, 1990). Throughout the study period, daylength and temperature did not appear to govern the onset of breeding. In temperate regions, photoperiod or photostimulation is known to influence and regulate the onset of breeding (Marshall, 1961; Follett, 1976; Wingfield & Farner, 1993), but there is little difference in daylength throughout the year in Sarawak. For instance, daylength at Niah, which is at a very similar latitude to Baram, varied by only 29 minutes throughout the year (Medway, 1962c). The temperature variations in the inner portion of caves where the swiftlets nest were minimal with little annual fluctuation. For example, the temperature within Lubang Salai was maintained at 25.5°C and 26.0°C with a relative humidity of 96 to 98% from 0800 to 1600 hours on 9 April 1997 (Figure 4.5). In contrast, the temperature a few meters outside the cave entrance varied from 24°C to 35°C and the relatively humidity varied from 57 to 96% with the driest period recorded at noon. These two external factors have been proven not to determine the breeding season of *A. maximus* and *A. salanganus* at Niah (Medway,

1962c). Fogden (1972) also came to the same conclusion that photoperiod seems unlikely to be a proximate factor in initiating breeding in Sarawak.

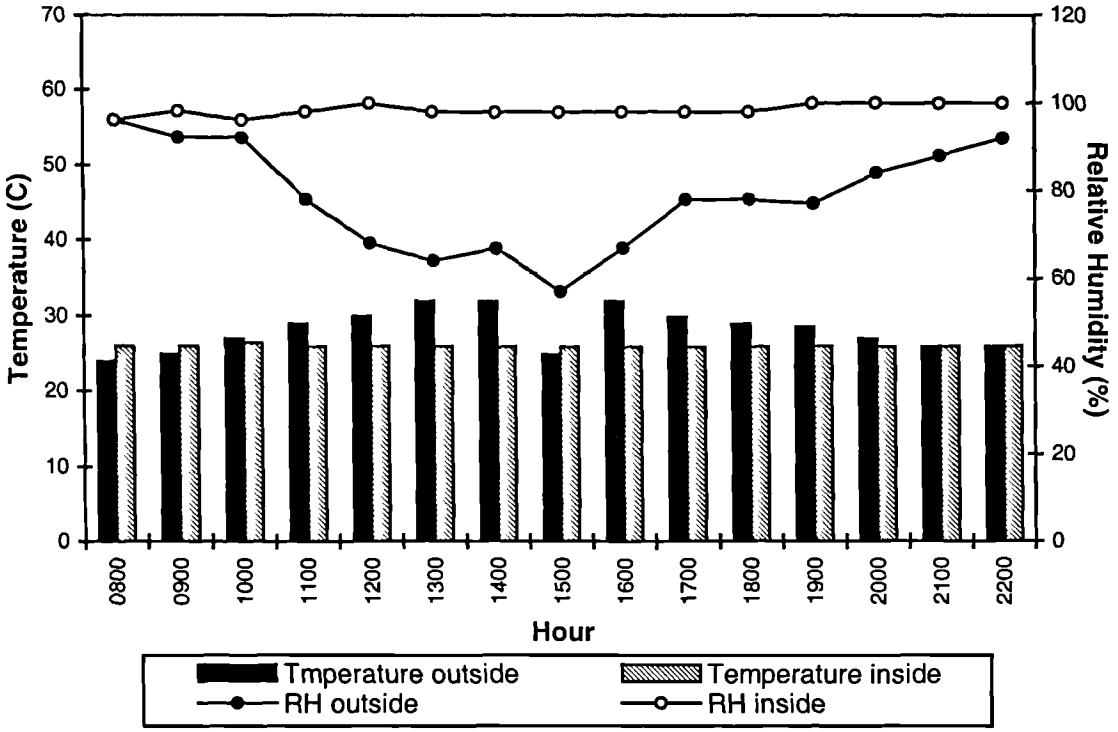

Figure 4.5 Daily temperatures outside and inside Lubang Salai with the respective relative humidity on 9 April 1997.

Generally, the slight differences in tropical photoperiod have been considered too insignificant to act as a proximate environmental cue to control breeding. However, recent research has shown that a species of Neotropical forest bird (*Hylophylax naevioides*) was able to perceive the one-hour difference between the longest and shortest tropical photoperiod. Even an increased of photoperiod by as little as 17 minutes was sufficient to cause physiological and behavioural responses, resulting in a dramatic increase of gonad size and song activities (Hau *et al.*, 1998).

Nevertheless, the most likely factor to stimulate the onset of the breeding of *A. fuciphagus*, and most probably other swiftlets in Sarawak, is a combination of internal physiological circa-annual rhythm and hormonal cycle, both of which are closely linked to abundance of food. Variations in the timing of breeding among bird species are under the constraining influence of energy reserves (Perrins, 1970), and seasonal changes in breeding activity are directly associated with the availability and abundance of food resources (Brinkhof & Cavé, 1997). Ward (1969b), suggesting that the level of tissue protein may have important repercussions on the timing of both reproduction and moult, and might even be the main regulating mechanism. Seasonal changes in the level of tissue protein of swiftlets must be directly correlated to changes in protein availability from the insect food supply. Therefore,

internal regulation by this process does not require any perception of an environmental change through any external sense organ (Fogden, 1972).

The production of saliva for nest construction in both sexes and the formation of eggs in the female must considerably deplete the energy reserved for reproduction. Egg formation is a process of great energy demand (Kang *et al.*, 1991; Heaney & Monaghan, 1995; Monaghan *et al.*, 1995), and can reach a maximum daily energy requirement of 50% of a female's basal metabolic rate in passerine birds (Ludvig *et al.*, 1995). Therefore, after one bout of breeding, the swiftlets will need to build up their energy reserves until they are sufficient for another breeding attempt. Hails and Turner (1985) reported that the protein and fat level in *C. esculenta* increased immediately before breeding and may act as the proximate stimulus initiating breeding. Such an internal trigger to mark the start of breeding is very useful and specifically important for birds in uniform tropical environment (Fogden & Fogden, 1979).

The increase in fat and protein in birds before breeding provides a store of nutrients to meet the demand of eggs production and incubation (Krapu, 1981). Bird muscle, and certain other tissues, are known to support a protein storage capacity for reproductive usage (Houston *et al.*, 1995b; Bradbury & Blakey, 1998). Furthermore, the utilisation of tissue protein to supplement egg production is very widespread. Birds have the ability to mobilise tissues selectively, for example the sarcoplasm and myofibrillar muscle, that can contribute scarce essential amino acids during laying (Houston *et al.*, 1995a). Therefore, it is postulated that any surplus resources for the daily expenditure energy and other physiological process such as formation of new feathers would be reserved to enhance bodily condition in anticipation of succeeding breeding. The remote effects of nourishment established well before the start of any breeding season has profound influenced on the quality and clutch size, as well as on reproductive success (Selman & Houston, 1996).

The breeding season of *A. fuciphagus* in Sarawak was timed whereby eggs laid during the first breeding bout hatched just before the north-eastern monsoon sets in. The succeeding breeding bout coincided with the entire period of the monsoon. The third breeding bout occurred during the receding months of the monsoon. *Aerodramus fuciphagus* in Vietnam were known to commence nest building in the dry season and bred during the first rainy season, at a time when aerial insects were most abundant and easily caught (Nguyen Quang, 1994). Many species of birds in tropical areas such as Peninsular Malaysia and Sabah have seasonal breeding. Food availability is either the ultimate factor determining the onset of breeding (Gibson-Hill, 1952; Gill, 1990) or serves as supplementary information for fine-tuning breeding events with local environmental resources (Wingfield *et al.*, 1992; Hau *et al*, 1998). In Sarawak, insects are available throughout the year in dipterocarp forest, with certain seasonal fluctuation in abundance. The months between December and May coincide with a period for which there is a good evidence that insects are most abundant (Fogden, 1972). Furthermore,

swarming termites, a readily and nutritious food supply, tend to occur after periods of heavy rain, particularly at the beginning of the monsoon.

4.3 BREEDING SUCCESS

4.3.1 Proportion Breeding At Various Periods

The proportion of swiftlets breeding in this study was based on the number of nests containing a clutch, regardless of whether this was of one or two eggs. The proportion breeding during different breeding bouts varied with the time of the year. Results from three successive bouts of breeding in Lubang Salai and Lubang Beruang are summarised in Table 4.1.

Table 4.1 Comparative values of the proportion breeding recorded from three bouts of breeding between April 1997 and March 1998.

Sampling sites	Proportion breeding (%)		
	First breeding bout	Second breeding bout	Third breeding bout
Lubang Salai	96.1	93.8	59.7
Pasen Avut, L. Beruang	84.6	80.0	46.7
Pasen San, L. Beruang	96.9	91.4	65.8

The breeding success for the first breeding bout is shown in Table 4.2. Almost all marked nests produced a clutch, reflecting the onset breeding activity. The number of adult pairs that bred was much higher (χ^2 = 19.99, df = 2, P < 0.05) than the previous bout of breeding for all sampling sites.

Table 4.2 Comparison of the breeding success during the first breeding bout.

	Lubang Salai	Pasen Avut, L. Beruang	Pasen San, L. Beruang
Proportion breeding (%)	96.1	84.6	96.9
Non-breeding pairs (%)	1.3	15.4	3.1
Nest abandoned (%)	2.6	0	0
Hatching successes (%)	63.3	66.7	75.9
Egg loss (%)	36.7	33.3	24.1
Nestling loss (%)	4.2	8.3	6.8

The breeding success recorded for the second breeding bout is shown in Table 4.3. The proportion breeding was 93.8% for Lubang Salai, while 80.0% and 91.4% for Pasen Avut and Pasen San of Lubang Beruang. The values recorded at all sampling sites did not differ (χ^2 = 0.03, df = 2, P > 0.05) from those of the first breeding bout.

Table 4.3 Comparison of the breeding success during the second breeding bout.

	Lubang Salai	Pasen Avut, L. Beruang	Pasen San, L. Beruang
Proportion breeding (%)	93.8	80.0	91.4
Non-breeding pairs (%)	6.2	20.0	8.6
Nest abandoned (%)	0	0	0
Hatching successes (%)	66.2	70.0	74.2
Egg loss (%)	33.8	30.0	25.8
Nestling loss (%)	1.0	7.1	6.5

The proportion breeding during the third breeding bout was approximately the same ($\chi^2 = 3.31$, df = 2, $P > 0.05$) for Lubang Salai and Lubang Beruang (Table 4.4).

Table 4.4 Comparison of the breeding success in the third breeding bout during the moulting period.

	Lubang Salai	Pasen Avut, L. Beruang	Pasen San, L. Beruang
Proportion breeding (%)	59.7	46.7	65.8
Non-breeding pairs (%)	21.0	46.7	34.1
Nest abandoned (%)	19.3	6.7	—
Hatching successes (%)	56.2	80.0	84.4
Egg loss (%)	43.8	20.0	15.6
Nestling loss (%)	3.6	0.0	10.5

Throughout the entire breeding season, there was an apparent slackening in breeding potential towards April as shown by the declining proportion of swiftlets breeding. Most adult pairs had produced at least one or two clutches in the first and second breeding bout (refer Appendix 2) and only a small percentage (22%) of the colony was attempting or capable of producing a third clutch. This kind of adaptive response of decreasing the reproductive capability at the end of the breeding season was also employed by the European Blackbird blackbirds (*Turdus meruda*), but such strategy was directly correlated to the declining food supply (Ludvig *et al.*, 1995).

4.3.2 Hatching Rate And Egg Loss

Hatching success did not show any differences between each breeding bout across three sites ($\chi^2 = 2.31$, df = 4, $P > 0.05$). There was no difference in the proportion egg loss between each breeding bout across three sites ($\chi^2 = 6.63$, df = 4, $P > 0.05$), with a range of 15.6% to 43.8% (Table 4.5). Therefore, it could be concluded that incidence of egg loss is indeed very high at all sampling sites and such losses are of natural occurrence.

Table 4.5 The percentage of hatching and egg loss for three observed breeding bouts between April 1997 and March 1998.

Breeding bout	Lubang Salai		Pasen Avut, Lubang Beruang		Pasen San, Lubang Beruang	
	Hatching (%)	Egg Loss (%)	Hatching (%)	Egg Loss (%)	Hatching (%)	Egg Loss (%)
First (Aug-Nov)	63.3	36.7	66.7	33.3	75.9	24.1
Second (Dec-Mac)	66.2	33.8	70.0	30.0	74.2	25.8
Third (Apr-Jul)	56.2	43.8	80.0	20.0	84.4	15.6

The hatching success recorded in this study is consistent with observations made elsewhere. For instance, Langham (1980) reported the hatching success of *A. fuciphagus* is 72.4% for the first clutch, 67.4% in the second, 65.0% in the third clutch. An 83% hatching rate was recorded for the same species at a colony in Singapore, while *A. maximus* at the same colony showed an 85% hatching rate (Lee & Kang, 1994). This reflects an egg loss during incubation within the range of 15 to 35%. The percentage of egg loss recorded at Niah was very high also. Medway (1962b) recorded 42% and 75% egg loss for *A. maximus* in 1957 and 1958 respectively. The other two species of swiftlets, *A. salanganus* and *C. esculenta*, also encountered a high proportion of egg loss. The author attributed egg loss to premature fall of nests, predation by a large gryllid (*Rhaphidophora oöphaga*) and the ejection by the adult, which is most likely to be accidental.

The contributing factors for egg loss are independent of the timing of breeding, but rather confined to the size of the nests. The huge margin of failure was mostly due to egg loss during the incubation period. The narrowness and shallowness of the nests were suspected to be the main cause of egg loss, especially when the incubating adults leaped off to the air. Egg loss was thus assumed accidental rather than deliberate ejection by the adult. For *A. fuciphagus* that produce a clutch of two eggs, there is an average interval of three days between the lay of the first and second egg (Langham, 1980; Kang *et al.*, 1991). Because the swiftlets start incubating when the first egg was laid, there is a delay between hatching date. However, not a single incident of egg ejection by the sibling was noticed throughout this study. In all single broods, the other egg was lost well before the successful one hatched.

During incubation, most swiftlets sit with their head facing the cave wall or at an angle, with the tail and wings protruding outward from the rim of the nest. When alarmed, the birds leap, followed by a sideways turn and few powerful flaps of the wings to get to the air. In Lubang Salai, a sudden squeaking noise from a Muller's Rat (*Sundamys muelleri*), a species that usually prowls the cave floor searching for food in the tranquillity of darkness, has been observed to cause a few impetuous incubating birds to startle, followed by a string of hysteria

and panic flight. This critical movement caused most eggs to be tossed out of the nest, particularly if they were caught between the feet of the incubating adults. Such moment had been witnessed at Niah when brooding *A. maximus* was startled from the nest and threw out the egg as they flew (Medway, 1962b).

4.3.3 Fledging Success

Newly hatched swiftlets have well-developed legs as compared to other altricial nestling birds. To a swiftlet chick, the feet are more important than any other organ during the brooding period. This is further evidenced by a well developed grasping reflex in the feet of one day old chicks and the rapid development of the tarsus (Tarburton, 1986a). Their powerful feet are vital for survival because the nestling will hold itself to the nest by clasping firmly to the bottom. Their clasp can be so powerful that it is difficult even to pull them out from their nests, and nestlings of Stage 3 to Stage 5 clinging firmly to falling nests have been observed during harvesting time. As soon as the nestlings have attained a complete plumage at Stage 4 to Stage 7, they usually spend most of the day clinging outside by the nest crest. The legs and claws have again proven their usefulness.

Throughout this study, the proportion of nestling loss was insubstantial. There was no significant differences among the values recorded at all bouts of breeding at three sites (χ^2 = 0.53, df = 4, P > 0.05). Fledging success was high at all sampling sites in all bouts of breeding (Table 4.6). Once the eggs hatched, the young nestlings evidently had a good chance of survival until they fledged. Not a single nestling was found dead inside the nests. There was no evidence of external predation, and therefore, nestling loss must have resulted from falling off the nest.

Table 4.6 The percentage of fledging success recorded from three bouts of breeding between April 1997 and March 1998.

Breeding bout	Lubang Salai (%)	Pasen Avut, L. Beruang (%)	Pasen San, L. Beruang (%)
First (Aug-Nov)	95.8 (n = 95)	91.7 (n = 12)	93.2 (n = 44)
Second (Dec-Mar)	99.0 (n = 98)	92.9 (n = 14)	93.5 (n = 46)
Third (Apr-Jul)	96.4 (n = 27)	100.0 (n = 8)	89.5 (n = 38)

Siblicidal behaviour may be deeply rooted in species behaviour and life history (Gill, 1990). Avian siblicide is normally the result of sibling competition, either from adaptive brood reduction during periods of food shortage (Braun & Hunt, 1983) or physical contact in which smaller or weaker chicks are killed by their larger siblings or die after being expelled from their

nest (Rodriguez-Gironés, 1996). Bryant and Tatner (1990) speculated that the pattern of nestling loss in a colony of *C. esculenta* points towards siblicide occurring when under nourishment induces the larger click to eject the weakened smaller chick. Observations from this study showed otherwise for *A. fuciphagus*. The incidence of sibling loss was minimal in all bouts of breeding (Table 4.7). Only nests with two nestlings were taken into account for possibility of sibling rivalry and this accounted for a negligible 4.8% and 4.3% loss during the first and second breeding bouts, respectively. Whenever both eggs hatched, almost all siblings grew until fledging.

Table 4.7 The number of double nestling broods and the percentage of sibling loss in each bout of breeding in Lubang Salai.

Breeding bout	First (Aug-Nov)	Second (Dec-Mac)	Third (Apr-Jul)
Number of nest	41	23	4
Sibling/nestling loss	2	1	0
Percentage sibling loss (%)	4.8	4.3	0

The fledging success reported for a house colony of *A. fuciphagus* in George Town, Penang, was 64.4%, 60.2% and 59.1% for the first, second and third broods, respectively, with an average success of 61.2%. The failure to fledge was attributed to nest fall (7%), accidental removal (13%), but 75% was due to the disappearance of the nestling (Langham, 1980). At another colony in Singapore, fledging success was recorded as 42% for *A. fuciphagus* and 76% for *A. maximus* (Lee & Kang, 1994). These values are clearly much lower than those recorded at Lubang Salai ($\chi^2 = 23.67$, df = 2, $P < 0.05$), or Lubang Beruang ($\chi^2 = 20.66$, df = 2, $P < 0.05$) of this study. One possible reason for the difference is that both the studies incorporated the measurement of nestling growth by removing them from the nest for weighing. This directly induced interference and stress to the nestling, which might fall off from the nests, especially when the eyes have already opened. Tarburton (1986b; 1987) discovered that his measuring attempts on the White-rumped Swiftlet (*A. spodiopygius*) increased the number of nestlings falling out of the nest during the first few minutes after they were returned. Decreasing such interference by reducing the frequency of visits to the nest showed a 92% fledging success for *A. spodiopygius* in Fiji, which does not differ from the value observed in this study under minimum disturbance ($\chi^2 = 0.15$, df = 1, $P > 0.05$). Nestling losses due to movements or sibling strife in the period of disturbance following handling have also been observed among *C. esculenta* (Bryant & Tatner, 1990).

In natural caves, nestling mortality could be caused by two main factors. One is the fall of loosely secured or deteriorating nests, unable to support the weight of the nestling. Another factor could be the accidental fall from the nest, perhaps while defecating over the nest rim, or inadequately fed nestlings that become restless and hypersensitive to neighbouring activities

until they leave the nest (Medway, 1962b). In middle Baram, all the nests are built on high locations and surfaces impossible to reach by crawling animals such as snakes or rodents. The large gryllid (*R. oöphaga*), with its powerful biting jaws that were known to attack vulnerable newly hatched nestling at Niah (Medway, 1962b), is absent among the caves in Baram. Blood-sucking bugs (*Paracimex borneensis*) infest colonies of *A. fuciphagus* and other swiftlets species in all caves visited in Baram. There was no evidence that such infestations contributed to premature death of nestlings (Medway, 1962b) or significantly reduced the success of breeding (Langham, 1980). In contrast, Brown and Brown (1986) demonstrated that the haematophageous swallow bug (*Oeciacus vicarius*) severely reduces the growth rate of Cliff Swallow nestlings (*Hirundo pyrrhonota*). Similarly, offspring mortality of Great Tit (*Parus major*) is significantly higher in broods that were experimentally infested with hen flea (*Ceratophyllus gallinae*) than the parasite-free broods, while the body mass of the latter brood is relatively heavier (Richner *et al.*, 1993). In this study, the consequence from infestation of ectoparasites was not investigated, but it appeared to have no significant effects on to the nestling or adults.

4.3.4 Reproductive Index (RI)

From the observations made in this study, it was evident that the first and second breeding bouts produced more nestlings, as shown by the proportion breeding (Table 4.1). The success of each breeding bout was measured by a reproductive index (RI), which is expressed as the mean number of nestlings raised per adult pair per bout (Table 4.8).

Table 4.8 The values of reproductive index (RI) of each bout of breeding for Lubang Salai and Lubang Beruang.

Breeding bout	First (Aug-Nov)		Second (Dec-Mac)		Third (Apr-Jul)	
	Salai	Beruang	Salai	Beruang	Salai	Beruang
Number of nestling fledged	101	41	79	36	27	—
Number of breeding pair	76	32	81	35	62	—
Reproductive Index (RI)	1.32	1.28	0.97	1.03	0.44	—

All RI values recorded in the first and second breeding bouts in this study were much higher than values reported in other studies. The average number of nestlings fledged per adult pair reported for *A. fuciphagus* in Penang is 0.94 (Langham, 1980). The highest values were recorded in the months of November and February with 1.06 and 1.10 nestlings produced by

each breeding pair. On the other hand, the reproductive index recorded for the *A. fuciphagus* colony in Singapore is 0.69 (Lee & Kang, 1994). The difference could be explained by fewer nestlings lost during the brooding period in this study because they were not subjected to the ordeal of handling and regular removal from their nests for weighing.

The RI for *A. fuciphagus* is also very high compared with other insectivorous passerine bird species that built open nests in Sarawak, for which the average reproductive success is 0.28 juveniles per pair (Fogden, 1972). This value can range from as low as 0.18 juveniles per pair for the Grey-headed Babbler (*Stachyris poliocephala*) to 0.86 for Red-tailed Tailorbird (*Orthotomus sericeus*). However, unlike other forest passerines that are constantly fed for four to six weeks after first leaving the nest, newly fledged swiftlets have to fend for themselves on their first maiden flight.

Offspring survival rate is generally not so dependent on the time of the breeding season for multi-brooded species. Therefore, the seasonal reproductive success is determined entirely by the total number of broods one pair can raise throughout the length of the breeding season, not simply by the success of any singular brood (Crick *et al.*, 1993; Svensson, 1995). Considering the overall breeding success as a collective result from several breeding attempts, it is anticipated that breeding will start as soon as environmental factors and intrinsic conditions permit, and continue in succession whilst favourable provisions persist. Such was the reproductive strategy adopted by *A. fuciphagus* in Sarawak and conceivably throughout its range. Evidence from this study showed that as many as three breeding attempts were possible in one year but two clutches were the norm.

4.3.5 Percentage Success For Experimentally Removed Nests

Thirteen nests were experimentally removed on 13 September 1997 in Lubang Salai. Eleven nests managed to produce a clutch within the first breeding bout, giving a proportion breeding of 84.6% (Table 4.9). After the nestling had fledged in the first two weeks of January, similar proportion breeding was recorded in the second breeding bout. The percentage of egg loss recorded was 31.6% but this value decreased to 21.1% in subsequent breeding bout, most probably because the nests were by then of larger size. As for the breeding productivity, the reproductive index calculated was 0.85 for the first breeding bout and a slight higher value of 1.15 for the second breeding bout.

Table 4.9 Comparison of breeding successes for experimentally removed nests on 13 September 1997 in Lubang Salai.

	First breeding bout	Second breeding bout
Proportion breeding (%)	84.6	84.6
Percentage of non-breeding pairs (%)	15.4	15.4
Hatching successes (%)	68.4	78.9
Percentage of egg lost (%)	31.6	21.1
Percentage of re-deposition	100	—
Reproduction Index (RI)	0.85	1.15

4.4 BREEDING AND BROODING

4.4.1 Incubation Period

The incubation periods calculated from three bouts of breeding observed in this study are shown in Table 4.10. There was no difference between the length of incubation for the three bouts ($F_{2, 93} = 0.81$, $P > 0.05$). The average of incubation period recorded for the first, second and third breeding bouts was 24 ± 1 days, 25 ± 1 days, and 26 ± 2 days.

Table 4.10 The incubation period (mean ± SE) of *Aerodramus fuciphagus* recorded from three breeding bouts observed at Lubang Salai.

Breeding bout	First (Aug-Nov)	Second (Dec-Mac)	Third (Apr-Jul)
Average (days ± SE)	24 ± 1	25 ± 1	26 ± 2
Range (days)	19 – 29	18 – 28	19 – 32
Sample size	n = 63	n = 20	n = 23

There is not much variation in the incubation for *A. fuciphagus* across the various geographical ranges. For instance, Langham (1980) reported that the average incubation period of 23 ± 3 days. Lee & Kang (1994) calculated the mean incubation period from a colony in Singapore at 25.5 days, while the incubation period ranged between 23 to 30 days with an average of 25 ± 2 days in Vietnam (Nguyen Quang, 1994).

Both sexes incubate among *A. maximus* (Medway, 1962b) and *A. fuciphagus*. Incubation starts after the first egg is laid (Langham, 1980) and usually happens when the parents return to roost at night, as well as during the day. In the latter case, many birds could be seen sitting in their nest during the normal routine check on the marked nests in Lubang Salai. For instance, on 17 May 1997, 21 adults were found sitting inside 34 nests containing at least one egg at one marked sample site in the cave from 1000 hours until 1500 hours. At other times, the nests were occasionally attended by only a few adults for the whole morning. The

longest incubation time recorded without any relief in edible nest swiftlet (e.g. *A. maximus*) is 30 hours 53 minutes, while the longest time an egg was left unattended is 18 hours 35 minutes (Medway, 1962b). This profound tolerance of prolonged exposure is because the daytime temperature within a cave is relatively constant. The interior temperature of Lubang Salai was maintained at 26 °C, with a maximum fluctuation of less than 1 °C. Such temperatures are certainly below what is needed to maintain full metabolism of incubation, but not low enough to be lethal.

Generally, the incubation periods of birds are positively correlated with the egg weight. However, low predation rate (Gill, 1990), scarce food resources (Boersma, 1982) and advanced development of hatching may favour longer incubation time. The safety provided by darkness of the caves and inaccessible nesting sites explains the relatively long incubation for *A. fuciphagus* egg, which is relatively small and weights 1.8 ± 0.4 g (n = 56). However, the minimum incubation period recorded was 18 days while the maximum period was 32 days. The huge deviation in the duration observed might be due to the unequal length of time the swiftlets spend sitting on the egg. Disparity of insect density and dispersion may prevent foraging adults from returning to the nest on schedule, resulting a longer neglect of eggs (Lack & Lack, 1951). It is possible that the disproportionate effort of bisexual incubation contributes to the dissimilar time spent of incubation (Nilsson, 1993). On the other hand, a long incubation period could also be an adaptation for species that need to leave their eggs unattended for distant feeding grounds (Boersma, 1982).

4.4.2 Fledging Period

Newly hatched swiftlets are naked and pinkish in colour. The feather sheaths on the main feather tracks begin to erupt after 7 to 15 days and the eyes are opened in another week. Similar development of nestling growth was also observed in *A. spodiopygius* where the feather sheaths broke through the skin on the eleventh day (Tarburton, 1986a). The limited nest confinement is barely large enough to accommodate two nestlings when they are roughly three weeks old, or at Stage-4. When they grow to Stage-5 where the tip of their wings has overshot the rectrices, most nestlings begin to cling to the side of the nest, and spend more and more time there. First trial flight will only be embarked in another 2 to 3 weeks.

There was no difference between the fledging period observed in all breeding bouts ($F_{2, 58} = 0.71$, $P > 0.05$). The average fledging periods for the first and second breeding bouts was 45 ± 1 days (Table 4.11). The average fledging period for the third breeding bout was 44 ± 2 days. This is similar to the period of 43 ± 6 days observed in Penang (Langham, 1980), and 45.9 days in Singapore (Lee & Kang, 1994). The fledging period of *A. fuciphagus* in Vietnam

was 40 ± 1.5 days (Nguyen Quang, 1994). The small variation in the average fledging period depends very much on the food supply at different localities, especially when these colonies are scattered over wide geographical ranges.

Table 4.11 The fledging period (mean ± SE) of *Aerodramus fuciphagus* recorded from three breeding bouts observed in Lubang Salai.

Breeding bout	First (Aug-Nov)	Second (Dec-Mac)	Third (Apr-Jul)
Average (day ± SE)	45 ± 1	45 ± 1	44 ± 2
Range (day)	37 – 52	40 – 50	37 – 54
	n = 31	n = 16	n = 23

The fledging period for single and double broods is shown in Table 4.12. There was no difference between single and double broods in all breeding bouts ($F_{5, 97} = 1.61$, $P > 0.05$).

Table 4.12 The comparison of fledging period (mean ± SE) for brood with single and brood with two nestling inside Lubang Salai.

Breeding bout	Single nestling		Two nestlings	
	Average (days ± SE)	Range (days)	Average (days ± SE)	Range (days)
First (Aug-Nov)	46 ± 1	37 – 52	47 ± 1	43 – 55
Second (Dec-Mac)	45 ± 2	40 – 50	45 ± 1	42 – 48
Third (Apr-Jul)	44 ± 2	39 – 52	44 ± 2	37 – 50

Adult swiftlets did not feed their young regularly. One observation from 0900 hours to 1700 hours on 11 June 1997 revealed that only a small number of nestlings were fed during the day (Table 4.13). Nestlings from 7 out of 27 (26%) marked nests were fed only once within this period. Another marked nest, where the single brood was fed three times within eight hours, fledged in 29 days. The rest of the nestlings were presumably fed when the adults returned to roost in the evening.

Table 4.13 The time and frequency of feeding for nestlings in 27 marked nests inside Lubang Salai on 11 June 1997.

Nest	Feeding time (hrs)	Number of nestling (growth stage)
S 018	1053	One (stage 6)
S 013	1145, 1240, 1530	One (stage 3)
S 021	1150	Two (stage 6 & stage 7)
S 008	1250	Two (stage 2 & stage 3)
S 022	1300	Two (stage 3 & stage 4)
S 003	1330	One (stage 2)
S 001	1345	One (stage 3)
S 015	1605	One (stage 3)

Another full-day observation was carried out in Lubang Salai from 0900 – 1745 hours on 8 October 1997. The feeding frequency at this time of the year was higher ($t_{18} = 1.83$, $P < 0.05$) than the previous observation (Table 4.14). More adults were able to return to feed their nestlings in a relatively shorter time. This indicates that food source may be comparatively more abundant during the rainy season in October than in the dryer month of June.

Table 4.14 Time and frequency of feeding observed on 8 October 1997 inside Lubang Salai.

Nest	Feeding time (hrs)	Number of nestling (growth stage)
S 123	0940, 1010, 1020, 1250	Two (stage 3 & stage 4)
S 003	0950, 1020, 1330	Two (stage 1 & stage 2)
S 064	0955, 1145, 1250, 1245	Two (stage 3 & stage 4)
S 102	0957, 1140, 1300, 1645	Two (stage 2 & stage 3)
S 073	1045	Two (stage 1 & stage 2)
S 050	1130, 1520	One (stage 4)
S 121	1135, 1335, 1400, 1425	Two (stage 2 & stage 3)
S 001	1245	Two (stage 2 & stage 3)
S 065	1245	Two (stage 4 & stage 5)
S 066	1245	Two (stage 3 & stage 4)
S 063	1400	One (stage 3)
S 026	1425	Two (stage 1 & stage 2)

The post-fledging success and failure could not be determined in this study. No attempt was made to investigate this aspect because the nestlings need to be ringed for capture and recapture experimentation. As an alternative, post-fledging activity was monitored with minimal disturbance to the colony. For example, the tip of the longest primary feather of a near-fledging nestling was dotted with quick dry paint and this individual fledged the next day after it was marked. A quick check that same evening confirmed that it returned to the same nest to roost. This suggests that newly fledged nestlings have the ability to return to the exact location of birth on their maiden flight, either with or without the guidance from their parents. In another example, three individuals of *A. fuciphagus* were seen on an isolated nest some distance from the main breeding colony. One bird was sitting inside the nest, while another two were clinging outside. Interestingly, this same nest was home to two nestlings that had fledged just twelve days earlier. This evidence strongly supports the assumption that newly fledged swiftlets are able to return to their natal nest site where they were raised.

4.5 INTER-CLUTCH INTERVAL

The last harvest before this study in Lubang Salai was on 12 March 1997, and the first egg of the third breeding bout was laid on 10 April. The average interval from nest removal to the lay of the first egg was 50 ± 4 days, with a range of 27 to 58 days. The interval from fledging to the lay of subsequent clutch between the third and the first breeding bout was 79 ± 9 days, with a range of 31 – 123 days (Table 4.15). Long intervals were recorded from nests with their clutch laid in middle of April, and their nestlings fledged in late June. In contrast, short intervals were associated with late breeding in the third breeding bout. Late breeders laid their eggs at the end of May, and their nestlings fledged in July. Neither early nor late breeders in the third breeding bout showed any difference in the interval of subsequent clutch, which were produced in between 8 and 26 September. Only five out of 19 pairs (25%) had exceptional long interval where the subsequent clutches were laid in late October.

Table 4.15 Interval from the previous brood or egg lost during the third breeding bout to the lay of subsequent clutch in the first breeding bout at Lubang Salai (mean ± SE).

	Interval of previous brood to subsequent clutch (days)	Interval of egg lost in last breeding bout to subsequent clutch (days)
Average (day ± SE)	79 ± 9	108 ± 14
Range (day)	31 – 123	71 – 144
Number of nest	n = 23	n = 13

Results for similar interval between the first and second breeding bout are shown in Table 4.16. The average interval from fledging to subsequent clutch was 41 ± 5 days. This was shorter than the value recorded previously ($t_{38} = 2.02$, $P < 0.05$).

Table 4.16 The interval from previous brood or egg lost during the first breeding bout to the lay of subsequent clutch in the second breeding bout at Lubang Salai (mean ± SE).

	Interval of previous fledge to subsequent clutch (days)	Interval of egg lost to subsequent clutch (days)
Average (day ± SE)	41 ± 5	47 ± 10
Range (day)	10 – 82	10 – 100
Number of nest	n = 42	n = 24

The average interval from egg loss in the third breeding bout to subsequent clutch was 108 ± 14 days (Table 4.15). Nests that lost their content did not have any replacement clutch until the beginning of the first breeding bout. The date of subsequent lay for nests with egg loss and nests with successful broods appeared to be the same, with most clutches produced in the first three weeks of September. When an egg was lost during the first breeding bout, the

average interval to the subsequent clutch was 47 ± 10 days (Table 4.16). This is approximately half the time taken in the previous breeding bout ($t_{22} = 6.45$, $P < 0.05$).

After successful breeding in the third breeding bout and the nests were not removed, 82% of the following clutch was laid in September. If egg loss occurred but the nests remained intact, 100% of the following clutch was also laid within September. However, if the nests were removed at the end of the breeding bout, the lay of the subsequent clutch was delayed by about a month regardless of the outcome of the previous breeding. The appearance of subsequent clutch in the first breeding bout can be grouped into weekly subdivisions as shown in Table 4.17.

Table 4.17 The appearance of the first egg in the first breeding bout for nests with successful breeding and those that lost their clutch in the third breeding bout.

	Successful breeding		Egg loss	
	Nest not removed n = 17	Nest removed n = 6	Nest not removed n = 9	Nest removed n = 4
1st week of September	2		2	
2nd week of September	6		1	
3rd week of September	4		2	
4th week of September	2		4	
1st week of October	1			
2nd week of October	1			1
3rd week of October		1		1
4th week of October	1	2		2
1st week of November		1		
2nd week of November		2		

Nineteen or 25.3% of marked nests inside Lubang Salai managed to produce one clutch in each breeding bout (Table 4.18). Langham (1980) reported that 16% out of 136 marked nests produce three clutches between September 1976 and April 1977 in a colony of *A. fuciphagus* in Penang. This shows that *A. fuciphagus* employed a multi-brooded reproductive strategy. Other species of cave swiftlets, namely *A. maximus* and *A. salanganus* also employ similar strategy (Medway, 1962b).

In Lubang Salai, 3 out of 32 pairs of swiftlets, or 9.4%, that had fledged their nestlings in the first breeding bout managed to produce another clutch within the same period. Nevertheless, the second clutch was laid in late November (Table 4.19). Only one pair in Lubang Beruang managed a second clutch within the same breeding bout after fledging one brood. In this case, the shortest interval for the first egg of the second clutch to appear was 11 days but this could be extended to 22 days.

On average, a female swiftlet that had fledged a brood needs at least 14 ± 6 days from the re-activation of the ovary to the formation and subsequent lay of an egg. The formation of one *A. fuciphagus* egg requires 3 to 5 days. This leaves 9 to 11 days for the stimulation and development of a follicle, as well as the deposition of egg yolk in the ovary to ovulation. This figure is realistic because the growth of a follicle and formation of an egg of domestic fowl can be achieved in 7 to 11 days (Johnson, 1986).

Table 4.18 Marked nests in Lubang Salai that have a clutch laid during each bout of breeding between April 1997 and March 1998.

Nest	April – July		August – November		December – March	
	Egg	Fledged	Egg	Fledged	Egg	Fledged or (egg loss)
S 001	11 May 97	12 Jul 97	8 Sep 97	12 Nov 97	5 Jan 98	28 Feb 98
S 003	30 May 97	23 Jul 97	13 Sep 97	20 Nov	20 Jan 98	Apr 98
S 006	20 Jun 97	18 Aug 97	13 Oct 97	15 Dec 97	20 Jan 98	(9 Feb 98)
S 008	11 May 97	15 Jul 97	20 Oct 97	25 Dec 97	15 Jan 98	(20 Jan 98)
S 012	17 May 97	23 Jul 97	26 Sep 97	12 Dec 97	15 Jan 97	(9 Feb 98)
S 013	5 May 97	8 Jul 97	30 Sep 97	6 Dec 97	20 Jan 98	Apr 98
S 015	11 May 97	15 Jul 97	1 Nov 97	5 Jan 98	16 Jan 98	Apr 98
S 017	19 Apr 97	23 Jun 97	13 Oct 97	5 Jan 98	15 Jan 97	Apr 98
S 018	21 Apr 97	25 Jun 97	30 Sep 97	12 Dec 97	20 Jan 98	Apr 98
S 021	10 Apr 97	20 Jun 97	8 Sep 97	20 Nov 97	15 Dec 97	19 Feb 98
S 022	26 Apr 97	8 Jul 97	28 Sep 97	1 Dec 97	5 Jan 98	(19 Feb 98)
S 023	21 Apr 97	5 Jul 97	13 Sep 97	26 Nov 97	5 Jan 98	12 Mar 98
S 025	3 May 97	12 Jul 97	18 Sep 97	26 Nov 97	9 Feb 98	Apr 98
S 033	5 May 97	13 Jul 97	23 Oct 97	5 Jan 98	23 Jan 98	Apr 98
S 037	11 May 97	23 Jul 97	11 Nov 97	12 Jan 98	2 Feb 98	(19 Feb 98)
S 041	5 May 97	12 Jul 97	15 Sep 97	20 Nov 97	2 Feb 98	Apr 98
S 056	22 Apr 97	5 Jul 97	11 Nov 97	12 Jan 98	9 Feb 98	Apr 98
S 060	22 Apr 97	5 Jul 97	20 Oct 97	24 Dec 97	9 Feb 98	Apr 98
S 061	11 May 97	15 Jul 97	20 Oct 97	5 Jan 98	19 Feb 98	Apr 98

Note: occurrence of egg lost was not indicated in April-July and first breeding bouts.

Table 4.19 Nests that have a second clutch within the first breeding bout after the first brood had fledged in Lubang Salai and Lubang Beruang.

Nest	First egg laid	Last nestling to fledge	Appearance of first egg in subsequent clutch	Interval (days)
S 047 (Salai)	29 Aug	4 Nov	26 Nov	22
S 050 (Salai)	24 Aug	1 Nov	11 Nov	10
S 052 (Salai)	24 Aug	4 Nov	20 Nov	16
B 008 (Beruang)	10 Sep	22 Nov	3 Dec	11
			average (days ± SE) =	14 ± 6

The period between recorded copulation to the lay of the first egg for *A. salanganus*, a species slightly larger than *A. fuciphagus*, is 8 days (Medway, 1962b). In birds, fertilisation normally occurs within one hour of ovulation, which in turn usually occurs about 24 hours before the egg is laid (Birkhead & Møller, 1992). Nevertheless, female birds are capable of storing sperm for several days or weeks following copulation, and depending of species, the fertile period is generally 6 days but can be as long as 45 days (Birkhead & Møller, 1993). Examination of ovarian sections and distribution of oocyte diameters of *C. esculenta* established that the rapid growth of follicle and yolk deposition occurs three days before ovulation, the egg passes down the oviduct in one day and is laid the next (Hails & Turner, 1985). This shows a minimum of four days for the formation of one *C. esculenta* egg. This suggests an estimate of 9 to 11 days for *A. fuciphagus* to produce a clutch right after raising a brood. However, this could only be achieved if the female is in optimal breeding condition in which bodily energy reserves and food supply are not the limiting constraints in breeding.

Many eggs were lost in every breeding bout in both Lubang Salai and Lubang Beruang. However, 10 nests (43%) at Lubang Salai had replacement eggs laid during the first breeding bout while, 7 replacement clutches (30%) were recorded in the second breeding bout (Table 4.20 & Table 4.21). Repeated egg loss was recorded in many nests. A few have several relays within the same breeding bout. For instance, nest S060 in Lubang Salai lost both eggs on 18 September, and one replacement egg was laid on 30 September. This replacement egg was later lost on 7 October but a second replacement egg laid on 20 October hatched and the chick survived until fledging. Lost eggs were not replaced during the third breeding bout.

Table 4.20 Nest with the lay of replacement egg during the first breeding bout in Lubang Salai.

Nest	Egg lost	Date of relay	Interval (days)
S 006	30 Sep	13 Oct	13
S 010	18 Sep	30 Sep	12
S 013	18 Sep	30 Sep	12
S 028	7 Oct	1 Nov	25
S 049	30 Sep	1 Nov	32 *
S 060	18 Sep	30 Sep	12
	7 Oct	20 Oct	13
S 061	30 Sep	20 Oct	20
S 065	9 Aug	16 Aug	7
S 068	13 Sep	7 Oct	24
S 074	7 Oct	27 Oct	20
		Average (days ± SE) =	17 ± 4

* appear to be an exceptional case

Replacement lay has been observed elsewhere. For instance, *A. maximus* at Niah replaced 27.6% of their lost clutches, while 26.2% had replacement clutches when the nestlings were lost. In addition, 11.1% produced a subsequent clutch after the nestlings had fledged. The interval between the loss of one clutch or brood, or the departure of the last nestling, and the lay of replacement or second clutch varied widely from less than one week to more than one month (Medway, 1962b). In a less refined treatment, 42% of the *A. fuciphagus* in Penang have replacement clutches after losing their eggs or nestlings (Langham, 1980).

Table 4.21 Nest with the lay of replacement egg during the second breeding bout in Lubang Salai.

Nest	Egg lost	Date of relay	Interval (days)
S 002	15 Jan	24 Jan	9
S 006	9 Feb	19 Feb	10
S 008	24 Jan	6 Feb	13
S 022	19 Feb	26 Feb	7
S 026	9 Feb	19 Feb	10
S 030	23 Jan	9 Feb	17
S 038	21 Jan	9 Feb	19
		Average (days ± SE) =	12 ± 3

Because all eggs were lost sometime after incubation, it could be assumed that the ovary of the swiftlets was in partial regression, as witnessed in *A. maximus* (Medway, 1962a). The average interval from egg loss to the lay of a replacement was 17 ± 4 days and 12 ± 3 days for the first and second breeding bout, respectively. The soonest was 7 days in nest S065, while the longest was 32 days. However, there was no difference in the intervals between both breeding bouts (t_{16} = 1.82, P > 0.05). Results from this study showed that re-laying occurred sooner if eggs were lost in the early stages of incubation rather than in the advanced stages. The *A. maximus* colonies at Niah relay less often after fledging their nestlings than after egg loss, and the consequence of earlier breeding attempts is presumably related to the involution of the reproductive organs (Medway, 1962c).

Only one marked nest in Lubang Salai, S057, lost both nestlings throughout the three breeding bouts. One nestling had reached a growth of Stage-4 and another at Stage-5 when they were last seen on 6 December 1997. Brooding was thus terminated. The first egg of the subsequent clutch did not appear until 26 February 1998, a long lapse of 82 days.

Regardless of whether a breeding attempt was successful, or suffered clutch loss, all pairs that bred in third breeding bout commence breeding at about the same time in the following breeding bout unless the nests were absent. The onset of breeding is likely to be correlated with the availability of food supply and the intrinsic physiological readiness of the swiftlets. Food availability, which depends very much on seasonal variation, present the most

critical factor that determine the fledging mass of Great Tit (*Parus major*) nestlings and the probability of a second clutch (Verboven & Verhulst, 1996). Therefore, one hypothesis for the observed variations in the date of laying after the third breeding bout is that the swiftlets would build up their protein and fat storage to prepare for the following breeding. Medway (1962a) showed that the female gonads of *A. maximus* have a cyclic alternation in weight in relation to breeding and moult. Although he did not point out the underlying principles behind this observation, it is now widely accepted that food supply, which in turn translates to assimilated energy, exerts an influential role between intrinsic physiological conditions and breeding.

Birds are known to utilise protein reserves during breeding (Hails & Turner, 1985). The level of protein content in the body might act as the proximate internal factor that initiates breeding as shown in the Yellow-vented Bulbul (Ward, 1969a) and Grey-backed Camaroptera (Fogden & Fogden, 1979). Ample food supply and good feeding result in a higher fat and protein levels that initiate reproduction. This correlation is clearly shown in *C. esculenta* (Hails & Turner, 1985) where the protein levels in the female increased by up to 170 mg immediately before the breeding season.

Kang *et al.* (1991) estimated that each *A. fuciphagus* needs 3.10 g of protein and 0.69 g of fat in excess of the energy required for daily physiological maintenance to construct a nest. To produce the eggs, the female needs 0.45 g of protein and 0.43 g of lipid. The assimilated insects yield per day per adult is 180 mg of protein and 24.1 mg of lipid. This implies that each adult will need to forage for 20 days to accumulate the protein needed and 46 days for the lipid requirement. As such, the increased energy demands to produce new feathers would not allow any replacement clutches in the third breeding bout during the main moulting period. Therefore, the biological time clock for the swiftlets is inactivated and waiting for the following season, which occurred in August and September. At this stage, the presence of the nest is extremely critical. It appears to act as an external stimulus that initiates the enlargement of the salivary glands if the nest is removed, or the activation of the gonads if the nest is intact. In the former, nest building commences and a new nest takes roughly 30 days to completion and approximately another 9 to 11 days before laying. This explains the delay in the lay of the first egg among the marked nests that were removed.

Nevertheless, the enlargement of salivary glands and the activation of the gonads do not overrule each other completely. Both allow a small margin of coexistence. This explains the occurrence of slight extension to the crest, or minor restoration at the base of the nests before each repeated lay. Another possibility is that the male swiftlets are responsible for nest restoration because one member of a pair has been noticed to spend more time building than the other (Kang *et al.*, 1991). To further strengthen this hypothesis, some female of *A. maximus* have totally inactive sublingual glands in full breeding condition, but all males have

hypertrophied glands (Medway, 1962a). Unfortunately, this could not be verified for *A. fuciphagus* in this study.

4.6 CORRELATION OF MOULT AND BREEDING

Moult consists of the orderly replacement of feathers. This is accompanied by the total regression of the reproductive organs and the cessation of lay for species that perform post-nuptial moult (Johnson, 1986). However, swiftlets are known to have a prolonged moult cycle that advances simultaneously with breeding (Medway, 1962a; Langham, 1980). In addition, the moult of the *A. maximus* was established as an annually recurrent event, and not a postnuptial one (Medway, 1962a). Generally, birds in the equatorial forest of Sarawak usually begin their moult shortly after the young have fledged in May, and continue moulting until the beginning of the dry season when food becomes scare (Fogden, 1972; Gill, 1990).

The primary feathers of swiftlets are moulted in descending order from the innermost outwards, or PF-1 to PF-10 of this study. In contrast, the secondary and tertiary feathers are moulted in ascending order while the rectrices are moulted centripetally, starting from the outer pairs working inwards (Chantler & Driessens, 1995). The months between April and August are traditionally considered as "bad season" for nests yield by swiftlet cave owners in the middle Baram and throughout the whole of Sarawak. Nests constructed during this period are smaller and have a relatively higher feather content even in the case of nests of *A. fuciphagus*, but particularly so for the nests of *A. maximus*. Results of feather count from this study proved that the swiftlets were going through a major moult during this time of the year, which caused more feathers to be incorporated in their nests.

A moderate number of feathers were collected during the third breeding bout. The highest count was recorded in June, a month generally referred as the "bad month". The number of feather shed gradually declined in between July and October. This was followed by the onset of a very productive breeding from August through March. The majority of the feathers collected in April 1997 were of PF-5 and PF-6. The moulting trend progressed forward from PF-6 to PF-10, where 64.2% of the feathers collected in August were the last primary feather (Table 4.22). The lowest feather count was recorded in September and October. A second period of moult occurred in November. Some 69.8% of the primary feather shed comprised the first four categories, namely PF-1 to PF-4. In addition, there were many body plumage, mainly small contour and down feathers. The ground inside the cave was covered with a layer of small fluffy feathers, a phenomenon observed only in November for a few days before they were eaten up by insect larvae in the guano. Another inspection in November 1998 revealed similar occurrence where 82.7% of the feathers collected were PF-1 to PF-4. The local

Table 4.22 Feather count for ten categories of primary feathers collected inside Lubang Salai between April 1997 and February 1998, including a collection in November 1998 for comparison.

Month	Categories of primary feathers										Sub-total	Total feathers collected (left + right)
	PF-1	**PF-2**	**PF-3**	**PF-4**	**PF-5**	**PF-6**	**PF-7**	**PF-8**	**PF-9**	**PF-10**		
April 97	7 (3.8 %)	21 (11.5 %)	27 (14.8 %)	30 (16.4 %)	35 (19.1 %)	37 (20.2 %)	20 (10.9 %)	2 (1.1 %)	1 (0.5 %)	3 (1.6 %)	183	316
May 97	4 (1.6 %)	16 (6.5 %)	28 (11.3 %)	36 (14.6 %)	53 (21.5 %)	45 (18.2 %)	59 (23.9 %)	6 (2.4 %)	0 (0.0 %)	0 (0.0 %)	247	444
June 97	1 (0.3 %)	7 (1.8 %)	11 (2.8 %)	18 (4.5 %)	41 (10.3 %)	82 (20.7 %)	126 (31.7 %)	36 (9.1 %)	27 (6.8 %)	48 (18.9 %)	397	746
July 97	0 (0.0 %)	2 (1.1 %)	1 (0.6 %)	5 (2.9 %)	5 (2.9 %)	9 (5.1 %)	12 (6.9 %)	35 (20.0 %)	44 (25.1 %)	62 (35.4 %)	175	304
August 97	0 (0.0 %)	0 (0.0 %)	1 (0.6 %)	3 (1.7 %)	5 (2.9 %)	9 (5.2 %)	9 (5.2 %)	13 (7.5 %)	22 (12.7 %)	111 (64.2 %)	173	313
September 97	1 (2.0 %)	0 (0.0 %)	5 (10.2 %)	8 (16.3 %)	6 (12.2 %)	7 (14.3 %)	7 (14.3 %)	2 (4.1 %)	3 (6.1 %)	10 (20.4 %)	49	80
October 97	0 (0.0 %)	2 (2.9 %)	1 (1.5 %)	1 (1.5 %)	9 (13.2 %)	9 (13.2 %)	7 (10.3 %)	5 (7.4 %)	6 (8.8 %)	28 (41.2 %)	68	111
November 97	69 (11.5 %)	92 (15.4 %)	141 (23.5 %)	116 (19.4 %)	77 (12.9 %)	44 (7.3 %)	27 (4.5 %)	16 (2.7 %)	5 (0.8 %)	12 (2.0 %)	599	1109
December 97	14 (3.8 %)	23 (6.3 %)	59 (16.1 %)	85 (23.2 %)	72 (19.7 %)	51 (13.9 %)	32 (8.7 %)	20 (5.5 %)	5 (1.4 %)	5 (1.4 %)	366	672
January 98	1 (0.7 %)	4 (3.0 %)	7 (5.2 %)	6 (4.5 %)	17 (12.7 %)	29 (21.7 %)	28 (20.9 %)	22 (16.4 %)	16 (11.9 %)	4 (3.0 %)	134	223
February 98	0 (0.0 %)	0 (0.0 %)	3 (7.5 %)	4 (10.0 %)	5 (12.5 %)	7 (17.5 %)	9 (22.5 %)	6 (15.0 %)	5 (12.5 %)	1 (2.5 %)	40	55
November 98	39 (19.3 %)	54 (26.7 %)	44 (21.8 %)	30 (14.9 %)	10 (4.9 %)	10 (4.9 %)	8 (4.0 %)	1 (0.5 %)	2 (1.0 %)	4 (2.0 %)	202*	351*

* represents one week of collection

communities from Long Laput claimed that there is a recognisable mid-moulting season or "*melaie pertengahan*" in November.

There was one obvious category of primary feather with the highest number count in every month. The beginning of the moulting period was marked by the appearance of large numbers of PF-1. In contrast, the end of the moult cycle was marked by the shedding of many long primary feathers, especially PF-9 and PF-10. The moult cycle of *A. fuciphagus* in Lubang Salai was a very long but slow process, starting in November and terminating in August the following year. This observation is in agreement with the speculation by Medway (1962a) regarding the moult of *A. maximus* at Niah Cave, roughly 90-km north-west of Lubang Salai. *Aerodramus fuciphagus* in middle Baram appeared to breed and moult concurrently between November and April. This was followed by a major moult in May and June when the lowest proportion breeding was recorded.

Figure 4.6 shows the correlation between the moult cycle and the breeding season of *A. fuciphagus* in Lubang Salai. The proportion breeding and the occurrence of the moult appear to be inversely related. The peak of each breeding bout corresponded with the least number of feathers collected throughout the breeding season, except for the third breeding bout. The first breeding bout occurred right after the heaviest moult. The first egg of the post-moulting breeding was noticed on 9 August in the marked nests, and 60 eggs were laid by mid-September. Furthermore, September was the month with the highest proportion breeding and the least number of feathers collected.

The proportion breeding was in the decline in November at the outset of the moult cycle because most of the eggs produced in September had hatched, and the swiftlets have entered the brooding phase. Only 20% of the marked nests contained eggs, while the others were packed with nestlings of various stages from Stage-5 to Stage-7. Another decline in the number of feathers collected was observed at the start of the second breeding bout.

It is a complicated task, physiologically and physically, to breed and moult simultaneously. Moulting imposes a severe strain on the birds because of the energy cost to produce new feathers is very high, especially in small birds (Rawles, 1960; Lindström *et al.*, 1993). At the same time, nest building and egg formation are processes of great energy demand (Kang *et al.*, 1991; Monaghan *et al.*, 1995). Furthermore, the loss of even one or two large primary feathers may jeopardise the aerodynamism of flight, and hinder foraging efficiency.

Moult is normally carried out at a slower rate if it overlaps with breeding (Morton & Morton, 1990; Lindström *et al.*, 1994) as observed in the *A. fuciphagus* colonies in middle Baram. However, a slower rate would be acceptable when the smaller primary feathers are in moult. As the moult progresses to larger primaries, it is important to replace these feathers as quickly as possible in order to increase the surface area of the wing because large primaries contribute substantially to the aerodynamic properties of the wing (Swaddle & Witter, 1994).

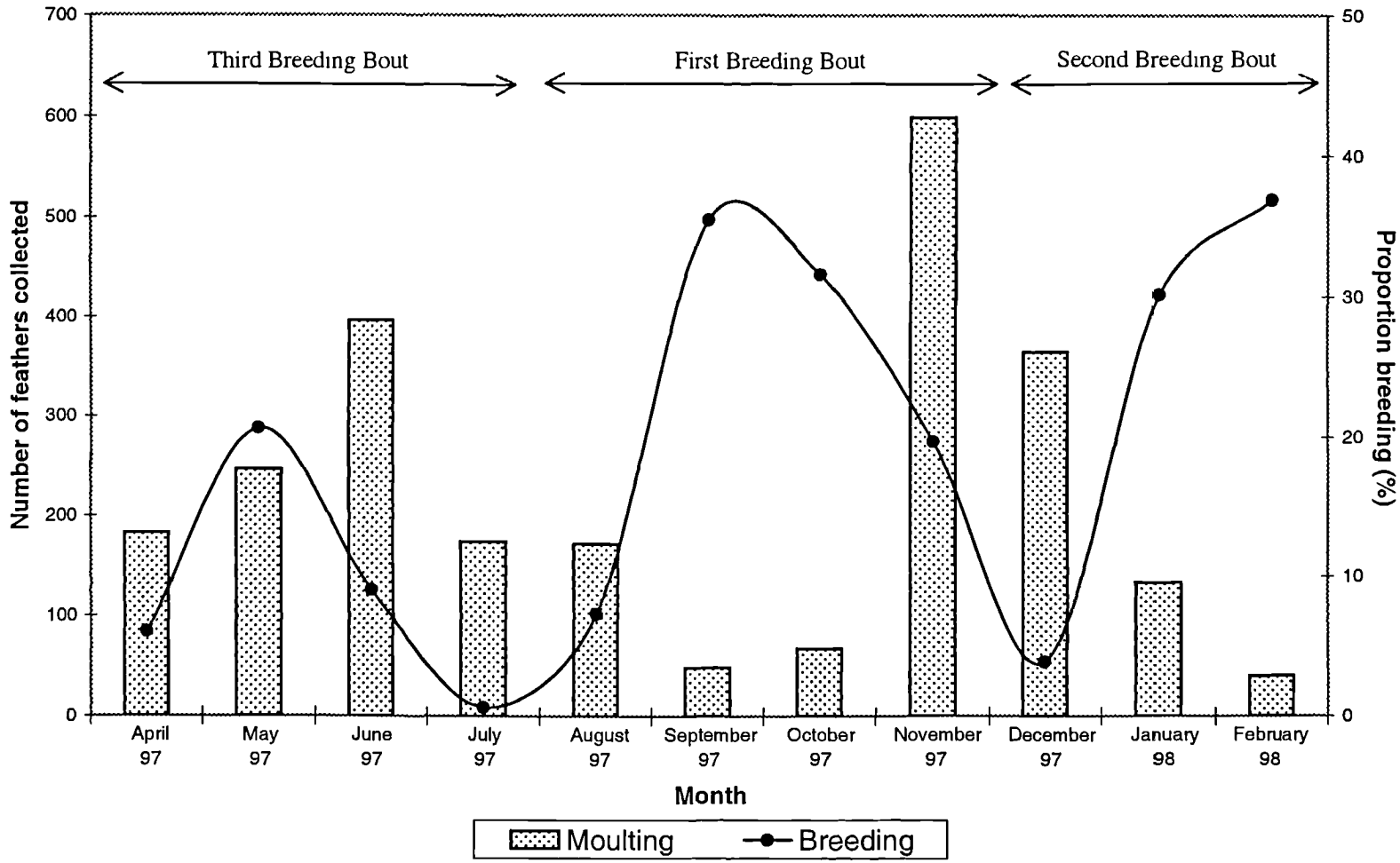

Figure 4.6 The correlation of moulting and breeding of *Aerodramus fuciphagus* in Lubang Salai.

This explains the sudden surge of many large primary feathers in June and July during the heavy moulting period. Consequently, these feathers were most probably re-grown at a faster rate, thus putting more energy demands on the swiftlets at the expense of the breeding productivity (e.g. lower proportion breeding).

The regulating mechanism of moult is undoubtedly complex. Höhn (1961) suggested that moult is regulated by hormonal and cyclic fluctuations in gonadal hormone production. In swiftlets, it was suggested that there might be direct endocrinological links between the reproductive cycle and the condition of the sublingual glands (Marshall & Folley, 1956). Medway (1962a) found that breeding was not necessarily accompanied by enlarged and active sublingual glands for *A. maximus* at Niah, nor were active glands always associated with reproductive condition in the gonads. This phenomenon was more apparent in females where totally inactive sublingual glands were associated with gonads in breeding condition. All these point to the possible occurrence of a negative feedback mechanism where the enlargement of sublingual glands suppresses, or decreases the gonad activities and accessory reproductive organs.

The physiological mechanisms that induce moult remain obscure. Nevertheless, the pituitary, thyroid, ovary and adrenal glands have been suggested as mediators (Payne, 1972). During the early phase of moulting, the metabolizable energy is reported to be high because additional energy is needed to fuel the increased heat production and tissue synthesis (Kendeigh *et al.*, 1977). Moulting is generally associated with an increase in thyroid activity, which is regulated by the hypothalamus, and hence an increase in the metabolic rate that culminate with the regeneration of flight feathers (Whittow, 1986). Concurrently, the secretion of the gonadotropins, namely luteinizing (LH) and follicle-stimulating hormone (FSH), is also controlled by the hypothalamic-hypophyseal complex situated at the base of the brain (Scanes, 1986). The hormone LH and FSH are necessary for the physiological control of the breeding cycle

In temperate avian species, the plasma concentrations of LH and FSH rise when they are exposed to long daylength, which subsequently leads to the rapid growth of the gonads (Follett, 1976; Silverin *et al.*, 1997; Sreekumar & Sharp, 1998). Because there is little change in the daylength and the annual temperature in equatorial regions (Fogden, 1972), the level of tissue protein and lipid must have important roles in regulating the timing of reproduction and moult (Ward, 1969b; Krapu, 1981; Hails & Turner, 1985). They are likely to be the proximate factors that regulate these processes in swiftlets (Ward, 1969a; Fogden & Fogden, 1979). It is hypothesised that an increased of tissue protein and lipid level exerts a positive feed back effect on the pituitary by stimulating it to secrete LH. This is supported by the fact that prolonged protein deprivation could depress the plasma concentration of LH in domestic fowl (Buonomo *et al.*, 1982) and broiler breeder hens (Bruggeman *et al.*, 1998). Another possibility is that the

adrenal gland, via the corticosterone, regulates the timing of the preovulatory LH surge and hence the onset of breeding (Wilson & Cunningham, 1980; Astheimer *et al.*, 1995). Seasonal changes in the plasma concentration of corticosterone in wild birds are affected by the nutritional and environmental conditions as well as physiological stresses (Harvey *et al.*, 1986).

In the domestic fowl, there is a preovulatory surge of LH secretion few hours prior to ovulation (Furr *et al.*, 1973). The plasma concentrations of LH then decreases dramatically during incubation, and remain low throughout this period and brooding (Burke & Dennison, 1980; Hector *et al.*, 1986; Scanes, 1986). The LH level of domestic hens gradually rises again towards the end of brooding, preparing for resumption of eggs laying (Sharp *et al.*, 1979). Brooding behaviour, on the other hand, is under the influence of prolactin (Schoech *et al.*, 1996). In birds, high concentration of prolactin induces incubation and brooding behaviour, but antagonistically inhibits gonadal functions in female birds via the hypothalamus (Scanes, 1986). If incubation is interrupted by egg loss, the plasma concentration of prolactin falls rapidly (El Halawani *et al.*, 1980).

The basal concentration of plasma prolactin, growth hormone, and LH are lower in moulting females than in laying hens (Scanes *et al.*, 1979). However, the pituitary content of LH is the same while the FSH activity is about twofold higher in moulting hens (Imai *et al.*, 1972). FSH is known to stimulate granulosa cell of the follicles to produce and secrete progesterone (Huang *et. al.*, 1979; Hammond *et al.*, 1981). By inference, the hormone progesterone must have an important regulatory role in order to achieve moult and breeding concurrently. Indeed, there is one substantiate study to uphold this deduction. Sturkie (1965) demonstrated that progesterone inhibits ovulation and induces moult when administered in large doses, but the actual mechanisms remain unclear.

All this evidence can explain the observations at Lubang Salai. The occurrence of huge number of feathers in June and November coincided with a high proportion of full-grown nestlings (Figure 4.2 & Figure 4.6). There ought to be some correlation between the endogenous rhythm of moult and the prolactin level towards the end of brooding. Consequently, the decline in prolactin level and gradual increase of LH at the end of brooding is followed by a surge of FSH and progesterone. Progesterone is postulated to induce moult instantaneously but gradually stimulate the development and maturation of follicles in the ovary. This correlates well with the increased of feathers shed towards the end of each breeding bout. Therefore, it clarifies the two reciprocal rhythms of marked increase in the breeding activities after a decline in the number of feather collected, or a sharp reduction in breeding when large number of feather were collected in June and November.

4.7 BEHAVIOUR IN AND AROUND THE CAVE

4.7.1 Foraging Patterns

On a normal fine day, the swiftlets at Lubang Salai begin to leave their roosting cave as early as 0600 hours. The number of emerging birds increases in a steady stream and reaches its peak around 0615 – 0630 hours (Table 4.23). The swiftlets normally flutter and glide above the forest canopy after emerging from the cave, or meander around the edge of the forest vegetation. When the sun is high above the horizon, they move on towards the river and forage above the vegetation along the banks, and disperse around midday. They appear to follow the insect swarms that are swept upward by rising thermals. According to Harrisson (1974), the vertical spread of swiftlets foraging ground is between 6 – 244 meter (20 to 800 feet), and only 2% were seen more than 300 meters (1000 feet) above the canopy. In addition, Waugh and Hail (1983) reported that different species of swiftlets occupy different vertical foraging space. *Aerodramus fuciphagus* in Baram never feed under the forest canopy. Even species that normally gather mosses hanging from branches (e.g. *A. salanganus* and *C. esculenta*) have never been seen foraging in the dense undergrowth of forest. They invariably flutter along the edge, preferring corridors of open areas flanked by forest.

Table 4.23 Three typical daily outward flights of swiftlets at each quarter from 0600 to 0700 hours at Lubang Salai.

Time (hours)	Outward flight (bird per minute)		
	6 April 1997	10 April 1997	17 May 1997
0600 – 0615	15	50	51
0615 – 0630	153	137	113
0630 – 0645	33	17	45
0645 - 0700	1	2	6

In a fine day, swiftlets begin to arrive near their roosting cave as early as 1600 hours, but swirling high in the sky. They usually form several concentrations of dense, but clearly defined groups at lower elevation. These groupings remain together for several minutes at a relatively fixed area. They then drift away mostly intact and very seldom breaking up entirely. This kind of grouping behaviour has also been observed in the colonial Cliff Swallows (*Hirundo pyrrhonota*), which utilise a distinctive vocal signal to recruit conspecific when food is discovered (Brown *et al.*, 1991). Large concentration of swiftlets have been observed feeding over swarming termites at Niah (Harrisson, 1974) and in Baram. Nevertheless, it is not clear if the grouping of *A. fuciphagus* are foraging packs, or they are merely drawn together by their colonial instinct.

The swiftlets invariably assembled in large flocks over rivers, or ponds in the afternoon. Here, they skilfully glide down and skim over the surface of the water, drinking in flight. At the nadir of their dive, both theirs wings are swept upwards, while their beak dip down to flick up a mouthful of water. Occasionally, a few clumsy individuals will hit the water hard before taking to the air again. The swiftlets retreat to their roosting cave after the afternoon splash. They sometimes trail and pursue one another in what appeared to be courtship displays, while whirling near the cave entrance unleashing a crescendo of squeaking calls. As dusk falls, streams of swooping swiftlets enter the cave to roost, while avoiding the emerging bats.

The outward flight continues even when there is a drizzle, and is only delayed when there is a heavy downpour. If this persists for several hours after dawn, the swiftlets will brave the shower when the torrential rain has subsided. Swiftlets normally do not revolve around the cave in the evening if they start to forage late. There was such a case on 23 June 1997 where not a single swiftlet was noticed inside or around Lubang Salai at 1845 hours. Suddenly, huge flocks of swiftlets appeared at 1850 hours, dropping down from the sky in succession and speedily dashed into the cave. Their timing was very precise. A few minutes apart make a difference between a few birds and several hundreds. In contrast, they normally return earlier than usual if there is an eminent thunderstorm in the afternoon.

4.7.2 Roosting Habits And Nest Site Fidelity

Aerodramus fuciphagus roost in pairs. The normal roosting place serves also as the nesting site during the breeding season. Each pair clings side by side on the uneven surface of the cave wall. When a nest is present, both individuals will cram inside it, or one cling by the side of the nest. The one outside either squats by the edge of the nest, or clings on the rock surface adjacent to it with its tail and wings pointing downward.

Observations of roosting swiftlets using a night scope inside Lubang Salai revealed that each pair has a permanent roosting site. Swiftlets are able to find the same nesting sites even when the nests are removed. One adult caught sitting inside its nest on 7 September 1997 was marked. The nesting site was also marked before the nest was removed. An inspection in the late evening showed that only one bird was sitting on the marked site. This individual was not the marked bird, but apparently its partner. However, another inspection early the next morning (≈ 0515 hrs) revealed that two birds were clinging on the marked site, including the marked individual. This strongly suggests that swiftlets are permanently paired with strong nest site fidelity.

Table 4.24 shows the distribution of roosting swiftlets at three locations inside Lubang Salai in October 1997. Generally, there were more birds sitting inside their respective nests than those clinging on the rock surface. This indicates that most pairs produced a nest during the peak of the breeding season, while individuals roosting far from any nest are most likely to be sexually unproductive pairs, or immature fledglings.

Table 4.24 The distribution of roosting swiftlets outside and inside a nest at three sections inside Lubang Salai on 30 October 1997.

Site	Roosting outside or without nest			Roosting inside a nest		
	Single	Double	Total	Single	Double	Total
A	10	0	10	12	64	76
B	20	6	26	6	27	33
C	15	9	24	4	60	64

A comprehensive account of the typical activity inside Lubang Salai during the brooding period, and the approach used by swiftlets to locate their nesting site is given in Appendix 4. A returning swiftlet can fly directly to its nesting site without difficulty when the environment inside the cave is silent, or with not many birds inside it. A squeaking call follow immediately by the echolocation call is normally heard as the bird entered the cave. Such vocalisation serves as a warning announcement to the birds inside the cave (Fullard & Barclay, 1993). Those individuals inside the cave spontaneously respond back with several squeaking calls, although they may not necessary their partners. A few individuals are able to locate and fly directly to their nests soon after entering the cave. Nevertheless, the swiftlets normally revolve several times inside the cave before flying to a particular section. Here, they flutter around and increase the rate of their echolocation clicks to get a clearer picture of the surrounding before alighting.

Physical contact between neighbouring birds is unavoidable because their nests are built adjacent to each other. Disputes around the nest site are very common, especially when large numbers of swiftlet have returned to roost. This often happen between individuals already at their roosts and neighbour that are trying to alight. The one at roost usually extends its neck with a show of threat, while screaming and squeaking from a position inside its nest, or clinging by the edge of it. It will peck the intruding bird if it sets down too close. However, such peaking appears to be harmless. The conflict is intensified when the alighting bird retaliates. Sometimes both are pushed off from their roost. Serious or fatal injuries by such action have never been observed.

Another associated behaviour is wing lifting. Nevertheless, the wings are not stretched, or raised upright, but merely lifted above the shoulder in a folding posture. This usually happen to a pair of birds when one partner is approaching and trying to alight. The squeaking and

squabble stop once the mutual bond is established. After a pair has set in, one will preen the head and neck of its partner accompanying by several soft chirps.

Many birds remain in the cave during daytime throughout the incubation period. It is dark and silent inside Lubang Salai except for the buzzing sound of a few hymenopteras digging burrows in the guano. The incubating swiftlets are very sensitive to sudden bursts of sound in such a tranquil surrounding. Therefore, they were alerted before any routine checks on the marked nests by making noises outside the cave such as clapping, or coughing. The purpose is not to startle the incubating birds, and caused a frenzy departure that might throw the eggs out from the nests.

4.7.3 Multiple Nests On One Site

Several new nests were built onto the old marked nests in Lubang Salai after several breeding bouts. This is referred as multiple-nest on single nesting site (Plate 8). This differs from the condition where adjacent nests are fused together at the edge because of space limitation. Three such nests were noticed among the marked nests in Lubang Salai throughout this study, but none at Lubang Beruang. These multiple nests only occurred among nests that have successfully fledged a brood. The most common structure is one additional nest attached to a "precursor" nest. A maximum of two has been recorded. The "precursor" nest is a nest with its base attached to the cave wall.

The new nest usually attaches to the side of the "precursor" nest. Its construction and development is similar to any typical nests, and both would produce a clutch each. This implies that different pairs were responsible for their construction. It is uncertain if the new pair was the newly fledged offspring from the "precursor" nest, or any other pairs. The former appeared to be true because multiple-nest only emerged on nests where several broods of nestling had been successfully raised.

4.8 CONCLUSIONS

This study has shown that the annual breeding periodicity of *A. fuciphagus* is a protracted process, lasting at least nine months from August to March. Three breeding bouts were observed within this period. However, not all sexually mature pairs would produce a clutch in every bout. The first breeding bout was the most productive in terms of proportion breeding, where almost 90% of the marked colony produced a clutch. In addition, a larger

number of nestlings were raised as reflected by the higher reproductive index of 0.97 to 1.32. There was a more vigorous egg laying with many replacement clutches within this breeding bout. The second breeding bout began in December, and the nestlings fledged in March, or April the following year. This breeding bout was also very productive, with a reproductive index of between 1.03 to 1.28. A slackening in breeding activity was noticed thereafter. Only one quarter to half of the colony would produce another clutch during the third breeding bout.

There was a longer interval from fledging to subsequent lay between the third and first breeding bout. This interval was significantly reduced between the first and second breeding bouts. This suggests a more favourable environmental condition, or an increased in food abundance to sustain a more dynamic breeding activities. None of the pairs that suffered egg loss in the third breeding bout produced any replacement clutch. The date of subsequent clutch was roughly the same regardless of the breeding successfulness. However, the time was postponed by approximately a month if the nests were removed at the beginning of the first breeding bout. This is roughly time needed to construct a full-size nest.

The most likely proximate stimulus to initiate reproduction is the intrinsic physiological conditions of the swiftlets in general, and the female in particular. Swiftlets probably store up any surplus energy in the form of protein, or lipid before each breeding bout until it reaches a critical level that initiates breeding. Similarly, the inter-clutch interval and number of breeding attempts depends exclusively on the intrinsic condition of the swiftlets and the amount of reserves available without jeopardising the health. The reproductive strategy adopted by *A. fuciphagus* showed a multi-brood tendency within a long breeding season. The swiftlets will attempt as many broods as possible because the success of this strategy is determined by the total number of nestling each pair can raise. Generally, two broods per year are the norm for this species, but some pairs managed to produce a third clutch.

Many eggs were lost during incubation in all breeding bouts. Swiftlet nesting sites are well protected from mammal predators. The potential insect predator, a large gryllid, is absent in all caves in middle Baram. Therefore, it is evident that egg loss is natural occurrence rather than caused by predation, or deliberate ejection by the adults. It was postulated that the size of the nests is one of the major factors affecting egg loss. The nestlings have a good chance of survival until fledging once the eggs hatched. Not a single nestling was found dead inside the nest throughout this study, suggesting that nestling loss is caused by falling off from the nest rather than starvation. The average incubation period for *A. fuciphagus* observed was 25 days, while the fledging period was 45 days.

Like other species of swiftlets, *A. fuciphagus* in middle Baram overlapped breeding and moult. The peak of each breeding bout in Lubang Salai coincided with the lowest number of feathers collected, or a lesser degree of moult. The only exception was the third breeding bout during the heavy moulting period, but not without any expense to the breeding productivity. It

is a complicated task to breed and moult concurrently. It requires a precisely co-ordinated and a perfect regulating mechanism. This can only be achieved through a complex hormonal control.

Chapter 5
Development Of The Nest

5.1 INTRODUCTION

Many swifts of the family Apodidae, including the swiftlets, bind together their nesting materials with a translucent mucilaginous secretion from the salivary glands, commonly known as the nest cement (Medway, 1969). Unlike other species of swiftlets, nests of the White-nest Swiftlet (*Aerodramus fuciphagus*) and Black-nest Swiftlet (*A. maximus*) contain a high proportion of salivary nest cement. This is more so for *A. fuciphagus* where the nest is composed almost entirely of whitish hardened saliva, arranged in thin irregular laminae, with occasional incorporation of few feathers between these layers (Medway, 1963). Nests of the latter species contain many feathers, sometimes about half the bulk of each nest or more (Medway, 1963), and as much as 10% of the dry weight (Kang *et al.*, 1991). The nesting cement is produced by a pair of sublingual salivary gland located underneath the tongue of the swiftlets (Marshall & Folley, 1956; Farner, 1960; Medway, 1962a).

Extra energy and nourishment are required for the production of saliva during nest building. Consequently, nest building and breeding undoubtedly places an immense constraint on the physiological processes of the bird. Swiftlet's ability to meet the energy demands of nest construction and breeding depends very much on the rate they can gather the necessary food supply from the environment (Kang *et al.*, 1991). Nest harvesting add further constraints to the swiftlet because it removes part of the energy allocated for reproduction. Therefore, a better understanding of the process of nest construction is critical and important for the sustainable management of the edible nest swiftlet.

Kang *et al.* (1991) studied the influence of nest harvesting upon the energetic requirements of nest and egg production of *A. fuciphagus* and *A. maximus* in Singapore. The rim of the nests was marked with different colour of food dye to monitor the progress of nest construction. This resulted in multi-coloured layers in a nest, each had been added over a known period. The nests were removed after the young had fledged, and the coloured strips were sliced, dried, and weighed to give a nest growth curve. Their study was limited to one season, or a breeding cycle, and did not investigate the recurrent annual nest building rhythm.

The application of morphometric measurements to determine the changes of nest size was first introduced by Nguyen Quang in Vietnam (1993, 1996, 1998). However, all these measurements were taken from nests harvested at intervals, which did not reflect the continuous development of nest when left unharvested in a natural environment.

Nest construction has not been studied previously under natural conditions for a full annual cycle. Therefore, the objective of this study was to measure *in situ* the development and extension of nest crest without removing them for one full year. This enabled the continuous observation of nest size changes over three breeding bouts of *A. fuciphagus* in Sarawak. The date and rate of each salivary deposition was recorded accurately to reflect the dynamic of this process.

In addition, some of the marked nests were experimentally removed at the beginning of the first breeding bout to emulate nest harvest. Subsequent replacement of nests, and their respective measurements, gave a comparison of the rate of nest building in different months of the year. Direct investigation of the activity of the salivary glands by dissecting individuals was prohibited by the cave owners. However, the rate of nest construction indirectly reflects the activity of the salivary glands. Medway (1962a) showed that the salivary glands and gonads of *A. maximus* have a cyclic alternation in weight in relation to the breeding season. Therefore, it is justified to assume that the faster a nest is built, the more active are the glands. This investigation aims to shed some insight on the stimulation and activation of the sublingual glands, and its correlation to breeding.

Most of the marked nests were left unharvested for observations on nest building activity when nest is present in subsequent breeding bouts. Furthermore, the correlation of moult, nest building and breeding were examined. Claims that swiftlets build token nests during the moulting season, or when not in breeding, were also investigated. The size of the nest when the first egg was laid in each bout of breeding was also determined.

In this chapter, the development of nest is described in Section 5.2. Section 5.3 compares the rate of nest building at different breeding bout, and the impact of nest removal is discussed in Section 5.4. The development of empty nests is described in Section 5.5, while the reoccupation of abandoned nests is described in Section 5.6. The seasonal variations of size and weight of nests is described in Section 5.7.

5.2 PROGRESSIVE GROWTH OF NEST

Nest construction begins as a patch of nest cement, usually in the shape of semi-circle, or crescent with both the reinforced ends sticking onto the wall pointing upwards. Then a rim is formed at the bottom of the crescentic structure, and layer upon layer of thin salivary laminae are added until the rim is extended to form a hollow bracket (Plate 9). Swiftlets exhibit a strong disposition for nest site fidelity (Medway, 1962b). At a site in Bau, some unusual crescent-shaped features embossed on the wall of a cave inhabited by *A. maximus* were attributed to the effect of repeated use of the same nesting site over the years (Medway *et al.*, 1967). Such occurrence was also observed in Baram.

Nest building involves a regurgitation movement as observed in *A. maximus* and takes place principally at night (Medway, 1962b). There are two peaks of building activities, one from midnight to 0100 hour, and another before dawn between 0500 to 0600 hours. The swiftlet clings to the side of the nest as it builds. The head is held low, the bill opens and shuts repeatedly, accompanied by retching movements of the throat as the saliva is regurgitated, and worked around in the mouth. This saliva is then smeared on the edge of the nest with the side and corner of the bill (Kang *et al.*, 1991; Kang & Lee, 1991). At the study site in middle Baram, *A. fuciphagus* has also been observed to construct nest in the early morning too.

5.2.1 Parameter D

After some trials and evaluations in the field, it was discovered that the parameter D served only as a good sign for initial nest deposition but was not suitable as an indicator for the rate of nest building. A short and thin layer of saliva was glued to the cave wall at the beginning of nest building. The length of the first deposition was only extended slightly during the nest building phase, if not delineating the final dimension, or diameter.

The mean of parameter D measured in Lubang Salai during the Apr-Jul breeding bout varied from 7.0 cm to 7.7 cm as shown in Table 5.1. The rate of growth calculated was between 0.1 – 0.9 mm/day. Nevertheless, the increment was not a continuous process, but occurred only at the beginning of nest building. The mean of D-value showed extremely little or no increment throughout the egg-laying and incubation period ($F_{3, 150} = 0.58$, $P > 0.05$). The length of parameter D did not increase when the nests were reused in the subsequent breeding bout as shown in Table 5.2 ($F_{3, 154} = 1.30$, $P > 0.05$). One distinctive difference when a nest was reused is that fresh saliva is deposited to reinforce the base, or the hinge of the nest before breeding.

Table 5.1 Successive measurements of parameter D from nests marked inside Lubang Salai between April and August (n = 48).

Date	10 Apr	16 Apr	19 Apr	5 May	11May	11 Jun	19 Jul	9 Aug	19 Aug
Mean (cm ± SE)	7.0 ± 0.2	7.4 ± 0.2	7.4 ± 0.2	7.5 ± 0.2	7.6 ± 0.2	7.7 ± 0.2	7.5 ± 0.2	7.3 ± 0.2	7.1 ± 0.2
Range (cm)	4.7 – 8.7	4.7 – 8.8	4.3 – 9.0	5.2 – 8.6	5.3 – 11.0	6.0 – 9.4	6.0 – 8.8	6.0 – 9.5	7.1 – 9.5

Table 5.2 Measurements of parameter D during from August to October in Lubang Salai (n = 45).

Date	29 Aug	13 Sep	30 Sep	7 Oct	12 Oct	20 Oct
Mean (cm ± SE)	7.2 ± 0.2	7.2 ± 0.2	7.3 ± 0.2	7.3 ± 0.2	7.3 ± 0.2	7.3 ± 0.2
Range (cm)	6.0 – 9.5	5.8 – 9.5	6.0 – 9.5	6.0 – 9.5	6.0 – 9.5	6.0 – 9.5

The mean value of parameter D for marked nests in Lubang Beruang during the third breeding bout is listed Table 5.3. The mean value did not change much in the following first breeding bout as shown in Table 5.4 ($F_{3, 53} = 0.34$, $P > 0.05$). As a summary, the diameter of the nests exhibit some increment only at the early stage of nest building, but the growth rate levelled off as the nests reach their maximum size, or final dimension.

Table 5.3 Successive measurements of parameter D for nests marked in Lubang Beruang from May to August (n = 15).

Date	7 May	15 May	9 Jun	1 Aug	11 Aug	25 Aug
Mean (cm ± SE)	6.2 ± 0.4	6.4 ± 0.2	6.5 ± 0.2	6.3 ± 0.3	6.3 ± 0.3	6.2 ± 0.3
Range (cm)	3.9 – 7.5	5.4 – 7.5	5.2 – 8.0	5.0 – 7.2	5.0 – 7.5	5.0 – 7.2

Table 5.4 Successive measurements of parameter D from September to October for nests left unharvested inside Lubang Beruang (n = 14).

Date	10 Sep	16 Sep	2 Oct	16 Oct	24 Oct
Mean (cm ± SE)	6.2 ± 0.3	6.2 ± 0.3	6.1 ± 0.2	6.1 ± 0.3	6.0 ± 0.3
Range (cm)	5.0 – 7.2	5.0 – 7.2	5.1 – 7.0	5.1 – 7.0	5.2 – 7.0

5.2.2 Parameter R

This parameter is the best indicator for measuring the development of the nests. The nest growth curve is sigmoidal, or curvilinear, and the rate of building tends to decrease near to the time of laying (Kang *et al.*, 1991). The mean value of R for nests marked in Lubang Salai increased steadily from 2.7 cm in April to 5.3 cm in May, but levelled off thereafter at around 5-cm (Table 5.5). The highest growth rate was recorded in April (Table 5.6), with a range of between 0.8 to 1.3 mm/day. Subsequent extension of R after middle of May remained uniform at a mere 0.1 mm/day, indicating that the nests were not enlarged any further.

Table 5.5 Measurements for parameter R from marked nests in Lubang Salai between April and August 1997 (n = 50).

Date	10 Apr	16 Apr	19 Apr	5 May	11 May	11 Jun	19 Jul	9 Aug	19 Aug
Mean (cm ± SE)	2.7 ± 0.2	3.7 ± 0.3	4.1 ± 0.3	5.3 ± 0.4	5.3 ± 0.4	5.7 ± 0.4	5.9 ± 0.3	5.9 ± 0.4	5.6 ± 0.5
Range (cm)	0.5 – 6.6	1.8 – 7.3	2.0 – 8.2	2.6 – 8.6	2.7 – 8.7	2.6 – 8.4	3.0 – 8.5	1.4 – 8.5	1.2 – 0.5

Table 5.6 Growth rate of parameter R from nests marked inside Lubang Salai between April and August 1997 (n = 50).

Date	10 Apr to 16 Apr	16 Apr to 19 Apr	19 Apr to 5 May	5 May to 11 May	11 May to 11 Jun	11 Jun to 19 Jul	19 Jul to 9 Aug	9 Aug to 19 Aug
Growth rate (mm/day ± SE)	0.8 ± 0.2	1.3 ± 0.3	0.7 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Range (mm/day)	0.0 – 2.8	0.0 – 4.3	0.0 – 2.3	0.0 – 1.3	0.0 – 0.7	0.0 – 0.7	0.0 – 0.8	0.0 - 1.4

The value of R for nests marked in Lubang Beruang between May and August is shown in Table 5.7, and the growth rate in Table 5.8. The means for both study sites were the same for May and June on a monthly comparison. However, the value in Lubang Beruang increased by an order of 1-cm from early August onwards, and the difference reached a remarkable 2-cm by the end of the month. This was because of the empty nests in Lubang Beruang were enlarged about a month earlier than those in Lubang Salai. Moreover, this contrasting difference was amplified by the narrow, but elongated nature of the nests in Lubang Beruang.

Table 5.7 Successive measurements of parameter R for nest marked in Lubang Beruang between May and August 1997 (n = 14).

Date	7 May	15 May	9 Jun	1 Aug	11 Aug	25 Aug
Mean (cm ± SE)	5.3 ± 1.0	5.6 ± 1.1	5.7 ± 1.0	6.8 ± 1.0	7.1 ± 0.9	7.6 ± 0.9
Range (cm)	1.3 – 8.6	1.9 – 8.8	2.0 – 9.0	2.6 – 9.2	3.2 – 9.5	3.2 – 10.9

Table 5.8 Growth rate of R for nests marked in Lubang Beruang between May and August 1997 (n = 14).

Date	7 May to 15 May	15 May to 9 Jun	9 Jun to 1 Aug	1 Aug to 11 Aug	11 Aug to 25 Aug
Growth rate (mm/day ± SE)	0.3 ± 0.3	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.2
Range (mm/day)	0.0 – 1.8	0.0 – 0.4	0.0 – 0.8	0.0 – 0.4	0.0 – 1.4

The correlation between nest building, the egg-laying phase, the incubation and the fledging phase for any typical nests with successful breeding is shown in Figure 5.1. Medway (1962a) showed that the epithelium columnar cells lining the salivary glands of *A. maximus* become hypertrophied at the onset of the breeding season. By inference, this corresponds with the more incline lines, indicating a faster rate of growth, or huge production of saliva before the egg-laying phase. Most nests were approaching, or had attained their maximum size at the onset of the egg-laying phase. This is represented by the more level lines. During the incubation

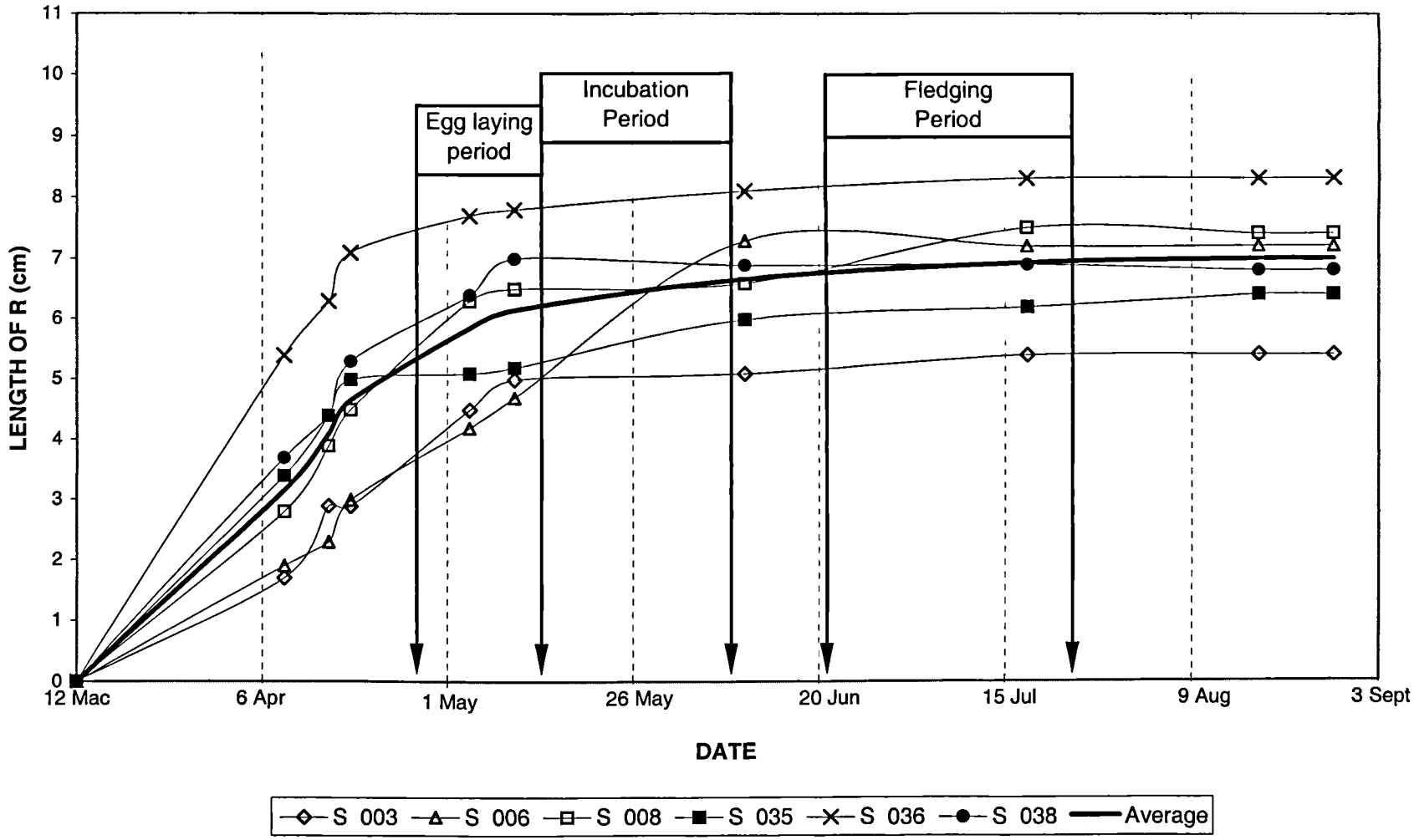

Figure 5.1 The increment of parameter R for several nests with successful breeding between March and September 1997 (lines represent different individual nests).

and brooding period, the nests hardly increased in size as illustrated by the horizontal lines stretching from middle of May to early September.

Figure 5.2 shows the increment of R-value for marked nests inside Lubang Salai that remained empty or without any clutch between April and September 1997. The more gradually inclining lines indicate that the nests were being built at a slower, but steady rate. However, the R-values were much lower nests with successful breeding, as illustrated by the dotted line. One explanation for this occurrence is that the saliva production might be suppressed, or diminished by the onset of the heavy moulting period. The inability to enlarge the nest any further suggested that these small token nests were constructed using the last remaining saliva in the sublingual glands at the end of the breeding season.

After the heavy moult in June and July, these empty nests were enlarged and reused in the following breeding bout. One good example is nest S 063, where this pair resumed enlarging their nest. Consequently, the R-value matched the mean value for nests with successful breeding four weeks after 9 August (Figure 5.2).

Table 5.9 shows the mean of parameter R for nests with successful breeding, empty nests, and nests harvested between April and August 1997, while the comparison is illustrated in Figure 5.3. The mean of R for nests with successful breeding is the highest. Empty nests have intermediate values, while the harvested nests were the shallowest with the lowest R-values because they have to be built from anew.

Table 5.9 Comparison of the mean value of R for nests with successful breeding (breeding nests); nests without any lay of a clutch or loss the content (empty) and harvested nests in Lubang Salai between April and August.

Date	Breeding nests (cm ± SE) n = 23	Empty nests (cm ± SE) n = 8	Harvested nests (cm ± SE) n = 13
12 March	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
10 April	3.5 ± 0.5	2.1 ± 0.5	1.9 ± 0.9
16 April	4.2 ± 0.5	2.3 ± 0.6	2.1 ± 0.7
19 April	4.6 ± 0.5	2.5 ± 1.2	2.2 ± 0.8
5 May	5.9 ± 0.6	3.5 ± 1.2	0.0 ± 0.0
11 May	5.9 ± 0.5	3.6 ± 1.3	0.1 ± 0.1
11 June	6.2 ± 0.5	4.0 ± 1.5	1.8 ± 0.6
19 July	6.4 ± 0.6	5.0 ± 1.1	3.3 ± 0.9
9 August	6.3 ± 0.6	5.8 ± 0.8	4.1 ± 1.2
19 August	6.3 ± 0.6	6.2 ± 0.6	4.1 ± 2.2

Table 5.10 shows the continuous measurement of R for nests left unharvested in Lubang Salai during the first breeding bout. The mean values had not change much since June ($F_{3, 140} = 0.06$, $P > 0.05$). This implies that most of the nests were reused without any

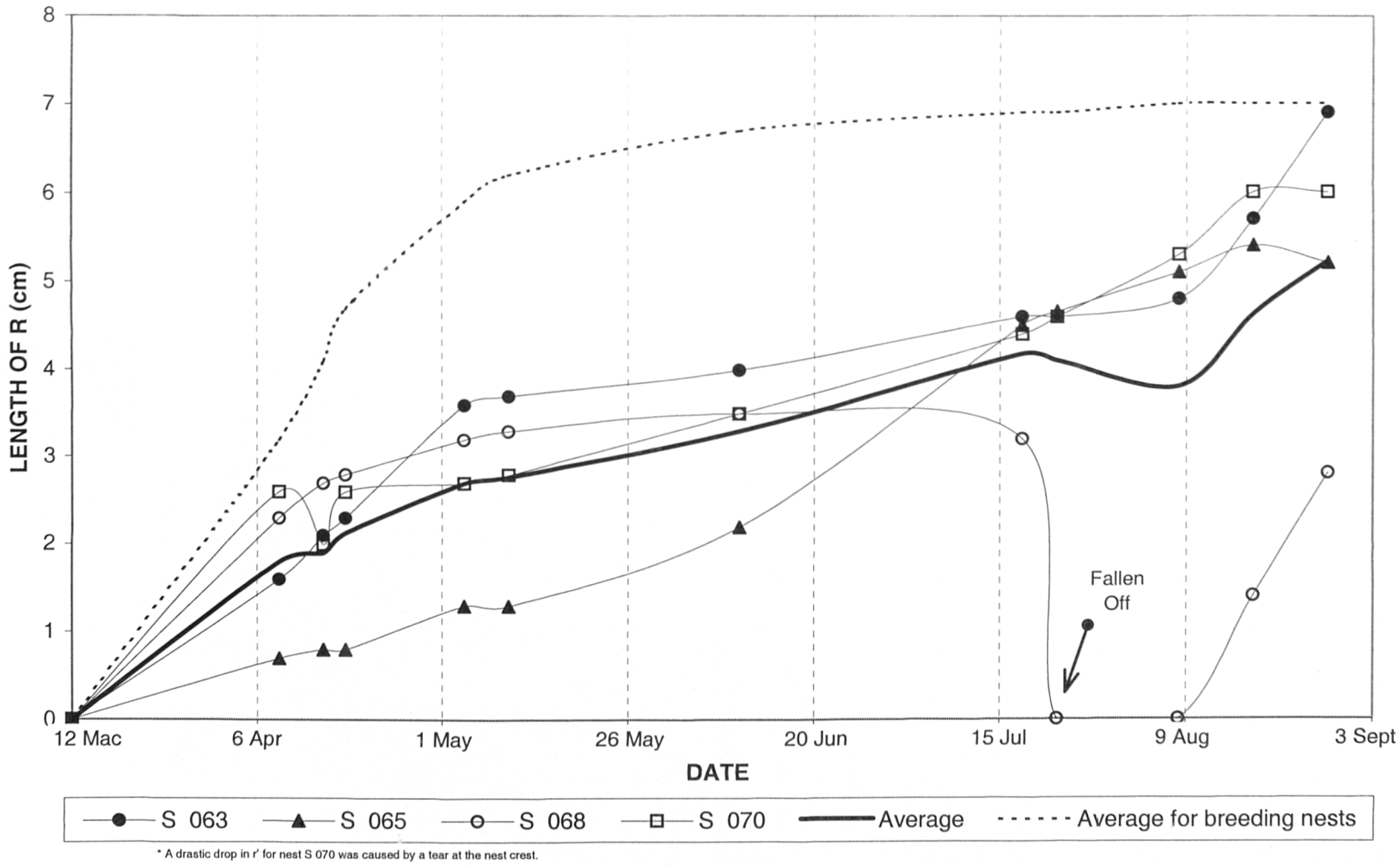

Figure 5.2 The increment of R-value for nests without any clutch laid from March to September (lines represent different individual nest).

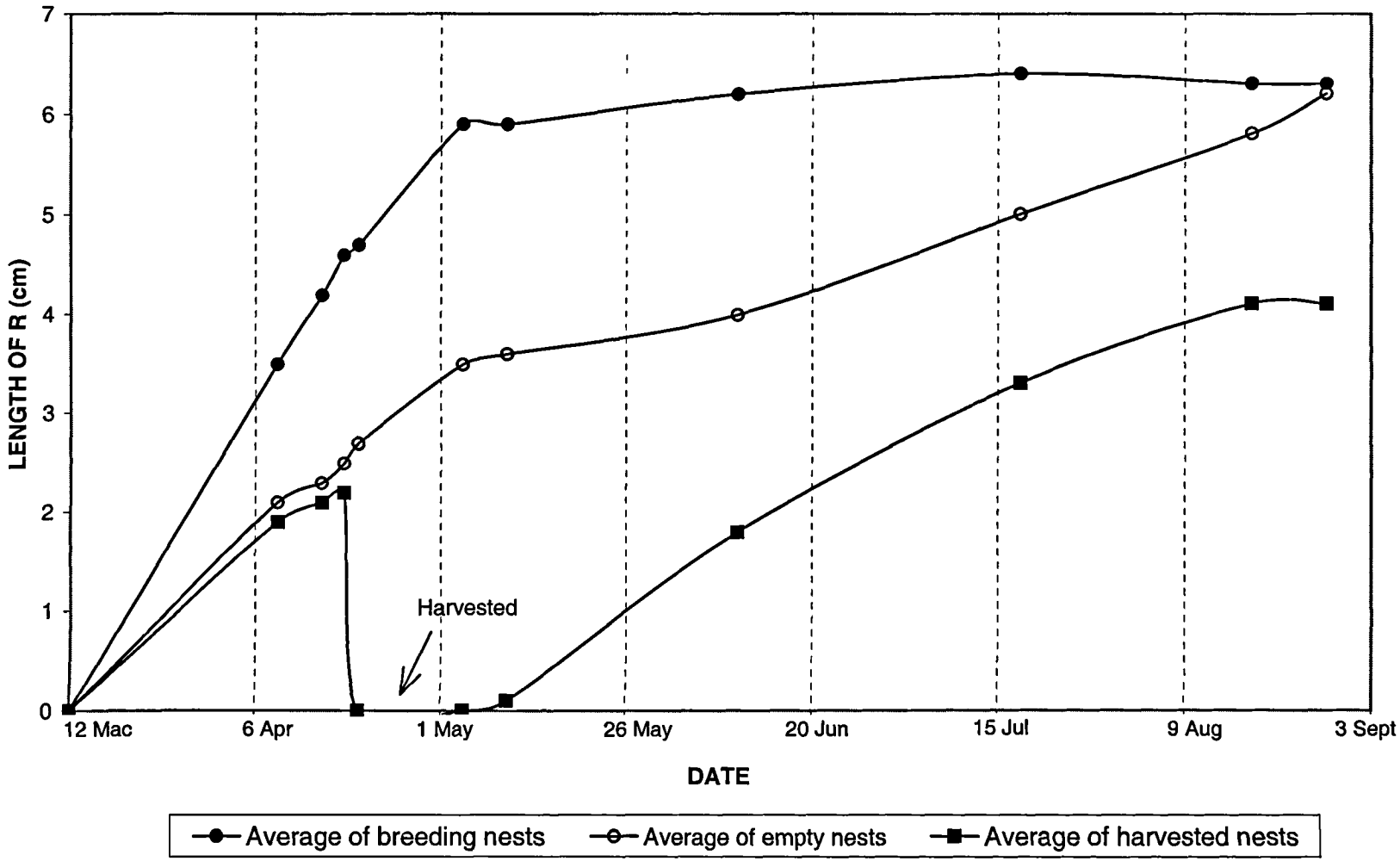

Figure 5.3 Comparison of the average of R-value for nests with successful breeding, without any clutch laid and harvested nest between March and September 1997.

extension to the nest crest. This is in agreement with observations made during routine checks on the nests. Old nests look yellowish after several months being left inside the cave and any new saliva deposited is readily distinguishable. Some nests were slightly enlarged but such extension was usually small and rarely more than 1.0 cm.

Table 5.10 Successive measurements of parameter R between August and December 1997 for marked nests left unharvested inside Lubang Salai (n = 49).

Date	29 Aug	13 Sep	30 Sep	7 Oct	27 Oct	11 Nov	26 Nov	1 Dec	6 Dec
Mean (cm ± SE)	5.7 ± 0.3	5.8 ± 0.3	5.9 ± 0.3	5.8 ± 0.4	5.9 ± 0.3	6.0 ± 0.4	6.1 ± 0.3	6.0 ± 0.3	6.1 ± 0.3
Range (cm)	3.1 – 8.5	3.1 – 9.2	2.7 – 9.2	1.1 – 9.2	1.4 – 9.2	1.3 – 9.2	1.9 – 9.2	1.9 – 9.2	1.9 – 9.2

There was a difference ($F_{3, 48} = 6.64$, $P < 0.05$) in the mean value of R between the second and third breeding bouts (Table 5.11). Nine out of fifteen, or 60% marked nests at Lubang Beruang showed not only clear enlargement before the first breeding bout, but a remarkable increment as well. For example, the R-value of five nests were extended by 0.5 to 0.9 cm, while six nests gained an additional 1.3 to 1.9 cm in between 25 August and 10 September 1997, or an interval of sixteen days. Another gained an exceptional 2.3 cm in the same period (Plate 10).

Table 5.11 Successive measurements of R-value between September and December for marked nests left unharvested at Lubang Beruang (n = 12).

Date	10 Sep	16 Sep	2 Oct	16 Oct	24 Oct	10 Nov	22 Nov	3 Dec
Mean (cm ± SE)	8.5 ± 1.0	8.7 ± 1.0	8.8 ± 0.8	8.9 ± 0.9	8.9 ± 0.8	9.0 ± 0.8	8.9 ± 0.8	8.9 ± 0.8
Range (cm)	5.5 – 12.2	5.5 – 12.2	6.1 – 12.2	6.1 – 12.2	6.1 – 12.2	6.1 – 12.2	6.1 – 12.2	6.1 – 12.2

The comparison of the rate of nest building at different months is shown in Table 5.12. The duration was calculated from the time when fresh saliva deposition was noticed. There was a marked contrast in the rate of nest building between all breeding bouts ($F_{5, 66} = 6.29$, $P < 0.05$).

None of the nests experimentally removed on 26 April 1997 rebuilt in the next 14 days, although flimsy re-deposition was noticed in half of the former nest sites. One site had new nesting materials deposited after two weeks, while the rests were enlarged after six weeks, but at a very slow rate. The rate of nest building could only matched that of the unharvested nests after nine weeks. The value of R of the second nests never reach anywhere near the mean of the breeding nest before the start of the first breeding bout, or produced any clutch (Figure 5.4).

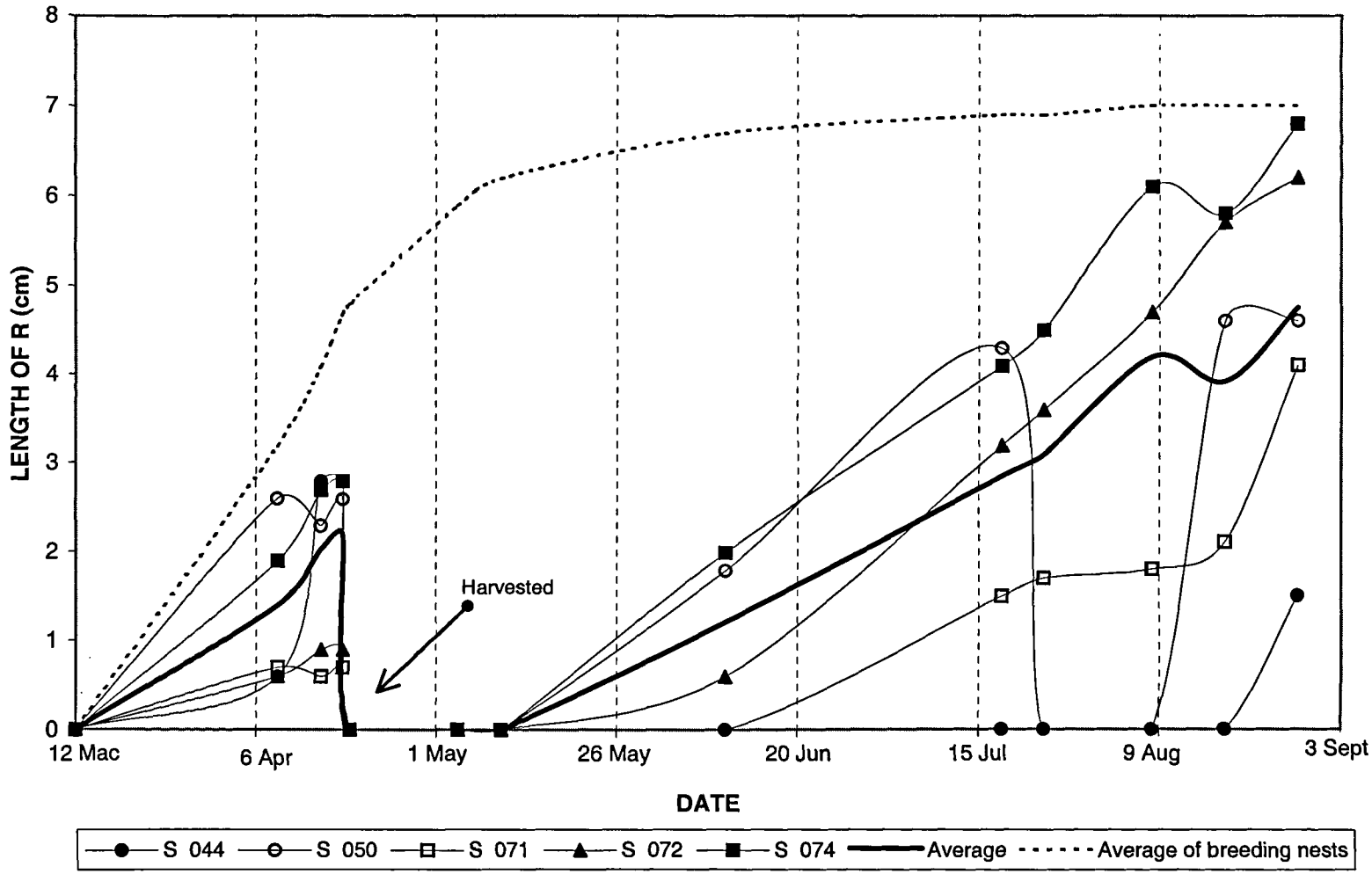

Figure 5.4 Pre-harvest and post-harvest profile of the increment of parameter R for several nests between March and September 1997.

Table 5.12 Comparison of the mean nest building rate for experimentally removed nests in Lubang Salai at different seasons.

	March			April			September		
	First week	Second week	Third week	First week	Second week	Third week	First week	Second week	Third week
Mean (mm/day)	0.8 ± 0.3	1.3 ± 0.5	0.7 ± 0.3	0.2 ± 0.1	0.3 ± 0.2	0.6 ± 0.5	2.2 ± 1.4	1.5 ± 0.7	1.3 ± 0.5
Range (mm/day)	0.0 – 2.8	0.0 – 4.3	0.0 – 2.3	0.0 – 0.6	0.0 – 0.7	0.0 – 1.6	0.0 – 3.8	0.0 – 2.6	0.0 – 2.0

The growth rate in the first week after nest removal for the first breeding bout was faster compared to the third breeding bout ($t_{59} = 4.20$, $P < 0.05$). On the second week, there was no significant difference in the growth rate of R for both breeding bouts ($t_{59} = 0.43$, $P > 0.05$). This was because all the nests removed in the third breeding bout were only rebuilt in the second week, while the difference was different again in the thrid week ($t_{59} = 2.57$, $P < 0.05$). The slower mean growth rate in April was caused by a large number of nests that were not enlarged, most probably due to the degeneration of the salivary glands.

5.2.3 Parameter P

The parameter P reflects the elongation of the outer circumscription of the nest crest. It was measured from the upper level part of the nest crest connected to the wall, or the hinge of the nest. The enlargement at the base was totally ignored. Each layer of laminae varies in length since the perimeter of the crest is not a mathematically perfect semi-circle, but a jagged crescent. The difference between these successive layers become smaller as the nest gets bigger.

The mean value of P for nests marked in Lubang Salai during the third breeding bout is shown in Table 5.13. No value was recorded in April because this parameter was introduced only in May when the majority of the nests were semi completed. That explained why the mean value stayed uniform from May until August at the magnitude of 13-cm. Nevertheless, the rate of growth was 0.7 mm/day in early May, but remained at a negligible rate of 0.1 mm/day thereafter (Table 5.14). This indicates a pause in nest building.

Table 5.13 Successive measurements of parameter P for nests marked in Lubang Salai between April and August 1997 (n = 50).

Date	10 Apr	16 Apr	19 Apr	5 May	11 May	11 Jun	19 Jul	9 Aug	19 Aug
Mean (cm ± SE)	—	—	—	13.2 ± 0.3	13.4 ± 0.3	13.5 ± 0.3	13.7 ± 0.2	13.7 ± 0.3	13.1 ± 0.6
Range (cm)	—	—	—	9.1 – 15.9	8.6 – 15.7	10.2 – 15.9	10.9 – 16.4	10.0 – 16.6	2.8 – 16.5

Table 5.14 The growth rate of the parameter P for nests marked in Lubang Salai between April and August 1997 (n = 50).

Date	10 Apr to 16 Apr	16 Apr to 19 Apr	19 Apr to 5 May	5 May to 11 May	11 May to 11 Jun	11 Jun to 19 Jul	19 Jul to 9 Aug	9 Aug to 19 Aug
Mean (mm/day ± SE)	—	—	—	0.7 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Range (mm/day)	—	—	—	0.2 – 3.7	0.0 – 2.2	0.0 – 0.9	0.0 – 1.0	0.0 – 1.8

The mean value of P for nests marked in Lubang Beruang is shown in Table 5.15, and the growth rate in Table 5.16. This value increased by 1.6 cm from 12.6 cm in early May to 14.2 cm in August. Only several nests exhibited some growth in early May when eggs were laid, with a growth rate of less then 1.5 mm/day. The growth rate was reduced to 0.2 mm/day in June, which gradually declined to 0.1 mm/day in July and completely no growth in August. The gradual reduction in the rate of nest building throughout this period corresponded with the incubation and brooding period. The mean growth rate subsequently recovered to 0.3 mm/day in middle of August when the nests were further enlarged, or restored during the first breeding bout.

Table 5.15 Successive measurements of parameter P for nests marked in Lubang Beruang between April and August 1997 (n = 15).

Date	7 May	15 May	9 Jun	1 Aug	11 Aug	25 Aug
Mean (cm ± SE)	12.6 ± 1.1	13.2 ± 1.1	13.7 ± 1.1	14.2 ± 1.0	14.2 ± 0.9	14.5 ± 1.0
Range (cm)	7.8 – 17.9	7.7 – 17.9	9.0 – 17.9	10.3 – 18.5	10.2 – 17.2	10.3 – 17.7

Table 5.16 The growth rate of parameter P for nests marked in Lubang Beruang between April and August 1997 (n = 15).

Date	7 May to 15 May	15 May to 9 Jun	9 Jun to 1 Aug	1 Aug to 11 Aug	11 Aug to 25 Aug
Mean (mm/day ± SE)	0.5 ± 0.3	0.2 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.3 ± 0.2
Range (mm/day)	0.0 – 1.5	0.0 – 1.2	0.0 – 0.8	0.0 – 0.2	0.0 – 1.4

The mean value of P for nests left undisturbed in Lubang Salai since April is shown in Table 5.17. The marked nests did not increase in size since the last breeding bout ($F_{3, 168} = 1.77$, $P > 0.05$), and the margin had attained on mean a mere 0.5 cm increment.

Table 5.17 Successive measurements of parameter P between August and December 1997 for nests left unharvested inside Lubang Salai (n = 54).

Date	29 Aug	13 Sep	30 Sep	7 Oct	27 Oct	11 Nov	26 Nov	1 Dec	6 Dec
Mean (cm ± SE)	13.7 ± 0.3	13.5 ± 0.4	13.9 ± 0.3	14.0 ± 0.3	14.1 ± 0.3	14.2 ± 0.3	14.2 ± 0.3	14.1 ± 0.3	14.0 ± 0.3
Range (cm)	8.9 – 16.7	8.0 – 16.0	11.0 – 16.7	11.3 – 16.7	11.3 – 16.7	11.5 – 16.8	11.5 – 16.8	11.5 – 16.7	11.5 – 16.7

The mean value of P during the first breeding bout in Lubang Beruang is shown in Table 5.18. Here, the extension of P was more distinctive, but not significantly different ($F_{3, 48}$ = 1.33, P > 0.05). Observations from both study sites showed that nests from the third breeding bout were restored with slight extension added to the crest at the beginning of the subsequent breeding bout.

Table 5.18 Successive measurements of parameter P between August and December 1997 for marked nest in Lubang Beruang (n = 12).

Date	10 Sep	16 Sep	2 Oct	16 Oct	24 Oct	10 Nov	22 Nov	3 Dec
Mean (cm ± SE)	15.2 ± 1.1	15.4 ± 1.1	15.5 ± 1.0	15.5 ± 1.1	15.5 ± 1.1	15.6 ± 1.1	15.5 ± 1.1	15.5 ± 1.1
Range (cm)	12.4 – 19.0	12.4 – 19.0	12.4 – 18.5	12.4 – 18.5	12.4 – 18.4	12.4 – 18.5	12.3 – 18.5	12.3 – 18.5

The growth rate of P for nests removed in Lubang Salai on 26 April and 13 September 1997 are shown in Table 5.19 and Table 5.20, respectively. There was not only a faster rate of nest building during the first breeding bout, but an immediate and simultaneous rebuilding after the nests were removed. In contrast, nests removed in April required 2 to 6 weeks before any new saliva was deposited.

Table 5.19 The growth rate of P for nests removed on 26 April 1997 in Lubang Salai (n = 14).

Date	5 May to 11 May	11 May to 11 Jun	11 Jun to 19 Jul	19 Jul to 30 Jul	30 Jul to 9 Aug	9 Aug to 19 Aug	19 Aug to 29 Aug
Mean (mm/day ± SE)	2.4 ± 1.8	1.6 ± 0.9	0.6 ± 0.4	2.3 ± 1.3	0.1 ± 0.1	2.1 ± 1.8	0.4 ± 0.4
Range (mm/day)	0.0 – 14.3	0.0 – 4.7	0.0 – 3.2	0.0 – 10.4	0.0 – 12.2	0.0 – 12.0	0.0 – 4.2

The growth rate during the first breeding bout was very high in the first week when fresh layers of saliva were deposited to form the base of the nest. This rate declined to 3.0 mm/day as the rim or the nest crest was being shaped. However, it was still much faster than the rate in the third breeding bout (t_{23} = 2.24, P < 0.05). There was a gradual and uniform

decline in the rate of growth three weeks after nest removal because most nests have reached their maximum size. There was a negligible prolongation of the perimeter throughout the incubation and brooding period, with a rate of only 0.1 mm/day.

Table 5.20 The growth rate of the parameter P for nests removed on 13 September 1997 in Lubang Salai (n = 11).

Date	13 Sep to 18 Sep	18 Sep to 30 Sep	30 Sep to 7 Oct	7 Oct to 13 Oct	13 Oct to 20 Oct	20 Oct to 27 Oct	27 Oct to 11 Nov	11 Nov to 20 Nov	20 Nov to 26 Nov
Mean (mm/day ± SE)	15.2 ± 1.3	3.0 ± 1.0	1.1 ± 0.4	0.6 ± 0.4	0.7 ± 0.4	0.4 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Range (mm/day)	11.8 – 19.0	0.0 – 7.4	0.0 – 1.9	0.0 – 2.5	0.0 – 2.0	0.0 – 1.0	0.0 – 0.1	0.0 – 0.1	0.0 – 0.1

Generally, swiftlets show preferences in selecting nesting sites. They tend to nest in aggregation, as featured in Lubang Beruang. Such aggregation might be the results of competition for available nesting sites, or because they are drawn by their colonial instinct to nest close together. Preliminary observations among *A. maximus* showed one member of the marked pair spends more time building the nest than the other (Kang *et al.*, 1991). If the contribution from each partner to reproduction is equal, it is reasonable to assume that male swiftlets ought to have excess resources equivalent to the amount allocated for egg production in female, and use this surplus energy for saliva production. Medway (1962a) showed that male *A. maximus* collected before the start of the breeding season have enlarged and active sublingual glands (71 – 91 g), while those taken during the breeding season have glands varying in weight between 34 to 131 g. In addition, four males collected during the moulting period in May also have enlarged glands.

Therefore, it was postulated that male swiftlets are the main nest builder, and contribute more based on the energy and resources preservation strategy. No doubts female swiftlets also contribute to nest building, but their participation is limited because she needs to allocate a portion of resources for egg production. In addition, the occurance of semi completed nests in Lubang Salai that were not enlarged between May and July suggested that the males might be solely responsible for their construction. Beside the daily maintenance of bodily functions in male swiftlets, excess energy assimilated from available food source during this time of the year is used for saliva production, and regrowth of new feathers. This surplus energy is most likely to be stored in the form of lipid, or protein in female swiftlets for future use in egg production.

5.3 COMPARATIVE RATE OF NEST BUILDING

The growth rate of parameter R during each bout of breeding was different ($F_{2, 72} = 9.09$, $P < 0.05$) throughout this study (Table 5.21). The growth rate during the third breeding bout was slower compared with the rate recorded during the first breeding bout ($t_{31} = 3.08$, $P < 0.05$), or the second breeding bout ($t_{37} = 2.69$, $P < 0.05$). However, there was no difference in the nes building rate for the two breeding bouts between August and December ($t_{12} = 1.72$, $P > 0.05$). Therefore, it could be concluded that nest building was most active in August at the beginning of the breeding season. In contrast, there was a slackening nest building rate starting from April until the end of July.

Table 5.21 The comparative rate of nest building at different bout of breeding recorded in Lubang Salai.

Breeding bout	First	Second	Third
Period	13 Sep – 7 Oct	15 Dec – 17 Jan	12 Mac – 10 Apr
Mean Rate (mm/day)	1.7 ± 0.3	1.4 ± 0.1	1.1 ± 0.1
Range (mm/day)	0.6 – 2.6 n = 13	0.8 – 1.8 n = 16	0.2 – 2.3 n = 49

Swiftlets build replacement nests at the same nesting sites when the nests are removed, or lost by natural nest fall (Manuel, 1937; Medway, 1962b; Nguyen Quang, 1994). This action is repeated if the replacement nests are subsequently removed again, producing a successive generations of nests built at different months of the year. In this study, the rate of nest building for several successions of nests constructed between September and January is shown in Table 5.22.

Table 5.22 Comparison of the rate of nest building for successive generations of nests that underwent multiple harvest in Lubang Salai.

	First batch	Second batch	Third batch
Period	13 Sep – 7 Oct	1 Nov – 20 Nov	15 Dec – 17 Jan
Mean Rate (mm/day)	1.7 ± 0.3	0.8 ± 0.2	1.4 ± 0.1
Range (mm/day)	0.6 – 2.6	0.4 – 1.6	0.8 – 1.8

The first harvest occurred on 13 September 1997, and the R-values of thirteen nests measured on 7 October showed a mean growth rate of 1.7 ± 0.3 mm/day. The second harvest took place on 1 November 1997, while the third harvest on 15 December 1997, with the growth rate of 0.8± 0.2 mm/day, and 1.4 ± 0.1 mm/day, respectively. The rate of nest building was different in all batches ($F_{2, 35} = 13.39$, $P < 0.05$). The growth rate of the second batch was clearly slower than that of the first ($t_{20} = 4.42$, $P < 0.05$), or the third batch ($t_{26} = 4.28$, $P < 0.05$). This slower rate was because the rebuilding of this batch of nests in November coincided with

the onset of the moulting season, as indicated by the large number of primary feathers PF-1, PF-2 and PF-3 collected inside the cave. The energy demand for producing new feathers is very high in small birds (Lindstrom *et al.*, 1993). The extra energy required for feathers formation, particularly to replace a sudden loss of many down feathers might place additional constrains on the capacity of saliva production.

On the other hand, there was no difference (t_{12} = 1.72, P > 0.05) in the rate of nest building between the first and third batch. This concurred with the observation by Kang *et al.* (1991) where neither *A. fuciphagus*, nor *A. maximus* build the second, or third replacement nest any faster. This suggests that the swiftlets were already building at the maximum rate and each swiftlets has its own limit in assimilating their food intake. Partial distribution and the channelling of this limited energy reserves to meet other physiological requirements such as moulting might constrained and slow down the nest building rate in November.

5.4 IMPACT OF NEST REMOVAL (HARVESTED NESTS)

Seven nests or approximately 50% of the 13 nests removed in Lubang Salai on 26 April 1997 have detectable quantity of nest material re-deposited within a week. This conformed with the observation by Kang *et al.* (1991) that the nest crest began to develop around 13 to 14 days after deposition of the base. The earliest sign of re-deposition by the remaining 50% was about 8 to 10 weeks later in between 11 July and 19 July. All except one nest that were harvested produced a clutch after August (Table 5.23). The mean interval from nest removal to the lay of subsequent clutch was 142 ± 17 (days ± SE), roughly 4 to 5 months.

Table 5.23 Nests that were experimentally removed in Lubang Salai on April 1997 with the subsequent re-deposition and the lay of a clutch.

Nest	Date of removal	First detected re-deposition	Subsequent clutch	Interval of removal to the lay of 1st egg (days)
S 042	26 Apr	29 Aug	13 Oct	171
S 046	26 Apr	11 May	—	—
S 048	26 Apr	11 May	13 Oct	170
S 049	26 Apr	11 May	8 Sep	135
S 050	26 Apr	5 May	24 Aug	120
S 051	26 Apr	29 Aug	1 Nov	189
S 052	26 Apr	5 May	24 Aug	120
S 071	26 Apr	11 Jun	3 Sep	130
S 072	26 Apr	6 Jun	24 Aug	120
S 074	26 Apr	6 Jun	24 Aug	120
			Mean (days ± SE) =	142 ± 17

Nest S042 could be considered a very small sized nest with a R-value of 0.5 cm when removed. Re-deposition was noticed by end of May, but this nest fell off by itself in June. Nothing was deposited again until 29 August, and the R-value had reached 4.1 cm by 13 September. The first egg appeared on 13 October when the R-value was 5.8 cm. For nest S046, re-deposition occurred 15 days after removal. However, the R-value had only increased by a mere 0.4 one month after removal. It then remained the same until another clear sign of enlargement was noticed on 29 August. The nest crest had extended to 3.8 cm by 7 October and 4.6 cm by 13 October, but remained empty until the end March in the following year. The R-value of nest S051 was 0.7 cm when removed. No nest material was deposited between April and July. The succeeding re-deposition was on 29 August. When the first egg appeared, the R-value was 2.6 cm. For nest S071, the R-value was 0.7 cm when removed. Re-deposition occurred on 11 June, and the R-value slowly increased. It reached 1.5 cm by 19 July, and 4.1 cm by 19 August. The R-value was 5.2 cm when the first egg was laid.

The chronicles of these four nests showed the subsequent development when small sized nests were harvested during or before the moulting period. There was very little rebuilding activity as shown by the extremely slow re-deposition rate of fresh saliva. Most nests had negligible enlargement, or maintained at the same size until the beginning of the first breeding bout. It could be assumed that the salivary glands were regressed between April and July, and they were apparently not actively secreting any salivary nest cement until the next breeding bout commenced.

Nest S048 was of moderate size with an R-value of 3.8 cm when it was removed. Re-deposition occurred on 11 May, but the replacement nest remained the same size until it fell off by itself on 11 June. The following deposition was only noticed on 29 August after 79 days, or 2½ months. The R-value had reached 6.0 cm when the subsequent clutch was laid. Similarly, nest S049 was another moderate sized nest with a R-value of 2.0 cm when it was removed. Little re-deposition was noticed, but the nest was not enlarged any further and it fell off on 20 June. Visible signs of re-deposition were noticed again on 30 July, a pause of 40 days. The R-value was 3.7 cm when the first egg was laid.

The chronicles of nests S048 and S049 showed post-harvesting development similar to that of any small sized nest, despite the fact that they had almost attained their maximum size when removed. Some depositions of fresh saliva were detected between April and July, but only in small quantities. When nests were removed in April, or during the heavy moulting period, no active nest rebuilding occurred until the end of July, or early August. In addition, the occurrence of nest fall was very frequent because nests constructed during this period were small, and thus lacked a strong support, or reinforcement at the base.

Three nests were removed twice between April and September in an attempt to experiment on the consequences of multiple nest harvest (Table 5.24). Although only three

marked nests were subjected to such trials, there were many other unmarked nests harvested at corresponding time. They too exhibited similar post-harvesting development.

Table 5.24 Nests that were experimentally removed twice between April and September in Lubang Salai.

Nest	First removal		Second removal		Subsequent clutch
	Date	R value (cm)	Date	R value (cm)	
S 043	26 Apr	5.6	23 Aug	3.5	13 Sep
S 044	26 Apr	2.8	13 Sep	5.3	27 Oct
S 075	26 Apr	0.7	13 Sep	5.9	–

The R-value of nest S043 was 5.6 cm, and it contained one egg when removed. Little re-deposition was noticed on 11 May, but the nest crest was not extended for another 30 days. Subsequently, the R-value reached 2.8 cm by 18 July and 3.5 cm when it was removed for the second time on 23 August. Fresh materials were deposited immediately where the R-value reached 1.5 cm in six days. The first egg of the subsequent clutch was laid when the R-value reached 5.5 cm, three weeks after the second removal.

The R-value of nest S044 was 2.8 cm when it was removed. It was rebuilt on 6 June, but the size remained the same until it fell off by itself on 23 June. New deposition did not occur until 9 August. The R-value had reached 5.3 cm when it was experimentally removed on 13 September. Subsequent deposition occurred 17 days later on 30 September, and the first egg appeared on 27 October when the R-value had reached 5.6 cm

As for nest S075, the R-value was 0.7 cm when it was removed. New nest material was not deposited until 9 August, an interval of 105 days. When it was removed for the second time, the R-value was 5.9 cm. After that, new deposits were noted on 1 November. This nest did not increased in size throughout November. The next obvious extension only occurred in early December, and the R-value reached 5.4 cm by 15 January. The absence of eggs in this nest even until March did not necessary mean that no subsequent clutch was produced. Alternatively, there is a possibility that the eggs were laid, but were lost before any routine check on the marked nest.

At the beginning of the first breeding bout, 12 nests from Lubang Salai and 7 nests in Lubang Beruang were removed to investigate the percentage of nest rebuilding. The result is shown in Table 5.25. The percentage of rebuilding was 100%, without any nest abandoned at all sites. This reflects a favourable breeding conditions where the salivary glands were very much active compared to the previous third breeding bout.

Table 5.25 Comparative data of nests harvested in Lubang Salai and Lubang Beruang on 13 September and 16 September respectively.

	Lubang Salai	Pasen Avut, L. Beruang	Pasen San, L. Beruang
Total nests harvested	12	2	5
Total number of nest re-deposited	12	2	5
Number of nests abandoned	0	0	0
Number of empty nests	3	1	1
Number of nests with a clutch laid in	8	1	4
Percentage of re-deposition (%)	100	100	100

Among the nests that were removed during the first breeding bout, 6 nests had experienced successful breeding in the previous breeding bout, and were removed after the young had fledged. The mean interval from the first brood to the subsequent clutch was 106 ± 12 (Table 5.26). This is 27 days longer ($t_{13} = 3.5$, $P < 0.05$) compared to the nests that were not removed (Table 5.15). The shortest interval was 84 days, while the longest was 125 days. Therefore, it could be deduced that subsequent lay in the first breeding bout was delayed by roughly a month if the nests were removed after the young from the third breeding bout had fledged.

Table 5.26 The date of fledging until the lay of subsequent clutches for nests that were removed after the young had fledged.

Nest	Fledged	Removed	Subsequent clutch	Interval between brood (days)	Interval from removal (days)
S 015	15 Jul	13 Sep	1 Nov	109	49
S 033	19 Jul	30 Jul	23 Oct	96	85
S 034	24 Jul	13 Sep	16 Oct	84	33
S 036	8 Jul	30 Jul	1 Nov	114	94
S 037	23 Jul	8 Aug	8 Nov	108	92
S 056	5 Jul	8 Aug	8 Nov	125	92
			Mean (days ± SE)	106 ± 12	74 ± 22

Two nests were categorised as abandoned, one with egg loss, and another three empty nests in the third breeding bout were also removed on 13 September (Table 5.27). There was a difference ($t_6 = 3.28$, $P < 0.05$) in the interval from nest removal to the subsequent clutch compared with the nests with successful breeding. Nests without any successful breeding required a mean interval of 37 ± 6 days compared with 74 ± 22 days for nests with successful breeding. Therefore, any pair of swiftlets that did not produce any brood in the third breeding bout were in better conditions to breed in subsequent attempt.

Table 5.27 Nests of various categories that were removed twice between April and November in Lubang Salai.

Nest	Previous category	First removal		Second removal		Subsequent clutch	Interval (days)
		Date	R (cm)	Date	R (cm)		
S 040	abandoned	8 Aug	2.8	13 Sep	6.0	20 Oct	37
S 045	abandoned	20 Jul	1.5	13 Sep	6.0	—	—
S 054	empty	8 Aug	6.0	13 Sep	7.0	1 Nov	49
S 057	empty	17 Jul	4.3	13 Sep	5.6	15 Oct	32
S 058	empty	30 Jun	4.8	13 Sep	4.9	15 Oct	32
S 062	egg lost	30 Jul	6.8	13 Sep	7.2	20 Oct	37
						Mean (days ± SE) =	37 ± 6

In dove species with a fixed clutch of two, the inter-clutch interval is shortened if they loose an egg or squab. In general, the correlation between the brood size and the inter-clutch interval is caused by the constraints on the females. Larger broods need more food, and this extra cost might delay the moment at which a female can reallocate resources to lay another clutch (Cate & Hilbers, 1991).

5.5 EMPTY NESTS

Thirteen out of 75 (17.3%) marked nests in Lubang Salai during the third breeding bout remained empty. All these nests had shallow nest crests with very small R-values. The percentage of empty nests during the subsequent first and second breeding bouts was reduced tremendously to 1.2% and 6.1%, respectively (Table 5.28). Similar observations were also recorded at all sampling sites in Lubang Beruang. This suggests that not all sexually mature pairs would produce a clutch during the third breeding bout. In contrast, most individuals in the colony, if not all, bred during the first and second breeding bouts.

Table 5.28 Percentage of nest that remained empty for each bout of breeding between April 1997 and March 1998.

Bout of Breeding	Lubang Salai (%)	Pasen Avut, L. Beruang (%)	Pasen San, L. Beruang (%)
First (Aug-Nov)	1.2	13.3	3.1
Second (Dec-Mar)	6.1	20.0	8.6
Third (Apr-Jul)	17.3	46.6	—

The value of R for the empty nests inside Lubang Salai during the third breeding bout only managed to reach a comparable value of the breeding nest after 170 days, or 5½ months (Figure 5.5). This time coincides with the beginning of the first breeding bout. Six out of the 13 empty nests had at least one egg by the end of August (Table 5.29). When the first egg

appeared among these previously empty nests, the mean value of R was 5.8 cm. This value falls in the mean value of 4.6 to 5.9 cm for nests with successful breeding.

Table 5.29 The date when the first egg was laid and the respective value of R and P for six marked nests that were empty in the April-July breeding bout.

Nest Number	Date of subsequent clutch	R-value when first egg laid (cm)	P-value when first egg laid (cm)
S 063	29 August	6.9	14.7
S 064	24 August	5.5	15.1
S 065	30 July	5.1	14.5
S 067	9 August	5.8	13.6
S 069	24 August	5.7	13.6
S 070	19 August	6.0	14.6

Seven out of 15 marked nests in Lubang Beruang were empty during the third breeding bout. These empty nests were only enlarged 55 days after removal, but neither the value of R reach the mean for the nests with successful breeding by the end of this breeding bout nor any egg was laid (Table 5.30). The first clutch of these nests was laid during the first breeding bout. This establishes the fact that many small nests with shallow nest crest were built between April and July, but no clutches were produced. Some of these nests were enlarged at a negligible rate, while many did not increase in size until the start of the following first breeding bout.

Table 5.30 Seven nests that remained empty at Pasen Avut during the April-July breeding bout and the date of the subsequent clutch.

Nest Number	Date of subsequent clutch	R-value when first egg was laid (cm)	P-value when first egg was laid (cm)
P 002	16 September	10.8	17.8
P 006	10 September	12.2	19.0
P 007	2 October	8.6	14.9
P 009	2 October	10.1	15.2
P 010	—	—	—
P 013	2 October	9.1	17.1
P 014	10 September	10.0	17.5

5.6 ABANDONED NESTS

Twelve nests in Lubang Salai were not reused after the marking in April 1997, and were categorised as abandoned. Possible factors that caused nest desertion include human interference, or the presence of the copper wire used for hanging the number markings (Plate 9). However, 9 nests were reoccupied, presumably by the same pairs. None of the marked nests was abandoned during the first and second breeding bout. All produced a clutch instead.

At one of the initial sites inside a long narrow tunnel in Lubang Beruang, all 60 pairs of birds abandoned their nests after their nests were marked in May 1997. Unfortunately, it was not certain whether any swiftlets used the abandoned site for roosting. The abandoned nests become soggy after few weeks. However, 36 nests were rebuilt by middle of August, representing 60% reoccupation, and the full complement of 60 nests was present by early February the following year.

It appears that the presence of humans seriously affected and frightened the colony of *A. fuciphagus* nesting in a small confined grotto inside Lubang Beruang, which led to nest desertion. Such disturbance was lessened, or diminished in larger cave such as in Pasen San, or Lubang Salai. Nest desertion and re-nesting are important components of breeding strategies, especially when predation is frequent (Bauchau & Seinen, 1997). Individuals may respond to a high probability of nest predation either by reducing their investment in any one breeding attempt (i.e. abandoning nest) and saving resources for future attempts (Cresswell, 1997). This was apparently the strategy adopted by the colony in Lubang Beruang. The whole colony was frightened by constant human presence and decided not to invest any further in their current breeding. The swiftlets reoccupied the nesting sites several months latter after that particular colony was left alone, and calmness was restored.

Nest desertion by adult swiftlets caused by disturbance or presence of human was observed in other species. Medway (1962b) discovered that the inspection platform permanently fixed near one group of *A. maximus* nests seriously disturbed the swiftlets and caused many to desert, at least temporarily. Kang *et al.* (1991) had to abandoned attempts to study nest-site loyalty because of the disturbance and desertion of nests affected by the catching and ringing process.

5.7 SEASONAL VARIATIONS OF SIZE AND WEIGHT OF NESTS

Random samples of nest harvested on 19 July, 8 September and 1 November were measured for the parameter R, P and their respective weight (Table 5.31). There is a significant difference in the mean weight of nest harvested in each season ($F_{2, 173} = 16.47$, $P < 0.05$). All the nests harvested in 19 July were built during the heavy moulting period between May and June. These nests were small and light. On the other hand, the mean weight for nests harvested on 8 September were highest because they comprised the first batch of nest built after the moulting season. Nests harvested on 1 November were the second, or replacement nest, and the mean weight was slightly lower than that of the previous batch constructed in September ($t_{116} = 3.71$, $P < 0.05$).

Table 5.31 The correlation of the mean weight and the P/R ratio for nests harvested from Lubang Salai at different seasons.

	19 July n = 32		8 September n = 61		1 November n = 82	
	Weight (g ± SE)	P/R ratio (unit ± SE)	Weight (g ± SE)	P/R ratio (unit ± SE)	Weight (g ± SE)	P/R ratio (unit ± SE)
Mean	6.0 ± 0.8	3.6 ± 0.4	8.7 ± 0.5	2.3 ± 0.1	7.3 ± 2.1	2.7 ± 0.2
Range	2.0 – 13.0	2.2 – 6.6	2.5 – 16.0	1.6 – 4.4	2.5 – 11.0	1.8 – 7.2
Correlation coefficient	– 0.74		– 0.42		– 0.46	

In addition, there is a significant correlation between the weight of the nest and the P/R ratio, where the weight is negatively correlated to the latter. This means that the heavier the nest, the smaller is the ratio. A smaller P/R ratio reflects a longer R, or a larger nest with a deeper crest. When nests from every season were categorised into their respective P/R ratio range, the seasonal variations were very distinctive as shown in Table 5.32. The mean weight of the nest in every month is different ($F_{4, 27} = 9.49$, $P < 0.05$ for 19 July, $F_{3, 57} = 4.61$, $P < 0.05$ for 8 September and $F_{4, 77} = 8.20$, $P < 0.05$ for 1 November). However, there is no difference in the mean weight if similar ratio category from different seasons were compared ($F_{2, 103} = 2.31$, $P > 0.05$ for the ratio range 2.0 – 2.9; $F_{2, 27} = 1.97$, $P > 0.05$ for the ratio range 3.0 – 3.9; $F_{2, 8} = 0.18$, $P > 0.05$ for the ratio range 4.0 – 4.9).

Nests harvested on 19 July varied tremendously in size and form. They comprised nests of various P/R ratios except for the range between 1.0 and 1.9, which is typical of large nests. Therefore, it is clear that nests constructed between April and July were small and shallow, with a small R-value. In contrast, 93.4% and 73.2% of nests harvested in September and November fell within the P/R ratio range of 1.0 to 1.9 and 2.0 to 2.9, respectively. The number of large nests was slightly reduced in the November harvest, indicating some decline in the nest building capability in subsequent breeding bout after multiple nest harvest.

Kang *et al.* (1991) reported that there was no difference in the final weight of three successive batches of nests in the same breeding season after repetitious removal. However, they noted fewer large nests appeared in successive harvests. Their study period corresponded with the third breeding bout as observed in Baram, and thus explains the fewer large nests owing to a slackening in the production of saliva.

Table 5.32 The average weight of nest from three harvests in Lubang Salai categorised into various P/R ratio ranges and its percentage.

P/R Ratio Range	19 July 1997				8 September 1997				1 November 1997			
	Mean (g ± SE)	Range (g)	n	Percentage (%)	Mean (g ± SE)	Range (g)	n	Percentage (%)	Mean (g ± SE)	Range (g)	n	Percentage (%)
1.0 – 1.9	—	—	—	—	9.9 ± 1.1	6.0 – 16.0	13	21.3	9.3 ± 0.7	8.0 – 11.0	8	9.8
2.0 – 2.9	8.4 ± 1.2	5.0 – 13.0	10	31.2	8.6 ± 0.6	2.5 – 14.5	44	72.1	7.7 ± 0.4	3.5 – 11.0	52	63.4
3.0 – 3.9	5.9 ± 0.8	2.2 – 7.5	12	37.5	8.5 ± 1.2	8.0 – 9.0	2	3.3	6.0 ± 0.9	3.0 – 9.5	16	19.5
4.0 – 4.9	4.6 ± 0.8	2.0 – 7.0	5	15.6	3.8 ± 0.7	3.5 – 4.0	2	3.3	4.4 ± 1.5	2.5 – 6.0	4	4.9
5.0 – 5.9	2.9 ± 0.3	2.8 – 3.0	2	6.3	—	—	—	—	—	—	—	—
6.0 – 6.9	2.8 ± 0.5	2.4 – 3.2	3	9.4	—	—	—	—	6.0 ± 0.8	—	2	2.4

5.8 CONCLUSIONS

The parameter D served as a good indicator for initial nest building activities. Nest construction begins in a form of thin flimsy crescentic patch of saliva sticking to the cave wall. More saliva is added until a rim is shaped, and this rim continues to extend until it reaches a size sufficiently large to accommodate two swiftlets. In contrast, the initial foundation will not be enlarged if nest building activity has slackened, or any crest formed.

Parameters R and P are good indicators for measuring the rate of nest building. The higher the R-value, the deeper is the crest and *vice versa.* There was a significant difference in the rate of nest building recorded at different months of the year. The rate of nest building was reduced between April and July. Then, a faster and more dynamic nest building activity was noticed at the beginning of August, which lasted until March the following year.

Nests removed during the third breeding bout were not rebuilt at once. Subsequent re-deposition was slow, and extended over a long period. These nests remained small throughout this period, and failed to form any deep nest crest. Such feeble nest foundations lacked a strong support. They usually fall off by themselves before the beginning of succeeding breeding bout, caused by the dampness in the cave that deteriorated the nest cement. The mean interval from nest removal in April to the subsequent lay was 142 days, or approximately 5 months. This interval was very long because of a lessening in nest building activities and the onset of the heavy moulting period between May and June.

In contrast, all nests removed in September were rebuilt immediately, and the re-deposition at all nesting sites was simultaneously. Re-building rate was 100%. The interval from nest removal to subsequent clutch during the first breeding bout varied, and depended particularly on the previous breeding performace and endurance. Any pairs that did not produced a clutch, or failed to raise a brood in the third breeding bout was in a better condition to breed in subsequent season. The mean of this interval was 74 days for any pairs that have successfully raised a brood in the previous breeding bout, and 36 days for pairs without any successful breeding.

A favourable breeding season was exhibited between August and March. There was a faster rate of nest building compared to the third breeding bout. Furthermore, there was a difference between the size and weight of nests constructed at different months of the year. Nests constructed between April and July were small and shallow, with a high P/R ratio. On the other hand, nests constructed between August and December have more large sized, or heavier nests. Nevertheless, repeated harvests reduced the number of large nests.

Chapter 6

Comparative Studies

6.1 INTRODUCTION

Of all the five species of swiftlets found in Sarawak (Smythies, 1960), several species can normally be found within a huge cave system with each having very specific niche (Medway, 1960). However, unlike the Gomantong cave in Sabah, there is not a single cave in Sarawak that is co-occupied by both Black-nest Swiftlets (*Aerodramus maximus*) and White-nest Swiftlets (*A. fuciphagus*). However, two other species of swiftlets can be found sharing a cave system among the edible-nest yielding caves. These species are the Mossy-nest Swiftlets (*A. salanganus*) and the White-bellied Swiftlets (*Collocalia esculenta*), which are locally referred as "*sarang lumut*". The lack of the echolocation capability has restricted *C. esculenta* to roost and nest near the light sections near the cave entrance where vision is not impaired. Although *A. salanganus* can echolocate and roost in the interior darkness of a cave, the soft consistency of their nest cement only allows them to nest on ledges or irregularities for additional support (Medway, 1966; Francis, 1987b). Therefore, there is some degree of niche separation between these species in the cave. Furthermore, the foraging pattern and feeding areas also differ (Medway, 1962c; Harrisson, 1974), and there is also some segregation in the type of insects food preferred (Lourie & Tompkins, 1998 in press).

In middle Baram, *A. salanganus* and *C. esculenta* are both encountered commonly and they can share the same roosting cave as *A. fuciphagus*, although the former is absent in both Lubang Salai or Lubang Beruang. The breeding biology and ecology of the mossy nest species is of great importance because they are found abundantly in all caves where the edible nest swiftlets have vanished because of over-exploitation. Therefore, there is great potential to make use of these species as surrogate parents in attempt to reintroduce the edible swiftlets back to their former habitat. For this undertaking, the smaller *C. esculenta* is more suitable than *A. salanganus* for several reasons. Firstly, *C. esculenta* is relatively more abundant than *A. salanganus*, occurring in large congregated colonies rather than as groups of scattered nests. Secondly, *C. esculenta* is known to readily occupy man-made structures such as tunnels, and inside, or along the eaves of buildings (Medway, 1961a). In Java, Indonesia, *C. esculenta* has been widely used to establish edible nest swiftlets in buildings (Nugroho & Whendrato, 1994; Nugroho *et al.*, 1994; Mardiastuti, 1996; Nugroho & Whendrate, 1996). For this reason, this species could be used to spearhead the establishment of "swiftlets farming" in Sarawak, as a secondary strategy for conserving the edible nest swiftlets.

Therefore, this chapter aims to to investigate the natural breeding periodicity of *C. esculenta* in their natural habitat, and to compare the timing of each bout of breeding with that of *A. fuciphagus*. The annual breeding periodicity of *C. esculenta* in three colonies is described in Section 6.2.1, while the incubation and fledging period is shown in Section 6.2.2. The cross-transfer experiment to investigate the best method and most suitable time to undertake such transfers is presented in Section 6.3.

6.2 COMPARATIVE STUDY OF *COLLOCALIA ESCULENTA*

6.2.1 Annual Breeding Periodicity

There was a marked difference between the breeding periodicity among the three colonies of *C. esculenta* observed in this study. The colony in Lubang Salai (Figure 6.1) showed recurrent patterns of sporadic breeding without any particular synchronisation. When the colony was initially marked in April, 62.5% of nests contained at least one egg, but most had two. The number of eggs laid throughout this month decreased sharply, and all egg laying ceased in May. An obvious non-breeding phase was observed between May and early July, in which all marked nests inside the cave contained neither eggs nor nestlings (Figure 6.2). These empty nests began to deteriorate, as nesting materials decayed and started to fall off. However, several frail nests were reused after minor repairs in early June. The bases of these nests were reinforced with new salivary secretion and fresh vegetable nesting materials were added. The first egg of the second breeding bout was laid on 19 July and the breeding reached its peak by early August. Even then only 50% of all the 36 marked nests contained eggs while the remainder were in a state of deterioration and had yet to be rebuilt.

Another small bout of breeding was observed in mid-October (Figure 6.1). Five out of 29 nests contained two eggs, two nests contained two nestlings each, while the remainder were empty or had fallen off. Among the five nests with eggs, three were empty since the last breeding in 14 June. This suggested an inter-clutch interval of 116 days or 4 months. The other two nests produced the second clutch 35 days after the last brood fledged in 3 September. From July until February, some of the marked nests inside Lubang Salai contained eggs or nestlings of various stages (Figure 6.2), suggesting that breeding occurred in a rather sporadic manner with no evidence of synchrony.

In contrast, the colony inside Lubang Ngawai had a clearly defined egg laying phase representing more synchronisation in breeding (Figure 6.3). The breeding periodicity in Lubang Ngawai exhibited a general pattern of three breeding bouts in a year with the first bouts in September followed by a subsequent bout in January and another in April or May. When the

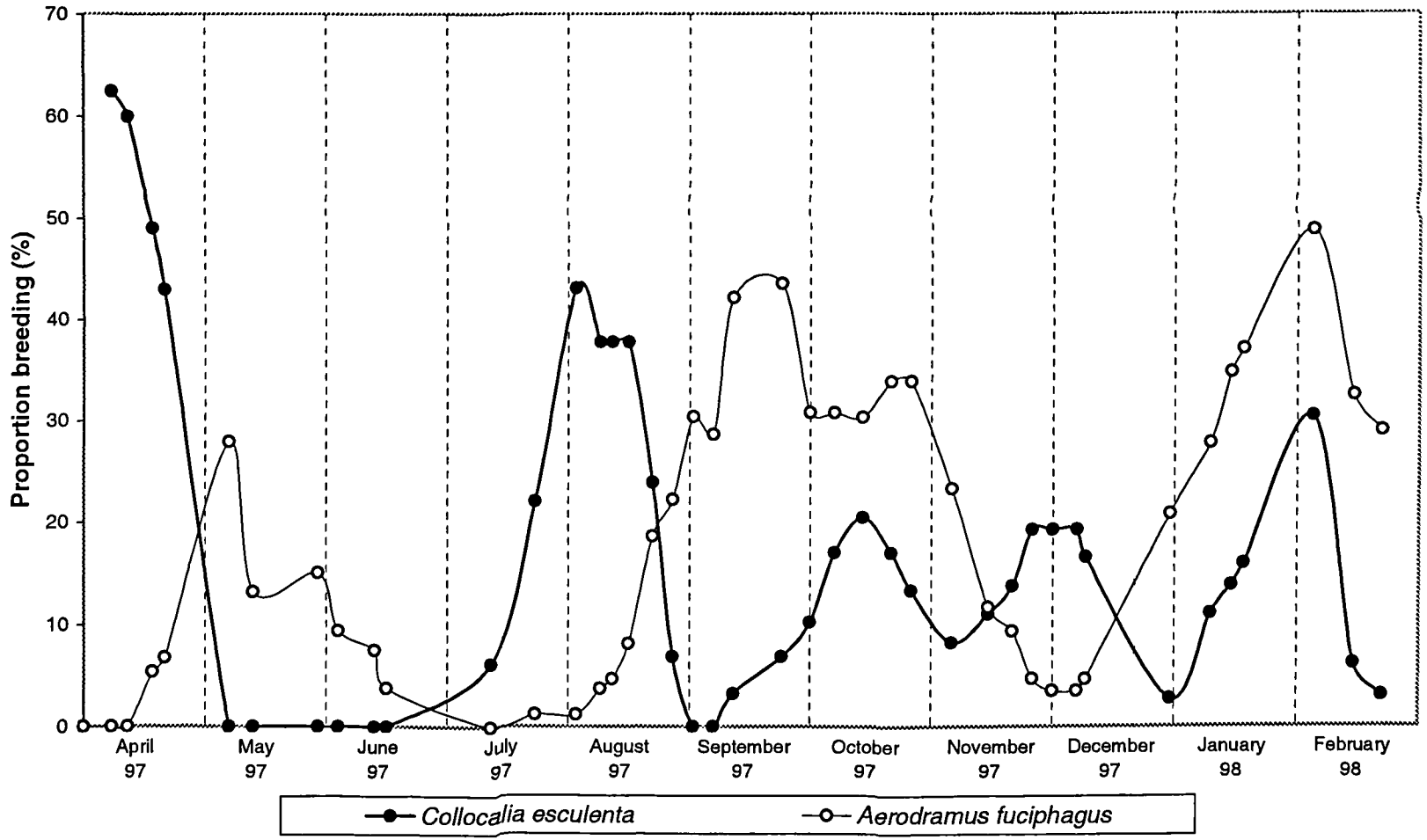

Figure 6.1 Comparison of the proportion breeding for *C. esculenta* and *A. fuciphagus* at Lubang Salai.

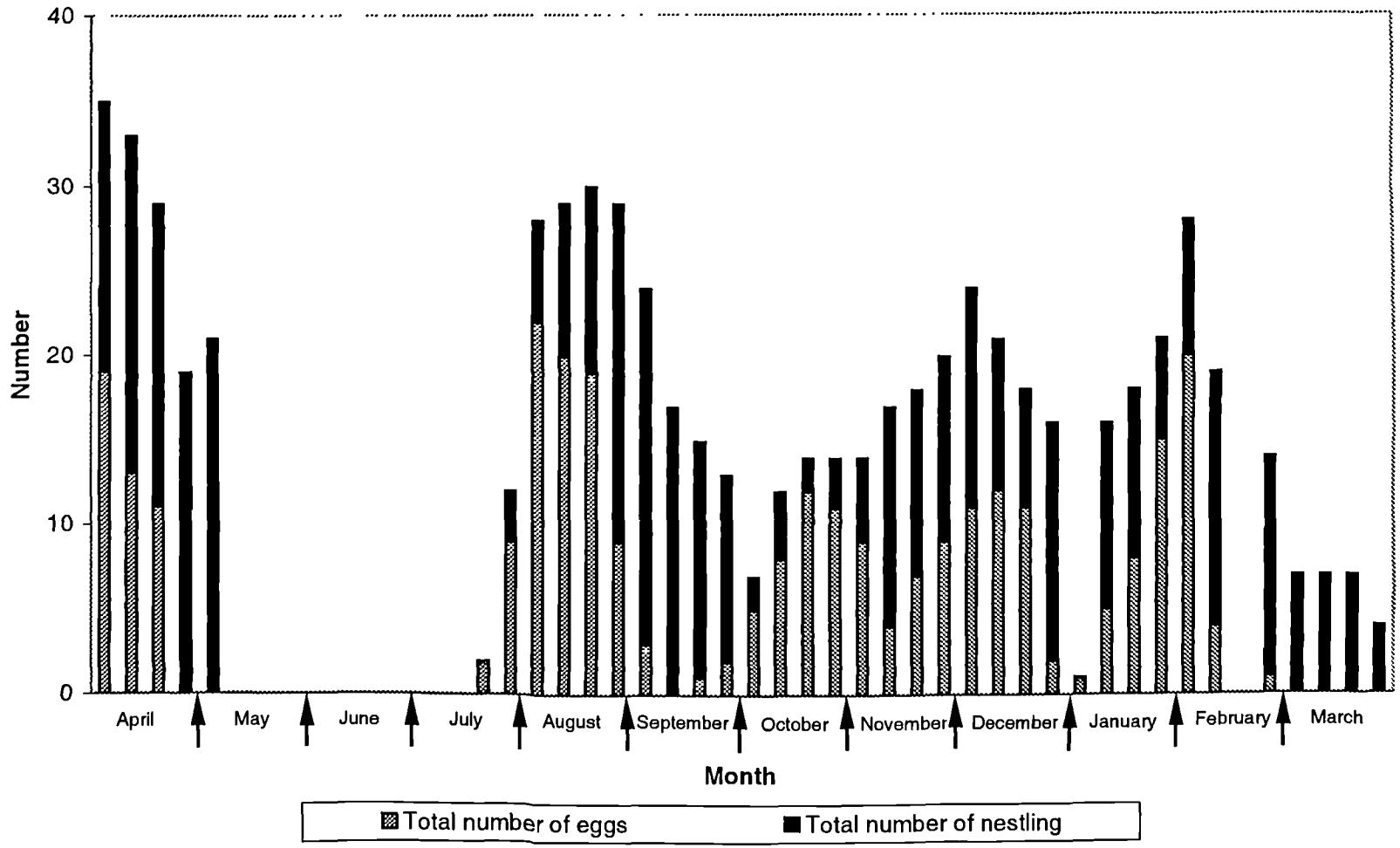

Figure 6.2 Total number of eggs and nestling of *C. esculenta* at Lubang Salai.

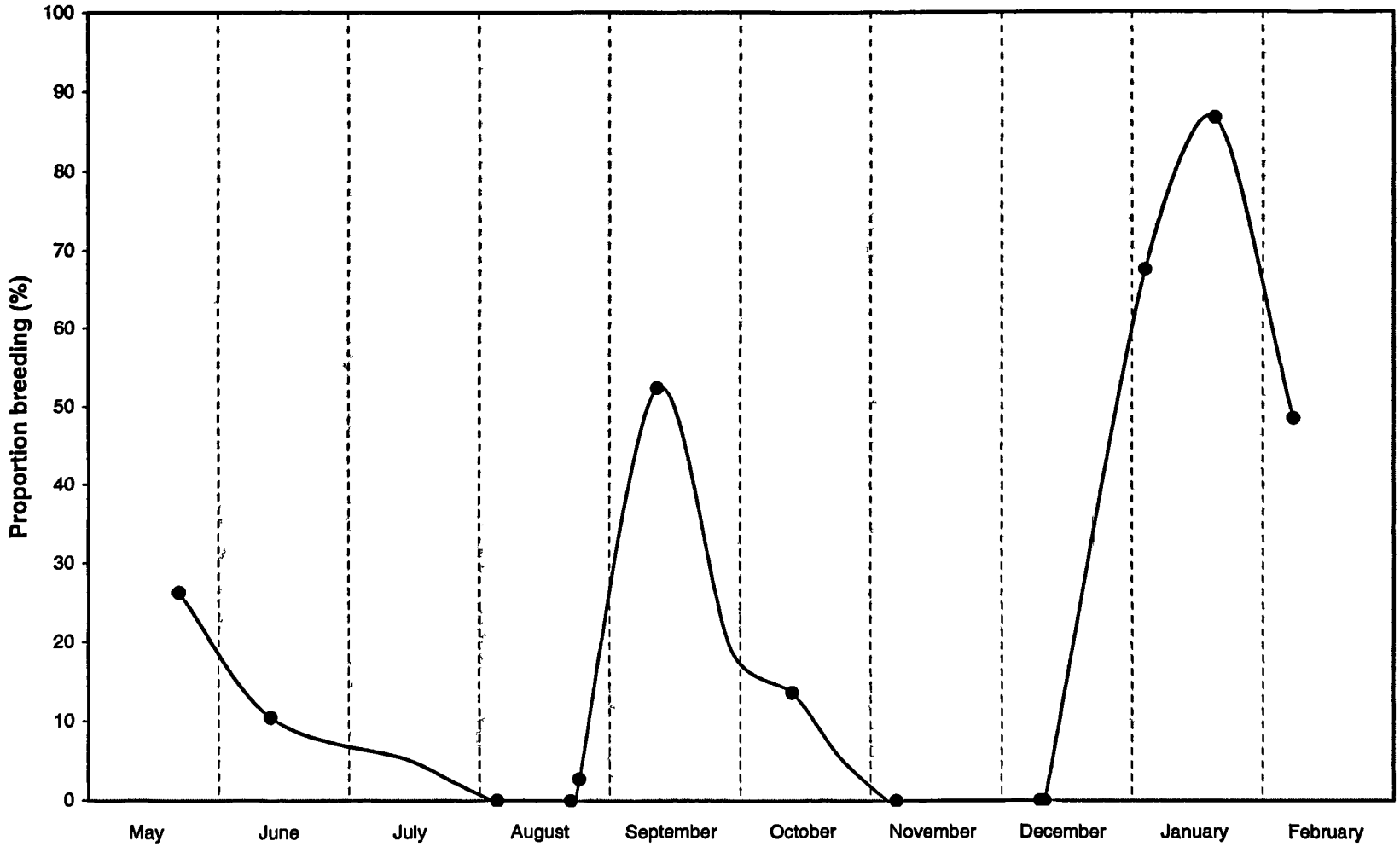

Figure 6.3 The proportion breeding of *C. esculenta* at Lubang Ngawai from June 1997 to February 1998.

nests were marked, 26% already contained eggs and no more were laid after that. The second bout of breeding was recorded in September, where 53% of eggs were laid within the first three weeks of that month, although one pair bred early in August. The proportion breeding subsequently declined until the third breeding bout was observed in January the following year. Because the majority of these nests were attached to a relatively smooth and sloping surface on the wall, most of them dropped off after the young had fledged. A *C. esculenta* colony in Peninsular Malaysia was also reported to exhibit three short breeding periods too with the egg-laying concentrated in April and declined slowly through May, June and July (Hails & Turner, 1985).

The colony of *C. esculenta* in Lubang Beruang contained about 300 to 400 breeding pairs that congregated their nests on a small ceiling area near the entrance. All the nests from this colony were destroyed by the owner during a nest harvest in April 1997. Some 80% to 85% of these nests contained nestlings of various stages but mainly Stage-5 and Stage-6. After their destruction, a well-defined synchronisation in breeding bout was noticed in early July (Figure 6.4). Two major egg laying periods were recorded between June 1997 and February 1998. The first bout of breeding occurred in early July, when 80% of the nests had at least one egg. Fewer eggs were laid after the first week of July. In contrast, many nestlings at different stages were present in the nests as the eggs began to hatch (Figure 6.5). From September until mid-October, the nesting site was completely silent. Most nests were in a state of semi-decay, or deteriorating. Not a single adult was seen flying out of the cave during routine checks on the site, indicating no incubation or nest building. A second bout of breeding occurred in November, for which the whole colony simultaneously began repairing and rebuilding their nests in early October. At this time of the year, many adult swiftlets were seen bringing nesting materials in and out of the cave during the day. The first egg was laid on 16 October but most eggs were laid in November, with 71% of pairs having laid by the end of November.

The three colonies of *C. esculenta* exhibited different timing for each bout of breeding. The asynchrony in breeding observed in Lubang Salai could arise from the same factors that contribute to the sporadic breeding patterns of *A. fuciphagus*, namely dampness and premature fall of nests. Nevertheless, the profiles of each breeding peak in 1997 were similar, except that the peaks for *A. fuciphagus* were delayed by about a month (Figure 6.1). Observations in Lubang Beruang suggested that the whole breeding profile could be delayed by premature termination of the early breeding bout as, happened in April. As with *A. fuciphagus*, the lay of the first egg was postponed by approximately one month when newly completed *C. esculenta* nests were destroyed, forcing the pair to rebuild a new nest. As such, this manipulation provides a possible means to defer and manipulate the timing of egg laying of *C. esculenta*, in order to synchronise it with *A. fuciphagus*.

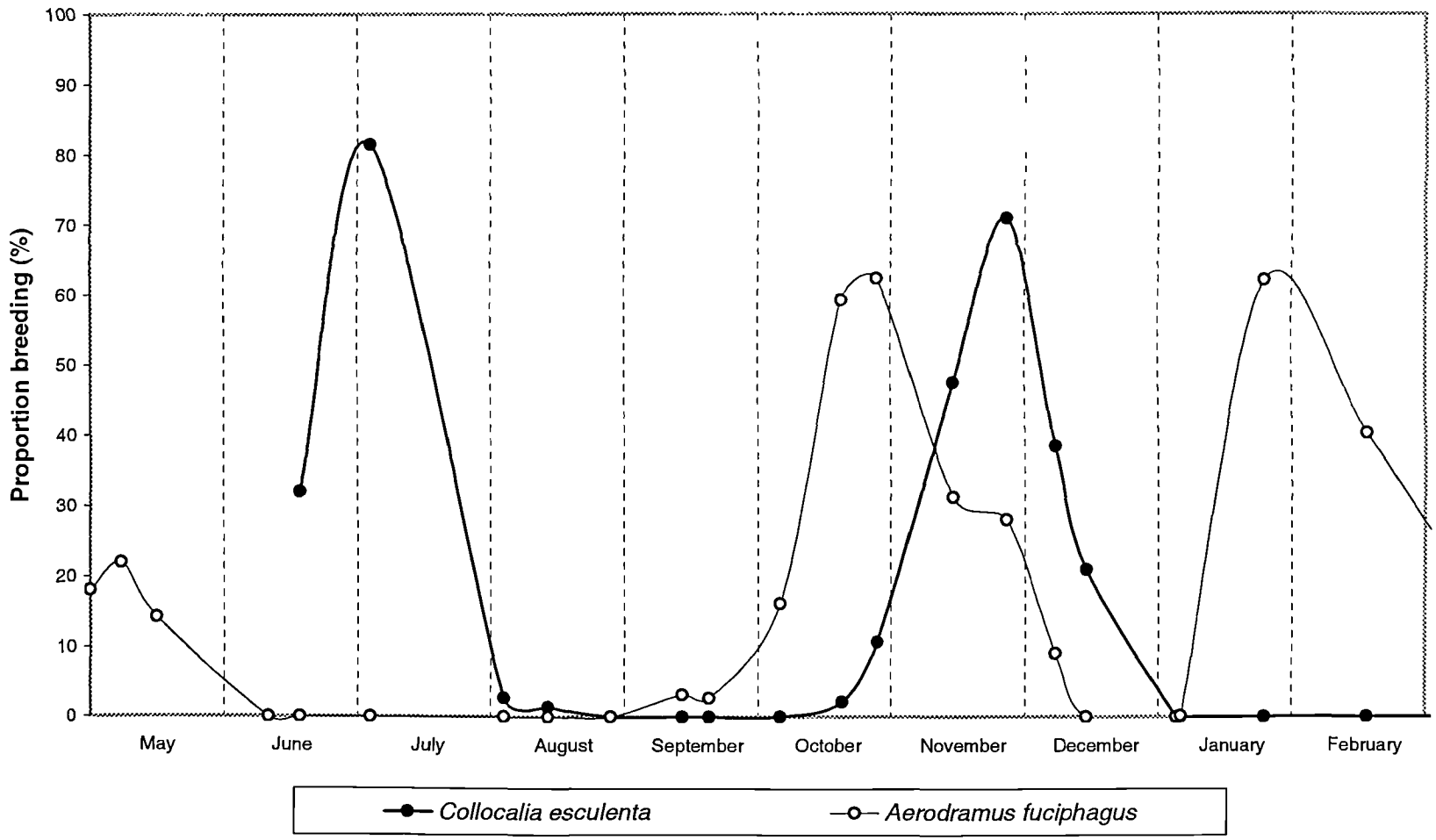

Figure 6.4 Comparison of the proportion breeding for *C. esculenta* and *A. fuciphagus* at Lubang Beruang.

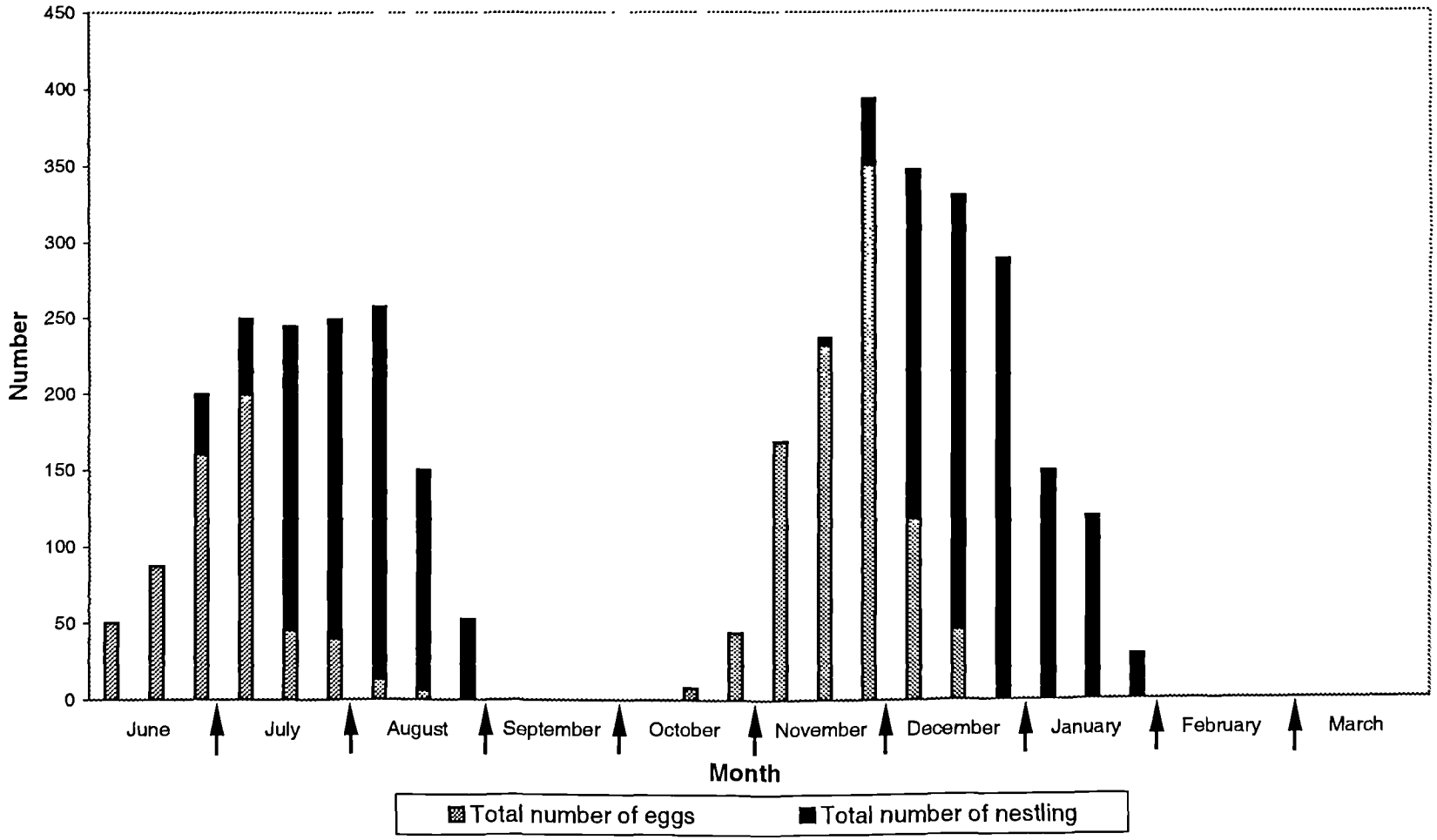

Figure 6.5 The total number of eggs and nestlings of *C. esculenta* at Lubang Beruang.

6.2.2 Incubation And Fledging Periods

The incubation and fledging period of *C. esculenta* is shown in Table 6.1. Its smaller egg required an average of 22 days to hatch, much shorter than the eggs of *A. fuciphagus* (t_{24} = 5.57, $P < 0.05$). The incubation period recorded in this study did not vary significantly (χ^2 = 0.06, df = 1, $P > 0.05$) with the mean of 21.5 days incubation period reported for *C. esculenta* by Medway (1962b) or Francis (1987a).

Table 6.1 The incubation and fledging period of *C. esculenta* from Lubang Salai recorded from beginning of June until November (mean ± SE).

	Incubation period n = 20	Fledging period single nestling n = 7	Fledging period two nestlings n = 8	Interval of 1st and 2nd egg n = 9
Average (day ± SE)	22 ± 2	37 ± 7	41 ± 3	3 ± 1
Range (day)	19 – 23	31 – 40	38 – 43	3 – 4

There was a slight difference (t_9 = 2.55; $P < 0.05$) in the fledging period between single nestling broods and for those nestlings with a sibling. Such disparity was not observed in *A. fuciphagus* brood. Single nestling brood took an average of 37 days to fledge while nestling with a sibling required an average of 41 days, but the ranges for both categories overlapped. The fledging period of *C. esculenta* was shorter than for *A. fuciphagus* nestlings regardless of single (t_8 = 6.12, $P < 0.05$) or two (t_{18} = 6.96, $P < 0.05$) nestling broods.

6.3 TRANSFER OF EGGS TO SURROGATE PARENTS

The natural phenomena of brood parasitism invovling surrogate parents is practised by at least seven families of bird (Gill, 1990), and the most familiar example being in the parasitic cuckoo (subfamily Cuculinae). A similar approach has been employed by some enthusiastic and enterprising people to convert colonies of *C. esculenta* and Linchi Swiftlets (*Collocalia linchi*) into remunerative colonies of *A. fuciphagus* (Nugroho & Whendrato, 1994; Nugroho *et al.*, 1994).

Throughout the study period, the inconsistent and unsynchronised breeding cycles of *A. fuciphagus* and *C. esculenta* only allowed a limited number of eggs to be transferred. Results of eleven transfers of *A. fuciphagus* eggs to *C. esculenta* nests between April and November in Lubang Salai are shown in Table 6.2. Six attempts were successful with *fuciphagus*-nestlings raised by their surrogate *esculenta*-parents surviving to fledge, representing 54.5% success rate. Five attempts were unsuccessful, with three cases of transferred *fuciphagus*-eggs being rejected or lost, and two cases from nestling fatality.

Table 6.2 The outcome of the transfering *A. fuciphagus* eggs into *C. esculenta* nests in Lubang Salai.

Nest	Date	Remark	No. of egg transferred	Original nest content
T3	26 Apr 97 11 May 97 8 Jul 97	Both *esculenta*-eggs destroyed. 2 chicks (stage 1 & 2). Fledged.	2 *fuciphagus*-eggs	2 *esculenta*-eggs
T4	26 Apr 97 11 May 97 6 Jun 97	Both *esculenta*-eggs destroyed. 2 chicks (stage 1 & 2). Fledged.	2 *fuciphagus*-eggs	2 *esculenta*-eggs
T5	26 Apr 97 6 Jun 97 18 Jul 97	Both *esculenta*-eggs destroyed. 1 chick (stage 1), the other egg lost. Fledged.	2 *fuciphagus*-eggs	2 *esculenta*-eggs
T1	5 May 97 6 Jun 97	Both *esculenta*-eggs destroyed. Empty (egg lost).	1 *fuciphagus*-egg	2 *esculenta*-eggs
T2	5 May 97 6 Jun 97	Both *esculenta*-eggs destroyed. Empty (egg lost).	1 *fuciphagus*-egg	2 *esculenta*-eggs
T5	8 Sep 97 13 Sep 97 1 Nov 97	1 punctured *esculenta*-egg included. 1 chick (stage 1). Fledged.	1 *fuciphagus*-egg	2 *esculenta*-eggs
T6	8 Sep 97 16 Sep 97 27 Oct 97	1 punctured *esculenta*-egg included. 1 chick (stage 1). Fledged.	1 *fuciphagus*-egg	2 *esculenta*-eggs
T7	8 Sep 97 13 Sep 97 27 Oct 97	The only *esculenta*-egg destroyed. 1 chick (stage 1). Fledged.	1 *fuciphagus*-egg	1 *esculenta*-egg
T8	8 Sep 97 13 Sep 97 20 Oct 97	1 viable *esculenta*-egg included. Both eggs presence. *fuciphagus* chick dead (stage 3), *esculenta* healthy (stage 5).	1 *fuciphagus*-egg	2 *esculenta*-eggs
T4	1 Nov 97 11 Nov 97 2 Jan 98	1 punctured *esculenta*-egg included. 1 chick (stage 1). Fledged.	1 *fuciphagus*-egg	2 *esculenta*-eggs
T9	1 Nov 97 11 Nov 97	1 punctured *esculenta*-egg included. Empty (egg lost).	1 *fuciphagus*-egg	2 *esculenta*-eggs

The results for ten transfers carried out at Lubang Ngawai are shown in Table 6.3. Four transferred eggs hatched, giving a hatching success of 40%. Three nestlings grew until fledging and one was lost. Six of transfer attempts failed because all the eggs were lost. However, the disappearance was of an accidental nature rather than a deliberate ejection, because all the transferred eggs were incubated for at least ten days before they were lost. This proved that the cross-fostering attempts were very successful in deceiving the surrogate parent. In addition, there appeared to be no difference in the outcome of various transfer techniques, because nests that had two *fuciphagus*-eggs substituted suffered the same losses as nests with only one *esculenta*-egg substituted and the other one punctured.

Table 6.3 Experimental attempts and the outcome of the transferred *A. fuciphagus* eggs into *C. esculenta* nests in Lubang Ngawai.

Nest	Date	Remark	No. of egg transferred	Original nest content
TN1	8 Sep 97 17 Sep 97 20 Sep 97	Both *esculenta*-eggs destroyed. 2 *fuciphagus*-eggs present. Empty (egg loss).	2 *fuciphagus*-eggs	2 *esculenta*-eggs
TN2	8 Sep 97 17 Sep 97 20 Sep 97	Both *esculenta*-eggs destroyed. Both transferred eggs presence. Empty (egg loss)	2 *fuciphagus*-eggs	2 *esculenta*-eggs
TN3	8 Sep 97 17 Sep 97 30 Sep 97	Both *esculenta*-eggs destroyed. 2 *fuciphagus*-eggs still present. Empty (egg loss)	2 *fuciphagus*-eggs	2 *esculenta*-eggs
TN4	8 Sep 97 17 Sep 97 30 Sep 97	Both *esculenta*-eggs destroyed. *fuciphagus*-egg still present. Empty (egg loss).	1 *fucihpagus*-egg	2 *esculenta*-eggs
TN5	8 Sep 97 30 Sep 97 18 Oct 97	Both *esculenta*-eggs destroyed. 1 chick (stage 2). Nestling loss.	1 *fucihpagus*-egg	2 *esculenta*-eggs
TN6	8 Sep 97 18 Sep 97	1 punctured *esculenta*-egg included. Empty (egg loss)	1 *fucihpagus*-egg	2 *esculenta*-eggs
TN7	8 Sep 97 30 Sep 97 29 Oct 97 11 Nov 97	1 punctured *esculenta*-egg included. 1 chick (stage 1). 1 chick (stage 6) Fledged.	1 *fucihpagus*-egg	2 *esculenta*-eggs
TN8	8 Sep 97 18 Sep 97	1 punctured *esculenta*-egg included. Empty (egg loss)	1 *fucihpagus*-egg	2 *esculenta*-eggs
TN9	8 Sep 97 30 Sep 97 29 Oct 97 11 Nov 97	1 punctured *esculenta*-egg included. 1 chick (stage 1). 1 chick (stage 6) Fledged.	1 *fucihpagus*-egg	2 *esculenta*-eggs
TN10	8 Sep 97 30 Sep 97 11 Nov 97 14 Nov 97	1 punctured *esculenta*-egg included. 1 chick (stage 1). 1 chick (stage 7). Fledged.	1 *fucihpagus*-egg	2 *esculenta*-eggs

All attempts involving the removal of both *C. esculenta* eggs and then replaced with two larger *A. fuciphagus* eggs were successful, with all *fuciphagus*-nestlings survived to fledge. On the other hand, both attempts to replace a 2 eggs clutch with a single *fuciphagus*-egg failed to deceive the surrogate parents. The loss of these replacement eggs might be purely coincidental but this small sample did not allow any statistical testing to verify this observation. Another experimental treatment was the substituting one *esculenta*-egg with one *fuciphagus*-egg while the other *esculenta*-egg was punctured but remained in the nest. For this, only one out of six attempts failed to hatch, resulting in 83% success rate.

For the transfer attempt on nest T8, the *esculenta*-egg left together with one *fuciphagus*-egg was not punctured, and both eggs hatched. However, the *fuciphagus*-nestling was found dead on 20 October after reaching growth Stage-3 while the *esculenta*-nestling had already attained Stage-5. There were no signs of external injuries on the dead nestling and it presumably died of starvation, with the larger *esculenta*-nestling apparently able to outdo its

smaller adopted sibling. Larger nestlings or those capable of attaining a favourable nest position such as the centre (in a cup-shaped nest) have a higher chance of being fed (Bryant & Tatner, 1990). Another possibility is that the surrogate parents are able to distinguish the adopted *fuciphagus*-nestling from its own offspring when one of each are present in the same nest and give preference to the latter. Lotem (1998) suggested that *Apus apus* parents were able to make active decisions regarding food provision rather than feeding nestlings on the basis of greater begging behaviour.

None of the nestlings raised by the surrogate parents could be monitored after they fledged. There were no signs of the *A. fuciphagus* nestlings raised in Lubang Ngawai even after a long wait inside the cave in the evening of the day the last nestling was seen. However, two *A. fuciphagus* nests were later constructed near to the *C. esculenta* nest in Lubang Salai in November 1998. One was built adjacent to nest-T4, where three adopted nestlings had been raised, two nestlings in 6 June 1997 and another fledged on 2 Jan 1998. The other *A. fuciphagus* nest was constructed directly on top of nest-T5 where two *fuciphagus*-nestlings were raised, one on 18 July 1997 and another one on 1 November 1997 by a pair of *C. esculenta*. The R-value of this nest was approximately 1 cm with strands of mosses attached to the rim. Judging from the unique composition of the nesting materials it was obvious that a pair of *A. fuciphagus* was competing for the same nesting site with another pair of *C. esculenta*. It could only be assumed that the nestling raised from nest-T5 by the *C. esculenta* returned to their birthplace.

The success of such cross-fostering transfers is generally low but cross-transfer is not impossible to achieve. In Java, it was reported that any cross-transfer undertaking, usually involving hundreds of substitutions, is considered successful when 10 – 30% of the fledglings return to nest (Nugroho *et al.*, 1994). Experience from this experiment showed that there was a difficulty in obtaining large number of *A. fuciphagus* eggs at the appropriate time for transfer into *C. esculenta* nests. One possibile resolution is to synchronise the breeding of these two species. The egg laying phase of *C. esculenta* could be delayed by destroying their nest so that they are compelled to build a new replacement nest. Results from this study showed that if the nests were destroyed after the eggs were laid, then the swiftlets would not rebuild their nests until the subsequent breeding cycle (Table 6.4). Under this circumstance, the subsequent breeding would not commence for the next 98 to 114 days. However, egg laying could be delayed by 25 to 35 days with nest destruction before any clutches were laid. Two good examples are nest-T6 and nest-T7 that were subsequently used for transfer experiments and produced two *A. fuciphagus* nestlings. Hence, nest destruction should be done after the nest is near completion but before any eggs have been laid to achieve the desired aims.

Table 6.4 The experimentation on the removal of *C. esculenta* nest at various stages and their subsequent development in Lubang Salai on 9 August 1997.

Nest	Condition when removed	Date rebuilt	First egg	Interval from removal (days)
T6	completed, empty	10 August	3 September	25
T7	completed, empty	16 August	8 September	35
T10	completed, empty	20 October	11 November	94
T11	two eggs	27 October	15 November	98
T13	two eggs	11 November	1 December	114
T17	two eggs	11 November	20 November	103

6.4 CONCLUSIONS

The three colonies of *C. esculenta* observed in this study showed variations in the timing of each bout of breeding. The colonies in Lubang Beruang and Lubang Ngawai showed a better synchronisation in breeding than the colony inside Lubang Salai. In the latter case, the occurrence of protracted breeding was attributed to the same reasons as those noted for *A. fuciphagus*, which is the dampness in the interior of the cave that caused premature nest fall. The incubation period recorded for the smaller *C. esculenta* was 22 ± 2 days while the fledging period varied between broods. Single nestling broods required 37 ± 7 days to fledge while double nestling broods took 41 ± 3 days.

Although the incubation and fledging period of *C. esculenta* is shorter than *A. fuciphagus*, cross fostering of eggs could be performed with considerable success. *Collocalia esculenta* has been proven to be efficient surrogate parents of raising artificially adopted *fuciphagus*-nestlings. Food quality and compatibility of parental care were apparently not an immediate constraint. Problems may lie in the egg laying period of the two species, and in acquiring enough *fuciphagus*-egg for transfer into suitable *esculenta*-nest. However, the egg laying phase of *C. esculenta* could be delayed by approximately one month if newly completely nests were destroyed before any clutch was laid, forcing the pair to build another new nest. This provides a means to manipulate the breeding rhythm and synchronise the breeding of both species.

In every cross-fostering attempt, evidence indicated that it was important to wait until both eggs of the surrogate pair were laid, and the number of eggs in the *esculenta*-nest after such transfer must be the same as before. If only one *fuciphagus*-egg is to be transferred, then one *esculenta*-egg must be removed and the second one destroyed by micro-puncture. Otherwise, there is a high possibility that the *esculenta*-nestling could out-compete the adopted sibling. This technique could be used for translocation scheme either to caves where *A.*

fuciphagus colonies formerly existed, or to specially constructed buildings for "swiftlet farming".

Chapter 7

Chemical Composition Of Nest

7.1 INTRODUCTION

The glutinous material produced by the edible nest swiftlets for nest construction is secreted from a pair of sublingual salivary glands (Medway, 1962a). Despite the widely acclaimed medicinal and therapeutic properties, there is a paucity of scientific research on the chemical properties of the nest (Lau & Melville, 1994). Some early analytical work has shown that the basic chemical constituents of edible bird nest include protein, carbohydrate and small amount of minerals (Wang, 1921; Kathan & Weeks, 1969), as well as reported traces of arsenic (Banks, 1986).

Several contemporary studies had been carried out to demonstrate the purported medicinal benefits of the edible nest. For instance, edible nest mucoid has been used as a substrate to investigate viral sialidase activity (Howe *et al.*, 1960) and the haemagglutination inhibiting actions against influenza virus (Howe *et al.*, 1961). Isolation of the active inhibitor in its homogeneous form from crude serum is technically difficult and time consuming. Therefore, it is of great interest to find an inhibitory substance, generally referred to as the collocalia mucoid, present in a biological secretion from which they can be fractionated in a relatively pure form with comparative ease (Biddle & Belyavin, 1963).

A more recent discovery was the first avian epidermal growth factor (EGF)-like activity in partially purified swiftlet's nest extract (Ng, *et al.*, 1986; Kong *et al.*, 1987). It is suggested that this water-soluble glycoprotein with a complex protein composition might affect more than one physiological parameter to effect its purported medicinal properties. The swiftlet nest EGF-like protein appears to assist in the proliferation of epidermal and epithelial tissues, stimulation of DNA synthesis and cell division within the immune system. However, this substance is present in such minute quantities, or perhaps is so tightly bound to the salivary matrix that prolonged heating is required to release it. One milligram of nest is estimated to contain 2.23 nanograms of EGF (Kong *et al.*, 1987).

Despite these interesting discoveries, no study addresses the inter-specific or seasonal variations of edible bird nests. Cranbrook *et al.* (1996) pointed out that there is a need to investigate the chemical composition of swiftlet nests, and the relation to the taxon, or geographical source, as well as the seasonal variations. Beside the contrasting quantity of incorporated feathers, nests produced by *A. fuciphagus* and *A. maximus* have distinctive morphological differences in texture and consistency. Within the same species, there are

noticeable morphological variations among nests from different caves or geographical areas (Banks, 1937).

Therefore, the objective of this study was to investigate the intra-specific variations, if any, in the chemical composition among batches of *A. fuciphagus* nests constructed at different month of the year. Information on the seasonal quality of nests might be useful for the management planners. In addition, inter-specific differences in the chemical constituents of nests of three species, namely *A. fuciphagus*, *A. maximus* and *C. esculenta*, were compared.

In this chapter, I present a detailed analysis of the carbohydrate and protein composition of *A. fuciphagus* nests constructed at different months, and compared with nests of *A. maximus* and *C. esculenta*. The carbohydrate composition is detailed in Section 7.2.1, which is divided into two sub-sections. The sialic acid content of each sample is presented in Section 7.2.1.1, while Section 7.2.1.2 deals with the neutral and amino sugars. The protein composition is described in Section 7.2.2. The seasonal varations of the *A. fuciphagus* nests is examined in Section 7.3, while the inter-species comparison of the chemical constituents of nest materials is discussed in Section 7.4.

7.2 CHEMICAL CONSTITUENTS

It has been recognised that the salivary secretion of swiftlets consists of a mucin-liked glycoprotein. Glycoprotein is a type of protein containing carbohydrate covalently attached to its amino acid residues of a protein backbone (Hughes, 1983; Beeley, 1985). As such, the principle behind the analytical work of this study is to split the core structure of the glycoprotein molecule into various protein and carbohydrate units by acid hydrolysis. Each subunit released from the hydrolysis was then labelled with appropriate florescent labels (i.e. PITC, 2-AA & DMB) and isolated using high-performance liquid chromatography (HPLC). These methods were chosen because of their sensitivity, repeatability and accuracy.

The most abundant of *O*-linked glycosylation is the mucin-type linkage between *N*-acetylgalactosamine and serine or threonine (Carraway & Hull, 1991). The molecular linkage in the edible nest is *O*-glycosidic. In addition, the sugars most frequently found linked to serine and threonine is *N*-acetylgalactosamine (Hughes, 1983; Beeley, 1985). Wang (1921) reported that edible nests contain approximately 11.6% moisture, 10.3% nitrogen and at least 17.36% carbohydrate, and a diet of bird nest fails to supplement a ration adequate in all respects, except the source of protein, in feeding experiments on rats. Kathan and Weeks (1969) revealed that the composition of edible bird nest is 20% inorganic ash, 32.3% protein and 38.7% carbohydrate, which can be further broken-up into hexose (16.9%), hexosamine (12.5%), fucose (0.7%) and sialic acid (8.6%).

7.2.1 Carbohydrate

7.2.1.1 Sialic acids

Sialic acids are nine-carbon sugars that are predominantly *N*- and *O*-acyl derivatives of the α-ketopolyhydroxyamino acid, known as neuraminic acid (Sharon, 1975; Candy, 1980). Sialic acid is usually found in glycoprotein as the terminal sugar of oligosaccharides (Varki, 1992). The sialic acid released after mild acid hydrolysis of dried swiftlets nest samples was identified as *N*-acetylneuraminic acid (Neu5Ac), which corresponded with a distinctive peak at the retention time of approximately 8.5 minutes (Figure 7.1). Nests of all threes species analysed had a similar peak in their respective chromatogram (Figure 7.2 to Figure 7.7). Pozsgay *et al.* (1987) isolated a new sialic-acid derived compound from hydrolysate of edible bird's nest by ion-exchange chromatography. The formation of this compound, 4,8-Anhydro-*N*-acetylneuraminic acid, suggests that in the glycoprotein of edible bird's nest at least a portion of *N*-acetylneuraminic acid is acetylated at HO-4. However, this compound was not detected as a different peak in the HPLC chromatogram in this study.

The concentration of Neu5Ac from *A. fuciphagus* nests constructed at different months of the year is shown in Table 7.1. All successive nest samples collected in April, July and August were from the same marked sites and it was assumed that they were each constructed by the same pair of swiftlets. Although the concentration differed from one nest to another within each batch of nests, there was no seasonal variation between different batches of nest ($F_{3, 18} = 0.30$, $P = 0.82$) as illustrated in Figures 7.5 and 7.6.

Table 7.1 The concentration of *N*-acetylneuraminic acid from *A. fuciphagus* nests constructed at different months of the year in Lubang Salai.

Nest	Concentration (μmol per mg of dried nest)			
	April	June	July (1st nest)	August (replacement)
S 040	3.54	—	0.43	1.91
S 045	1.05	—	1.76	1.01
S 056	0.84	—	4.86	1.60
S 057	1.59	—	2.05	1.00
S 058	1.73	—	0.97	1.90
S 062	1.59	—	0.78	0.88
m 01	—	1.78	—	—
m 02	—	1.11	—	—
m 03	—	3.75	—	—
m 04	—	1.53	—	—
Mean ± SE	1.72 ± 0.78	2.04 ± 0.96	1.81 ± 1.32	1.38 ± 0.39

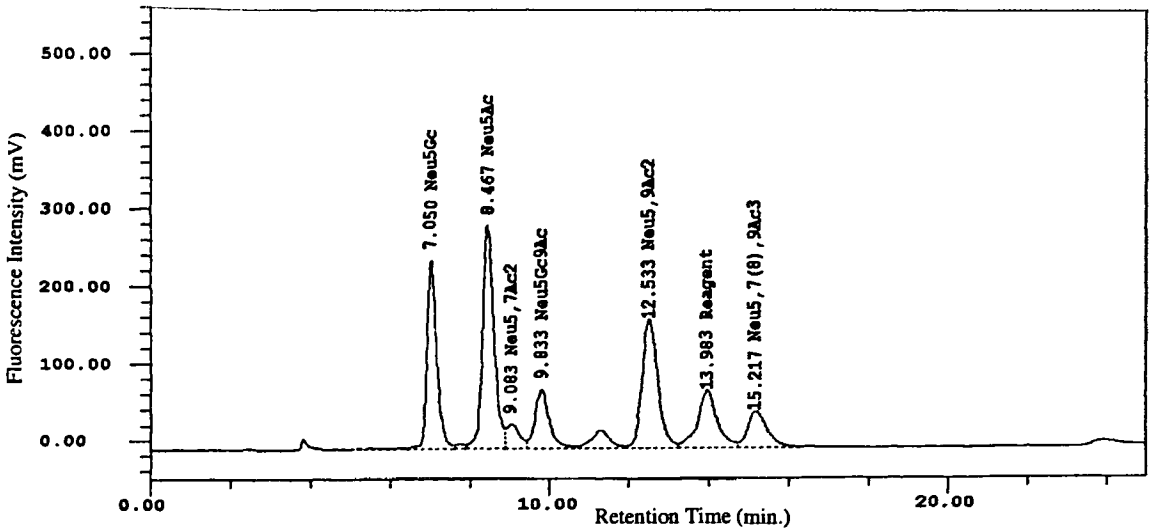

Figure 7.1 Chromatogram of the DMB derivatives of neuraminic acids standard mixture.
(Neu5Gc = *N*-glycolylneuraminic acid; Neu5Ac = *N*-acetylneuraminic acid; Neu5,7Ac2 = *N*-acteyl-7-*O*-acetylneuraminic acid; Neu5Gc9Ac = *N*-glucolyl-9-*O*-acetylneuraminic acid; Neu5,9Ac2 = *N*-acetyl-9-*O*-acetylneuraminic acid).

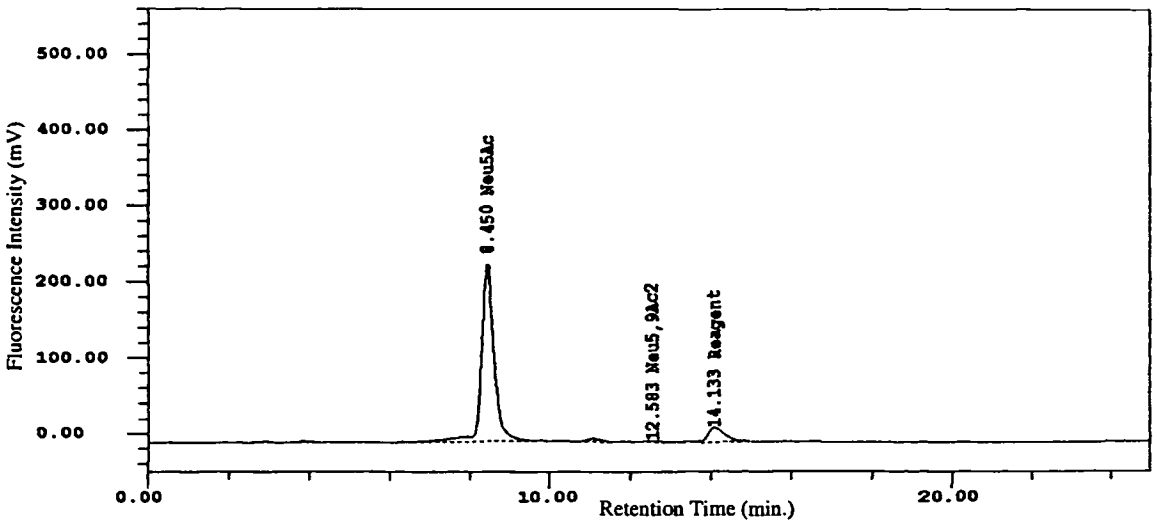

Figure 7.2 Chromatogram of the DMB derivatives of neuraminic acid for *A. fuciphagus* nest constructed in April 1997 (marked nest S045).

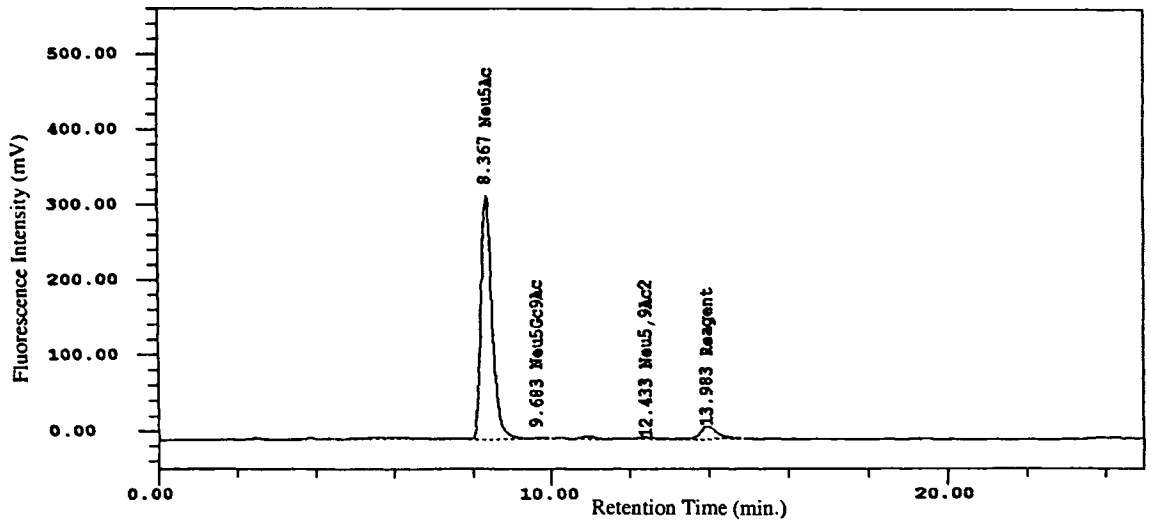

Figure 7.3 Chromatogram of DMB derivatives of neuraminic acid for *A. maximus* nest.

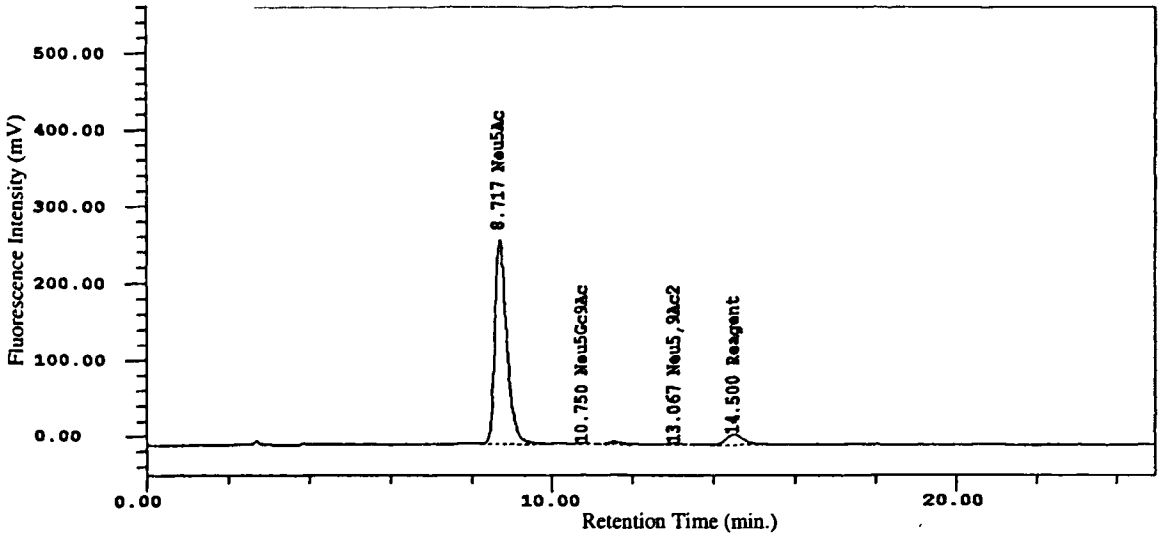

Figure 7.4 Chromatogram of DMB derivatives of neuraminic acid for *A. fuciphagus* nest constructed in June during the heavy moulting period or "*melaie*".

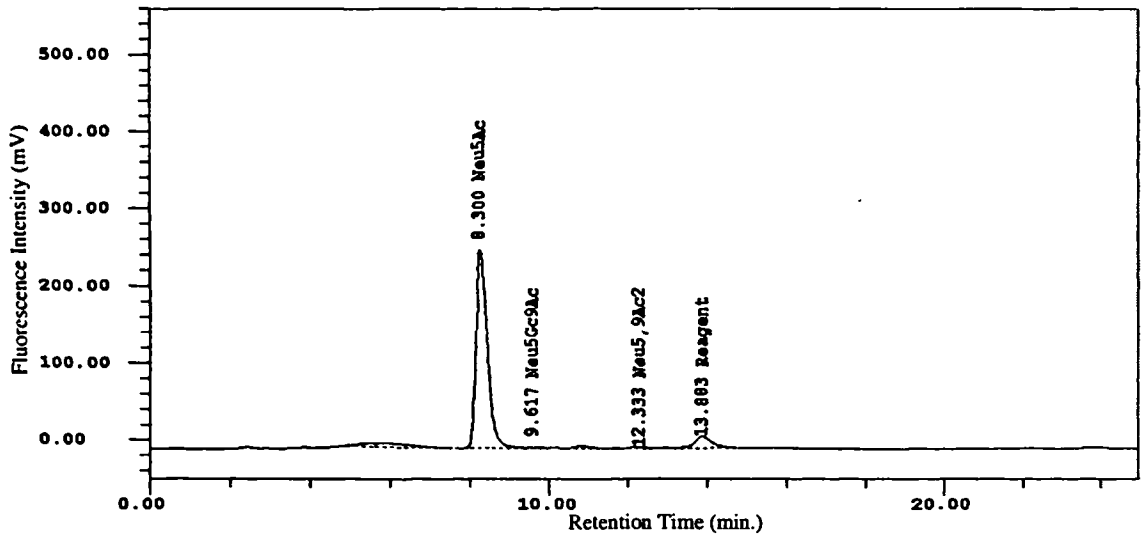

Figure 7.5 Chromatogram of DMB derivatives of neuraminic acid for *A. fuciphagus* nest constructed in July (marked nest S045).

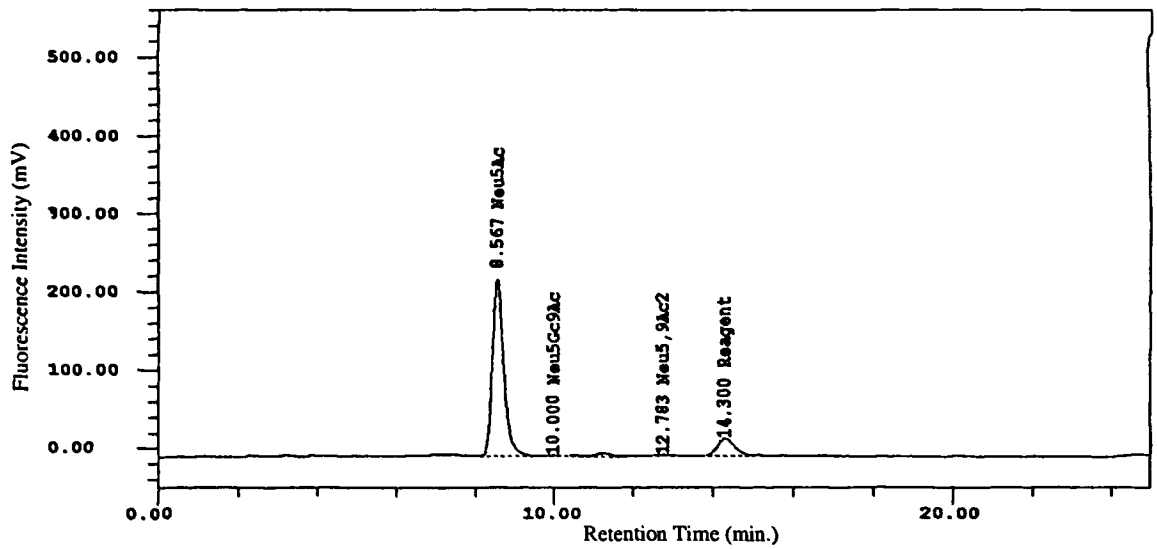

Figure 7.6 Chromatogram of DMB derivatives of neuraminic acid for replacement nest of *A. fuciphagus* constructed in August (marked nest S045).

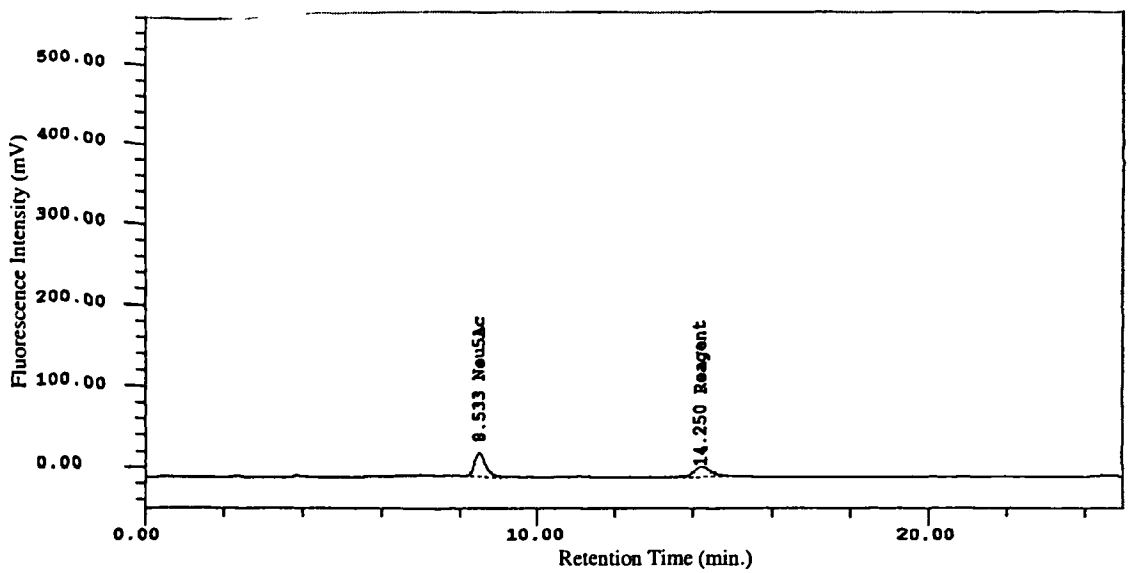

Figure 7.7 Chromatogram of DMB derivatives of neuraminic acid for *C. esculenta* nest.

The concentrations of Neu5Ac for *A. maximus* and *C. esculenta* nests (Table 7.2; Figures 7.3 and 7.7) show inter-species difference in the sialic acid content of the salivary secretion between these two species ($t_5 = 4.40$, $P = 0.003$). Similarly, there was a difference ($t_{13} = 5.24$, $P = 0.00007$) in the concentrations of Neu5Ac found in the nesting cement of *A. fuciphagus* and *C. esculenta*. However, nests produced by the two species of edible nest swiftlets, *A. fuciphagus* and *A. maximus*, did not show any difference ($t_7 = 0.83$, $P = 0.22$) in the concentrations of Neu5Ac with an overall mean of 1.71 ± 0.39 μmol/mg and 2.08 ± 0.70 μmol/mg, respectively.

Table 7.2 The concentration of *N*-acetylneuraminic acid for *A. maximus* and *C. esculenta* nests.

Species	Concentration (μmol per mg of dried nest)					Average
	unmark 1	unmark 2	unmark 3	unmark 4	unmark 5	
A. maximus	3.22	2.20	2.49	1.44	1.06	2.08 ± 0.70
C. esculenta	0.06	0.13	0.57	—	—	0.25 ± 0.23

7.2.1.2 Neutral and amino sugars

Two amino sugars and four neutral sugars were identified in the hydrolysate of all nest samples (Figure 7.9 to Figure 7.14). The amino sugars are, in sequence from shorter to longer elution time, glucosamine (GlcN) and galactosamine (GalN) with corresponding elution peaks at approximately 9 minute and 10 minute respectively in the standard monosaccharides solution (Figure 7.8). Three hexoses, namely galactose (Gal), mannose (Man) and glucose (Glu) were

identified from all nests sample in accordance to their respective elution sequence. The quantity of each monosaccharide for nest samples from three species of swiftlets analysed is shown in Table 7.3. Generally, the two hexosamines were the most abundant sugars found in the glycoprotein of edible swiftlet's nest. Galactose was always present in nests from all three species in relatively high concentration. On the other hand, there appeared to have been some disparities in the quantity of mannose and glucose in some samples. Fucose (Fuc), the only deoxyhexose identified in the hydrolysate, was only detected among nests sample from *A. fuciphagus* and *C. esculenta* at the elution time of approximately 27 minute but was absent in all *A. maximus* nests analysed (Figure 7.13).

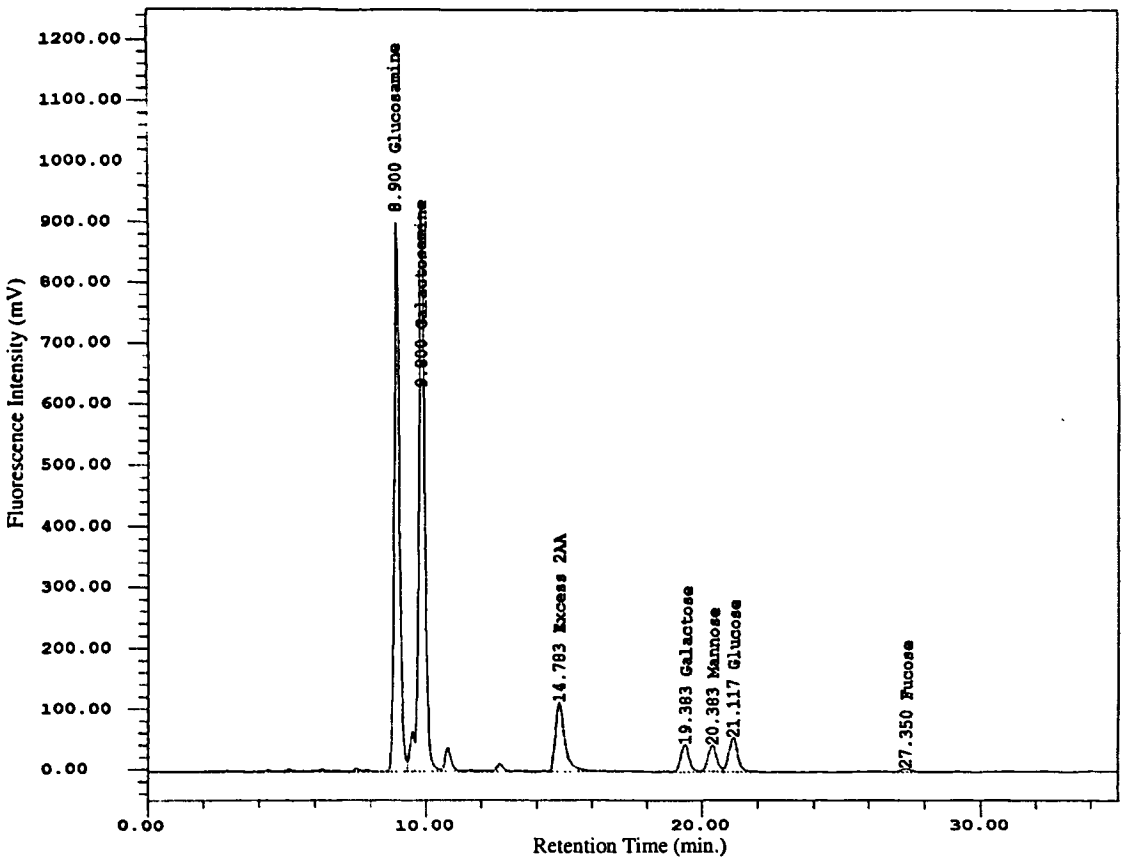

Figure 7.8 Chromatogram of 2-AA labelled monosaccharides from a standard solution. (Elution sequence: Glucosamine, Galactosamine, Excess 2-AA, Galactose, Mannose, Glucose and lastly Fucose).

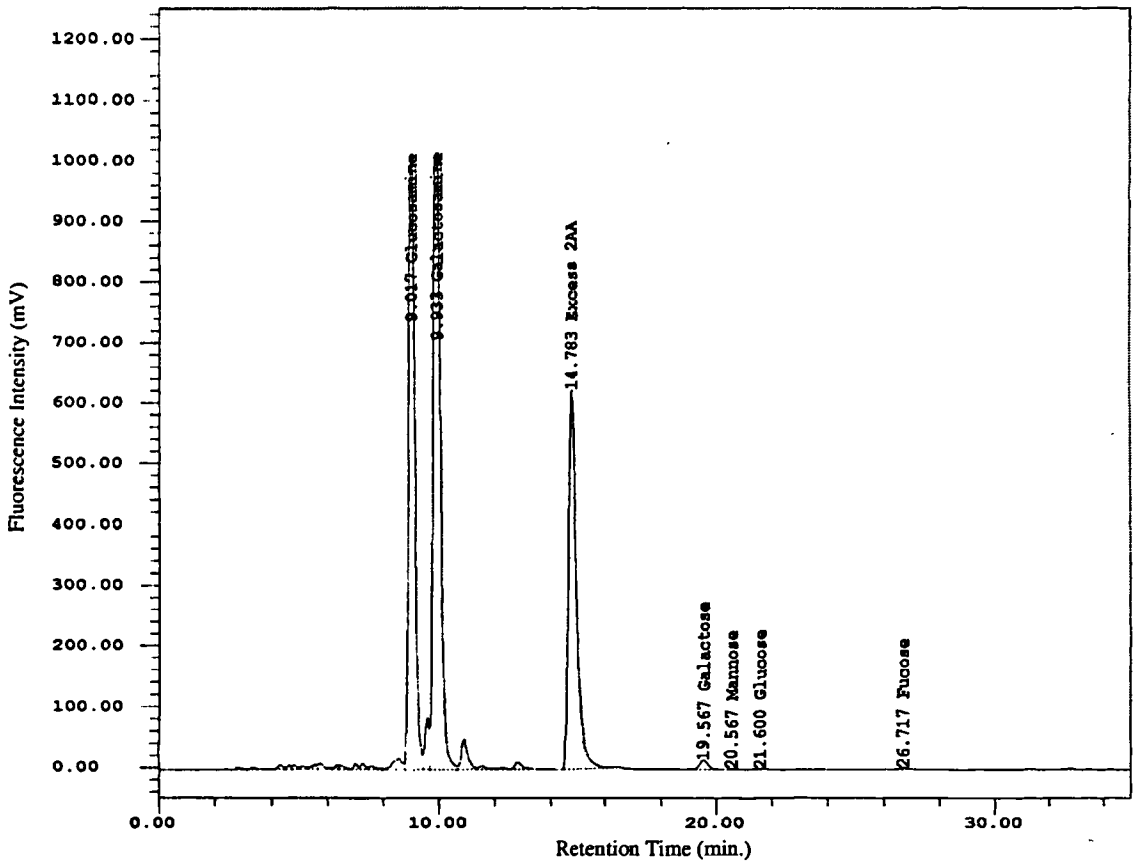

Figure 7.9 Chromatogram of 2-AA labelled monosaccharides for *A. fuciphagus* nest constructed in April (marked nest S 040).

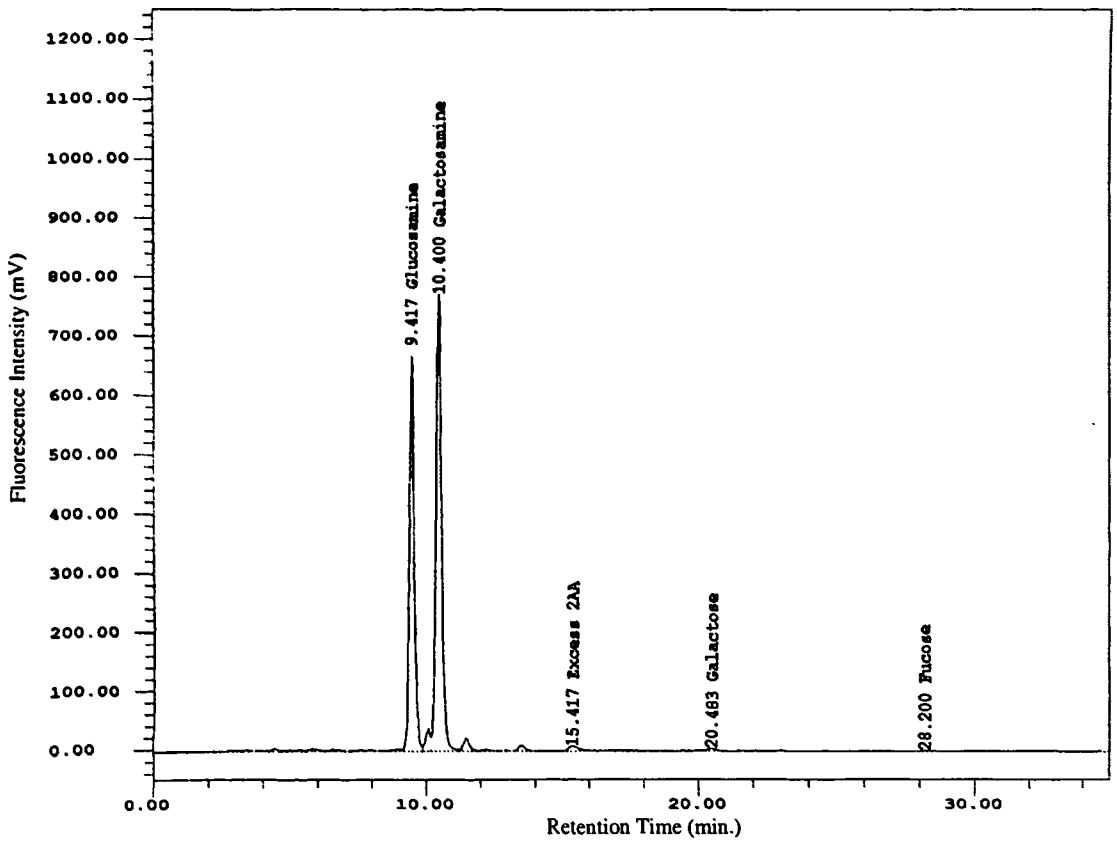

Figure 7.10 Chromatogram of 2-AA labelled monosaccharides for *A. fuciphagus* nest constructed in June during the heavy moulting period (unmarked nest).

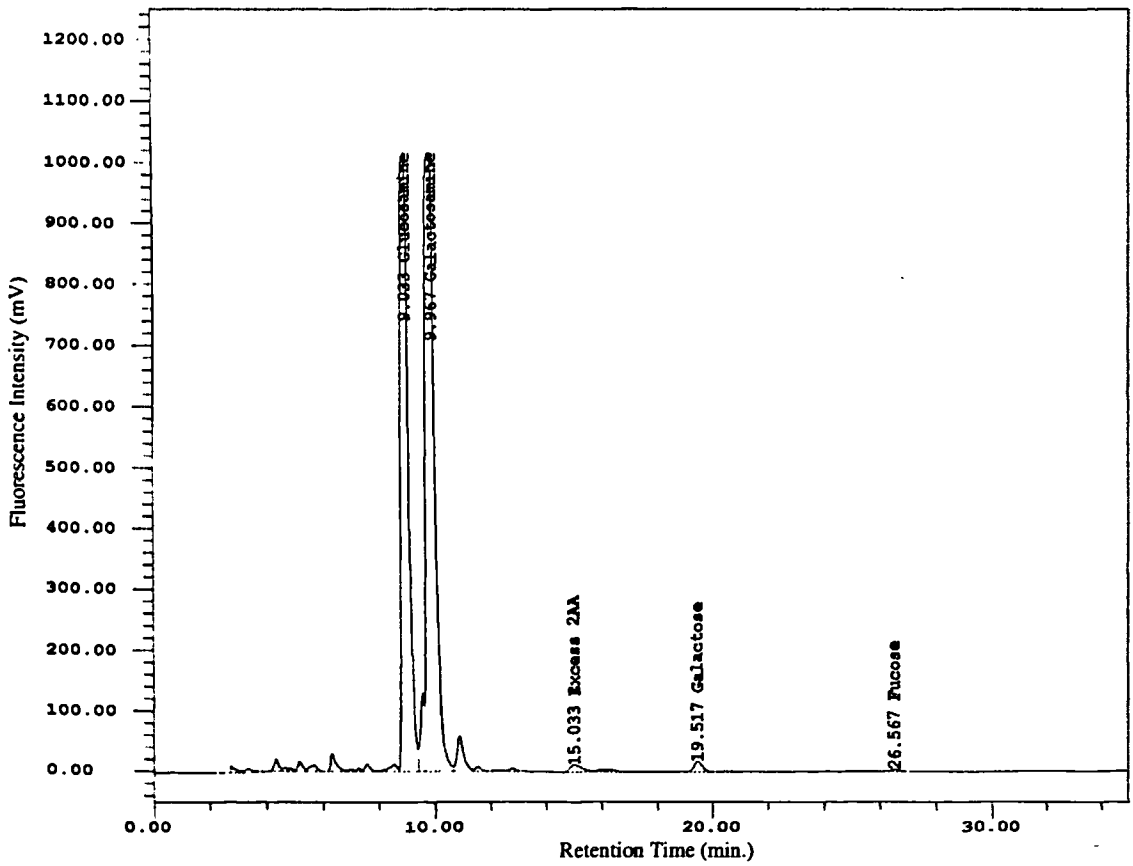

Figure 7.11 Chromatogram of 2-AA labelled monosaccharides for *A. fuciphagus* nest constructed in July (marked nest S 040).

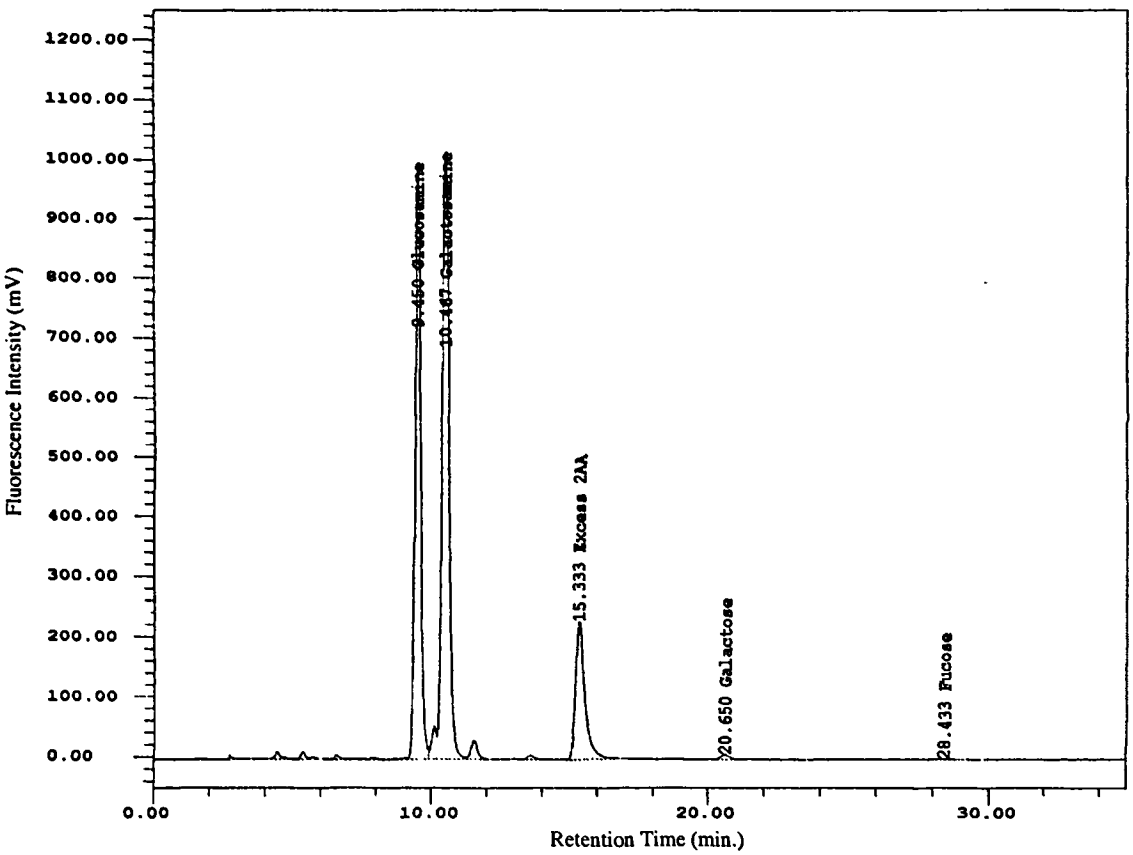

Figure 7.12 Chromatogram of 2-AA labelled monosaccharides for replacement nest of *A. fuciphagus* constructed in August (marked nest S 040).

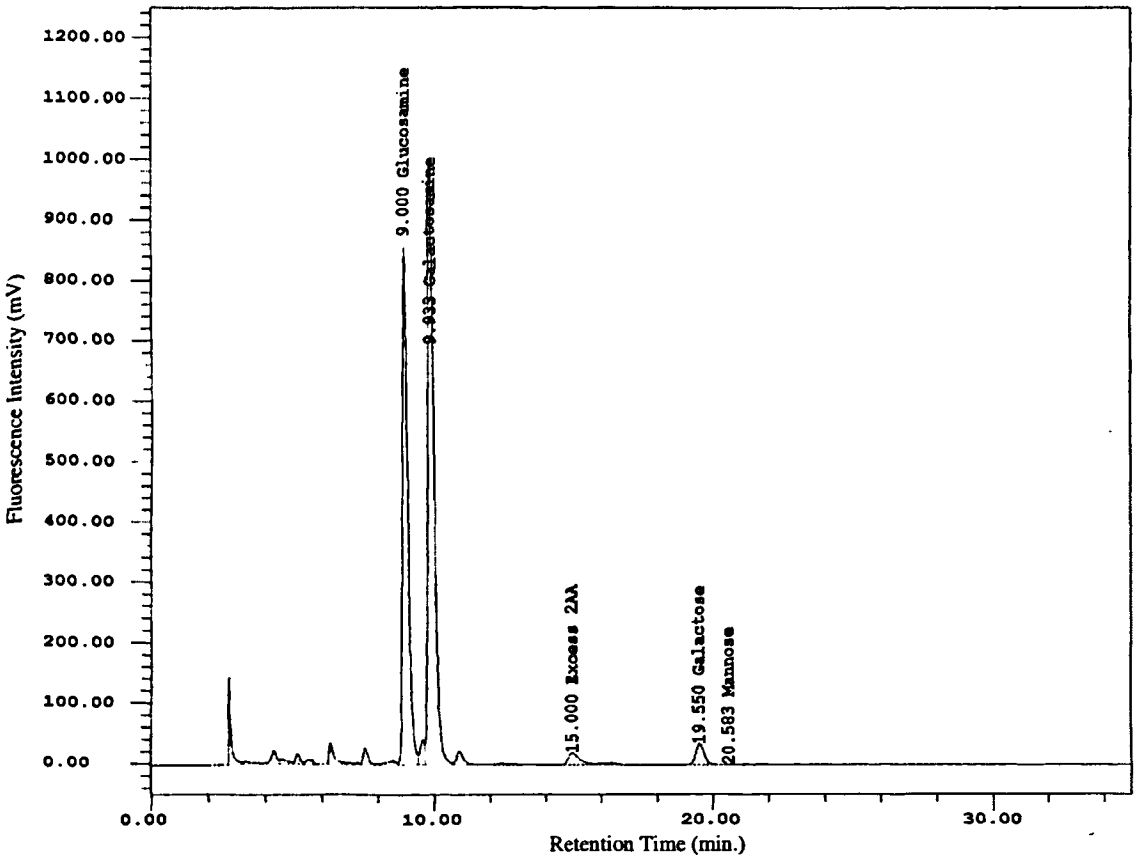

Figure 7.13 Chromatogram of 2-AA labelled monosaccharides for *A. maximus* nest.

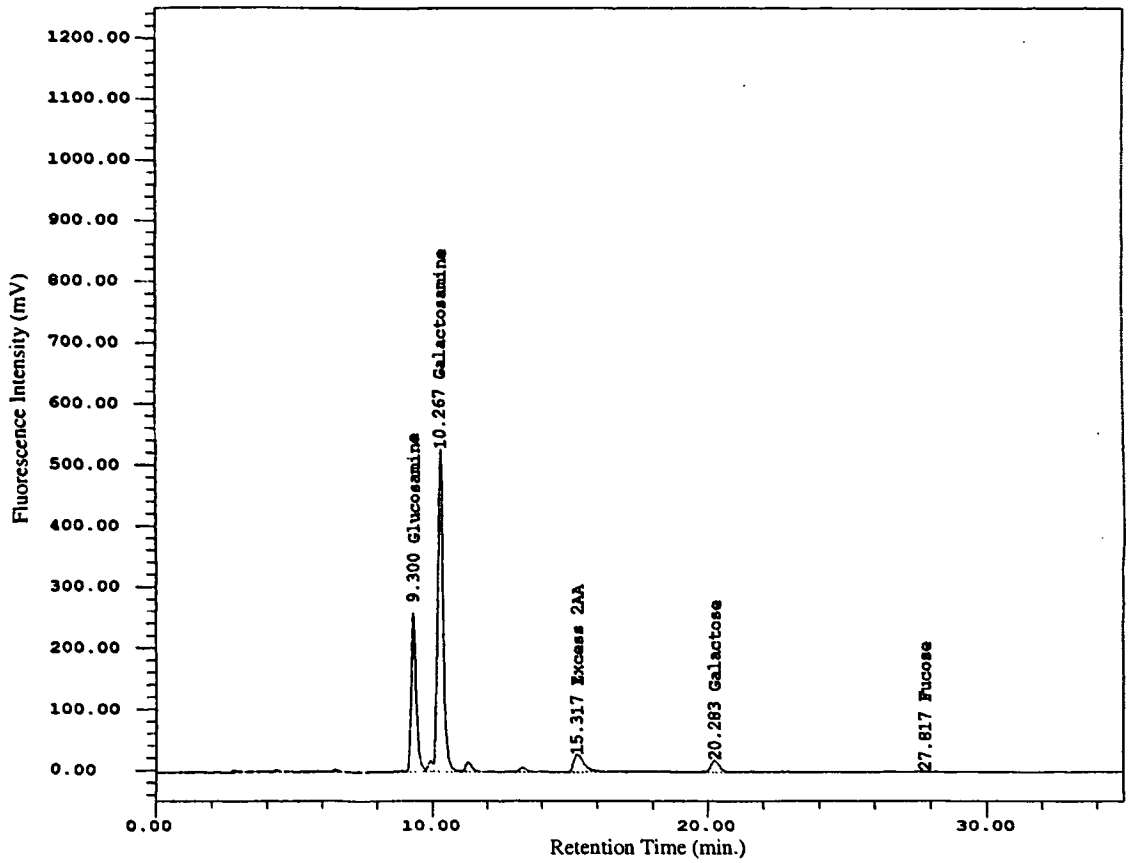

Figure 7.14 Chromatogram of 2-AA labelled monosaccharides for *C. esculenta* nest.

Table 7.3 The concentration of released amino and neutral sugars from hydrolysed edible nest samples produced by threes species of swiftlets.

Species	Month	Nest	Concentration (nmol per mg of dried nest)					
			Glucosamine	Galactosamine	Galactose	Mannose	Glucose	Fucose
Aerodramus fuciphagus	April	A 040	102.9	108.8	25.8	1.7	3.2	38.6
		A 045	19.3	39.7	66.8	3.4	1.4	14.8
		A 056	156.2	164.4	32.8	1.6	0.0	52.2
		A 057	60.8	70.1	13.5	0.0	1.0	12.8
		A 058	95.2	99.8	40.4	2.2	1.8	52.3
		A 062	95.2	99.8	40.4	2.2	1.8	52.3
	June	m 01	59.2	71.2	27.1	0.7	0	31.4
		m 02	136.2	166.4	29.6	0	0	13.0
		m 03	188.0	114.6	17.2	0	0	20.2
		m 04	118.6	145.0	20.2	0	0	35.0
	July	Au 040	79.7	90.2	19.1	0	0	63.6
		Au 045	63.0	67.4	10.5	0	1.0	10.4
		Au 056	123.6	128.6	38.7	1.4	0.5	44.6
		Au 057	85.8	90.2	26.0	0.6	0.8	16.7
		Au 058	93.1	116.9	14.9	0	0	7.2
		Au 062	86.0	108.0	19.6	0	0	8.0
	August	Se 040	199.4	227.4	36.2	0	0	49.0
		Se 045	112.8	136.2	10.5	0	0	12.0
		Se 056	130.5	144.0	33.6	0	0	13.5
		Se 057	219.3	232.5	43.2	0	12.6	15.0
		Se 058	205.7	241.4	24.5	0	0.5	16.3
		Se 062	54.6	64.1	9.5	0	0.2	3.4
Aerodramus maximus		bn 1	34.3	53.5	6.3	0	0.4	0
		bn 2	102.7	141.6	17.8	0	2.4	0
		bn 3	36.4	47.3	32.8	0.5	0	0
		bn 5	42.5	51.7	19.4	0.5	0	0
		bn 6	49.6	57.6	16.6	0	0	0
C. escu-lenta		e 1	79.7	117.1	59.3	0	3.6	70.6
		e 2	57.6	116.9	109.4	0	0	57.4
		e 3	180.8	234.0	20.0	0	0	11.0

The mean values of each monosaccharide for *A. fuciphagus* nests constructed at different months of the year are shown in Table 7.4 and the pooled percentage values are shown in Table 7.5. Most (89%) of the amino and neutral sugar comprised glucosamine, galactosamine and fucose, with an average percentage of 37.3%, 43.1% and 8.6% respectively. For the three hexoses, 8.8% was galactose, leaving a negligible 2.2% for mannose and glucose. There were no significant seasonal differences for most groups of monosaccharides ($F_{3, 18}$ = 2.81, P = 0.07 for glucosamine; $F_{3, 18}$ = 0.65, P = 0.60 for galactose; $F_{3, 18}$ = 0.68, P = 0.58 for glucose; $F_{3, 18}$ = 0.30, P = 0.82 for fucose).

Table 7.4 The concentration of amino and neutral sugars from *A. fuciphagus* nest constructed at different time of the year in Lubang Salai (mean ± SE).

	Concentration (nmol per mg of dried nest)			
	April	June	July	August
Glucosamine	81.2 ± 39.1	125.5 ± 53.4	88.5 ± 16.4	153.7 ± 53.3
Galactosamine	89.4 ± 37.1	124.3 ± 41.5	100.2 ± 18.1	174.3 ± 58.3
Galactose	32.2 ± 16.4	23.5 ± 5.8	21.4 ± 8.1	26.3 ± 11.4
Mannose	1.5 ± 1.1	0.2 ± 0.2	0.3 ± 0.3	0
Glucose	1.2 ± 1.0	0	0.4 ± 0.4	2.2 ± 2.2
Fucose	28.6 ± 18.0	24.9 ± 10.2	25.1 ± 19.3	18.2 ± 12.9

Table 7.5 Inter-specific comparison of the concentrations of various monosaccharides from nest of three species of swiftlets (shown as the mean ± SE with the percentage in parenthesis)

	Concentration (nmol per mg of dried nest)		
	A. fuciphagus (n = 22)	*A. maximus* (n = 5)	*C. esculenta* (n = 3)
Glucosamine	111.0 ± 20.1 (37.3%)	53.1 ± 25.5 (36.7%)	106 ± 87.2 (27.2%)
Galactosamine	121.8 ± 21.0 (43.1%)	70.3 ± 35.9 (48.0%)	156 ± 89.7 (40.7%)
Galactose	26.1 ± 5.0 (8.8%)	18.6 ± 8.5 (14.3%)	62.9 ± 59.5 (18.2%)
Mannose	0.5 ± 0.3 (0.3%)	0.2 ± 0.1 (0.2%)	0 (0%)
Glucose	1.0 ± 0.9 (1.9%)	0.6 ± 0.4 (0.8%)	1.2 ± 1.2 (0.3%)
Fucose	24.1 ± 6.7 (8.6%)	0 (0%)	46.3 ± 41.5 (13.6%)

There was a difference in the concentrations of galactosamine in batches of nests constructed in different seasons ($F_{3, 18} = 3.57$, $P = 0.03$). However, there was no difference in the concentrations of galactosamine from April to July ($F_{2, 13} = 1.08$, $P = 0.37$). Hence, the concentration of galactosamine was highest in August 174.3 ± 58.3 nmol/mg. In the course of the analysis, the elution peak for galactosamine of several nest samples overshot the detection limit. This resulted in failure to quantify less than an estimated 10% to 20% of the total galactosamine concentration, but nevertheless, this shortcoming did not seem to affect the final result.

There was also a difference in the concentrations of mannose in batches of nest constructed at different seasons ($F_{3, 18} = 4.47$; $P = 0.01$). The concentration of mannose for nests constructed in April differed from nests constructed from June to August ($F_{1, 13} = 1.10$, $P = 0.36$), with the concentration of 1.5 nmol/mg. The difference observed could be experimental errors because mannose occurs in very small concentrations, ranging from 0.5 nmol/mg to 3.4 nmol/mg or a mere 0.3% of the total. This might be caused by the dilution factor used that was

suitable for the detection of the amino sugars, but not for mannose. Similarly, this would explain the failure to detect any glucose in the nest samples constructed in June.

On the overall percentage composition of nest produced by the other two species of swiftlets, corresponding results for glucosamine and galactosamine were obtained. These two amino sugars made up 84.7% and 67.9% of the sugar in *A. maximus* and *C. esculenta* nest respectively (Table 7.5). The mean concentrations of various monosaccharides are shown in Table 7.5. The values for *A. fuciphagus* nest samples constructed at different months were pooled for comparison.

There were no differences among the two amino sugars ($F_{2, 27} = 2.48$, $P = 0.10$ for glucosamine and $F_{2, 27} = 2.56$, $P = 0.09$ for galactosamine), or for mannose ($F_{2, 27} = 0.74$, $P = 0.49$) and glucose ($F_{2, 27} = 0.09$, $P = 0.91$) for nests of all species. However, several interesting inter-specific differences were noted in the concentrations of galactose and fucose. Although galactose was present in the nest of all three speceis, there was a difference in the concentration in each species ($F_{2, 27} = 6.78$, $P = 0.004$), particularly for nests of *C. esculenta.* The concentration of galactose is higher in *C. esculenta* when compared to *A. fuciphagus* ($t_2 = 3.21$, $P = 0.001$), or *A. maximus* ($t_2 = 2.24$, $P = 0.03$). On the other hand, the galactose content in the nests of *A. fuciphagus* and *A. maximus* did not show any inter-specific difference ($t_{28} = 1.15$, $P = 0.13$), with a mean of 26.1 ± 5.0 nmol/mg and 18.6 ± 8.5 nmol/mg, respectively.

Finally, it was discovered that nests of *A. maximus* did not contain any fucose (Figure 7.13 and Table 7.5), even when a higher titre of sample was injected into the HPLC for analysis. However, fucose was present in relatively high concentration in the nests of *A. fuciphagus* ($t_{21} = 2.89$, $P = 0.004$), and *C. esculenta* ($t_2 = 3.51$, $P = 0.006$). In addition, the concentration of fucose in nests of *A. fuciphagus* is slightly higher compared to nests of *C. esculenta* ($t_2 = 1.82$, $P = 0.04$).

7.2.2 Protein

Seventeen amino acids were identified from the hydrolysate of dried edible nest (Appendix 7). These were, according to the rate of elution, Aspartic acid (Asp), Glutamic acid (Glu), Serine (Ser), Glycine (Gly), Histidine (His), Threonine (Thr), Arginine (Arg), Alanine (Ala), Proline (Pro), Tyrosine (Tyr), Valine (Val), Methionine (Met), Cystine (Cys), Isoleucine (Ile), Leucine (Leu), Phenylalanine (Phe) and Lysine (Lys).

In this study, nests produced by *A. fuciphagus* at different months (April, June, July and August) were analysed. The detailed results for each nest sample are shown in Table 7.6 and summarised in Table 7.7. Generally, the concentration of each amino acid varied from one nest to another, as shown in the relative height of peaks in the respective HPLC chromatogram

Table 7.6 The amount of various amino acids from the hydrolysate of dried edible bird nest from three species of swiftlets.

Species	Month	Nest	Amount (nmol per mg of dried nest)																
			Asp	Glu	Ser	Gly	His	Thr	Arg	Ala	Pro	Tyr	Val	Met	Cys	Ile	Leu	Phe	Lys
Aerodramus fuciphagus	April	A 040	15.33	27.70	80.78	62.61	35.82	71.29	35.07	37.72	75.66	29.21	71.57	9.32	106.06	30.30	71.81	52.90	25.39
		A 045	5.42	7.61	29.71	28.04	12.77	26.17	17.69	23.37	60.30	6.39	50.69	6.31	79.08	22.31	48.22	33.94	17.84
		A 056	45.10	73.31	280.05	209.53	173.18	214.33	137.97	122.66	236.95	120.02	225.88	24.44	40.91	126.62	249.68	178.97	19.85
		A 057	9.92	21.06	71.58	56.90	29.41	66.18	33.66	35.22	78.53	21.45	71.52	8.52	149.56	31.05	71.19	50.03	21.59
		A 058	14.46	23.48	65.01	49.72	27.33	58.96	29.40	31.88	63.46	27.69	61.26	8.98	70.14	25.60	61.49	46.03	23.35
		A 062	41.38	73.57	259.09	192.15	157.72	191.14	129.76	112.17	211.38	109.37	203.95	24.56	35.37	117.00	223.30	162.08	17.42
	June	m 01	16.28	30.62	81.48	64.63	33.19	68.36	35.98	36.61	79.41	33.81	66.23	6.94	40.69	30.68	70.68	52.77	26.46
		m 02	46.20	59.46	110.26	78.91	43.37	82.38	65.00	40.76	86.04	48.62	70.25	7.50	8.37	35.17	77.78	58.44	31.87
		m 03	7.07	15.22	54.08	47.04	19.16	45.04	24.80	27.33	66.77	5.56	52.76	6.30	93.70	24.40	55.30	40.53	22.31
		m 04	8.41	20.30	71.00	57.91	27.81	58.66	30.66	31.13	71.59	21.45	58.09	6.07	62.91	27.59	62.03	46.46	24.29
	July	Au 040	15.14	29.51	80.26	59.09	34.01	69.43	36.19	33.94	70.11	37.03	63.17	8.96	17.07	27.99	64.38	48.00	24.65
		Au 045	86.88	152.00	379.07	253.26	206.22	252.13	172.89	122.94	244.12	139.19	238.40	26.41	48.26	127.19	265.53	186.84	24.17
		Au 056	10.90	20.81	71.18	58.01	33.07	67.41	33.61	34.64	74.73	35.06	69.72	8.93	37.40	30.63	69.32	50.90	23.80
		Au 057	61.35	119.67	327.79	225.78	173.35	224.67	147.99	109.56	222.42	121.83	226.97	25.56	49.50	114.63	239.61	166.85	25.23
		Au 058	9.60	21.82	75.74	61.82	31.15	67.55	31.46	33.72	79.64	22.38	68.13	9.69	145.47	30.18	69.16	51.64	24.38
		Au 062	20.26	38.51	95.75	71.97	41.45	84.85	47.69	37.18	82.85	45.36	73.64	10.06	7.34	32.25	75.12	57.13	26.96
	August	Se 040	30.51	52.05	104.24	76.89	41.65	79.55	61.56	37.38	83.73	47.09	69.39	7.35	9.51	34.70	75.73	57.52	30.92
		Se 045	161.44	192.26	386.15	244.94	200.54	228.56	202.57	108.39	221.38	14.52	207.84	25.03	18.17	113.31	233.60	167.98	24.87
		Se 056	24.99	47.04	100.76	76.87	41.70	78.88	56.82	37.63	83.86	46.95	67.65	7.28	9.35	33.49	74.44	56.76	30.24
		Se 057	191.93	235.24	472.54	291.76	250.06	279.68	248.72	32.83	261.59	170.59	246.74	27.39	19.66	141.08	276.36	201.24	28.36
		Se 058	27.03	45.16	95.11	71.05	36.06	71.50	56.49	33.29	77.26	42.17	60.27	6.79	6.66	29.17	66.78	50.80	28.58
		Se 062	35.57	61.67	123.30	89.93	52.04	90.57	75.37	42.43	95.09	53.10	77.14	7.81	15.51	39.75	87.42	62.89	32.37
Aerodramus maximus		bn 1	44.91	63.18	113.77	84.07	42.31	92.40	78.58	45.63	81.28	49.24	67.29	9.49	7.69	36.43	81.70	59.22	33.61
		bn 2	42.54	61.15	113.98	84.40	41.59	90.17	77.57	45.51	84.10	51.29	69.50	10.10	6.33	36.78	83.03	60.13	32.52
		bn 3	13.05	29.13	89.79	69.94	32.66	78.51	45.99	39.58	81.63	45.08	64.57	9.31	2.49	32.82	75.13	54.74	25.72
		bn 5	30.25	55.52	122.76	87.61	47.89	97.59	75.07	46.98	95.69	54.79	79.29	9.80	0.99	40.25	91.58	66.08	31.36
		bn 6	62.53	71.72	122.97	86.52	46.98	89.31	75.85	53.20	90.18	55.82	79.39	7.46	16.55	42.46	92.98	66.58	34.86
Collocalia esculenta		e 1	7.15	8.69	35.35	35.18	9.56	24.45	19.36	26.63	67.30	4.04	53.13	5.67	49.08	24.62	48.23	33.93	17.54
		e 2	6.72	9.23	35.13	34.44	9.29	24.55	20.61	27.37	77.47	4.46	57.89	6.06	50.35	28.41	51.81	34.67	20.17
		e 3	30.47	44.88	106.27	75.64	27.15	75.56	53.12	42.66	86.77	42.81	70.63	6.56	14.73	40.46	72.41	56.52	29.90

(Figures 7.15 to Figure 7.18). However, statistical analysis showed that there was only a seasonal difference in the concentrations of lysine ($F_{3, 18} = 7.90$, $P = 0.01$). The other sixteen amino acids did not vary between different months ($F_{3, 18} = 2.07$, $P = 0.14$ for Asp; $F_{3, 18} = 1.94$, $P = 0.16$ for Glu; $F_{3, 18} = 0.96$, $P = 0.43$ for Ser; $F_{3, 18} = 0.81$, $P = 0.50$ for Gly; $F_{3, 18} = 0.77$, $P = 0.52$ for His; $F_{3, 18} = 0.83$, $P = 0.49$ for Thr; $F_{3, 18} = 1.34$, $P = 0.29$ for Arg; $F_{3, 18} = 0.62$, $P = 0.61$ for Ala; $F_{3, 18} = 0.60$, $P = 0.62$ for Pro; $F_{3, 18} = 0.65$, $P = 0.59$ for Tyr; $F_{3, 18} = 0.66$, $P = 0.59$ for Val; $F_{3, 18} = 0.83$, $P = 0.49$ for Met; $F_{3, 18} = 3.02$, $P = 0.57$ for Cys; $F_{3, 18} = 0.60$, $P = 0.62$ for Ile; $F_{3, 18} = 0.62$, $P = 0.61$ for Leu and $F_{3, 18} = 0.63$, $P = 0.61$ for Phe).

Table 7.7 The concentration of various amino acids from *A. fuciphagus* nests constructed at different month of the year in Lubang Salai (mean ± SE).

Amino acid	Concentration (nmol per mg of dried nest)			
	April (n = 6)	June (n = 4)	July (n = 6)	August (n = 6)
Aspartic acid (Asp)	21.9 ± 13.9	19.5 ±15.0	34.0 ±26.6	78.6 ±63.1
Glutamic acid (Glu)	37.8 ± 23.4	31.4 ±16.3	63.7 ± 47.0	105.6 ± 70.0
Serine (Ser)	131.0 ± 89.6	79.2 ±19.4	171.6 ±116.8	213.7 ± 139.5
Glycine (Gly)	99.8 ± 65.2	62.1 ±11.0	121.7 ± 75.6	141.9 ± 81.6
Histidine (His)	72.7 ± 59.6	30.9 ± 8.3	86.5 ± 66.4	103.7 ± 78.7
Threonine (Thr)	104.7 ± 64.1	63.6 ±13.0	127.7 ± 71.1	138.1 ± 75.3
Arginine (Arg)	63.9 ± 44.9	39.1 ±14.7	78.3 ± 52.9	116.9 ± 70.5
Alanine (Ala)	60.5 ± 36.6	34.0 ± 4.9	62.0 ± 34.8	48.7 ± 24.2
Proline (Pro)	121.0 ± 66.3	76.0 ± 7.0	129.0 ± 66.8	137.2 ± 67.5
Tyrosine (Tyr)	52.4 ± 40.4	27.4 ±14.0	66.8 ± 41.3	62.4 ± 45.0
Valine (Val)	114.1 ± 64.8	61.8 ± 6.5	123.3 ± 69.8	121.5 ± 68.3
Methionine (Met)	13.7 ± 6.9	6.7 ± 0.5	14.9 ± 7.1	13.6 ± 8.1
Cystine (Cys)	80.2 ± 35.2	51.4 ±29.6	50.8 ± 40.6	13.1 ± 4.4
Isoleucine (Ile)	58.8 ± 40.3	29.5 ± 3.8	60.5 ± 38.7	65.3 ± 40.2
Leucine (Leu)	130.9 ± 74.3	66.4 ± 8.1	130.5 ± 78.1	135.7 ± 77.0
Phenylalanine (Phe)	87.3 ± 53.5	49.5 ± 6.4	93.6 ± 53.4	99.5 ± 55.0
Lysine (Lys)	20.9 ± 2.6	26.2 ± 3.4	24.9 ± 0.9	29.2 ± 2.1

Nests from *A. maximus* and *C. esculenta* analysed in this study contained all the seventeen amino acids present in very similar quantity (Figure 7.19 to Figure 7.20). The mean concentration of various amino acids for each species is listed in Table 7.8. Similarly, there were no inter-specific variations in all amino acids identified ($F_{2, 27} = 0.45$; $P = 0.64$ for Asp; $F_{2, 27} = 0.78$; $P = 0.47$ for Glu; $F_{2, 27} = 1.07$; $P = 0.36$ for Ser; $F_{2, 27} = 1.13$; $P = 0.34$ for Gly; $F_{2, 27} = 1.52$; $P = 0.23$ for His; $F_{2, 27} = 1.50$; $P = 0.24$ for Thr; $F_{2, 27} = 0.86$; $P = 0.44$ for Arg; $F_{2, 27} = 0.62$; $P = 0.54$ for Ala; $F_{2, 27} = 0.98$; $P = 0.39$ for Pro; $F_{2, 27} = 1.08$; $P = 0.35$ for Tyr; $F_{2, 27} = 1.23$; $P = 0.31$ for Val; $F_{2, 27} = 1.36$; $P = 0.28$ for Met; $F_{2, 27} = 2.36$; $P = 0.11$ for Cys; $F_{2, 27} = 0.88$; $P = 0.43$ for Ile; $F_{2, 27} = 1.15$; $P = 0.33$ for Leu; $F_{2, 27} = 1.23$ and $P = 0.31$ for Phe) except for lysine ($F_{2, 27} = 5.38$; $P = 0.01$).

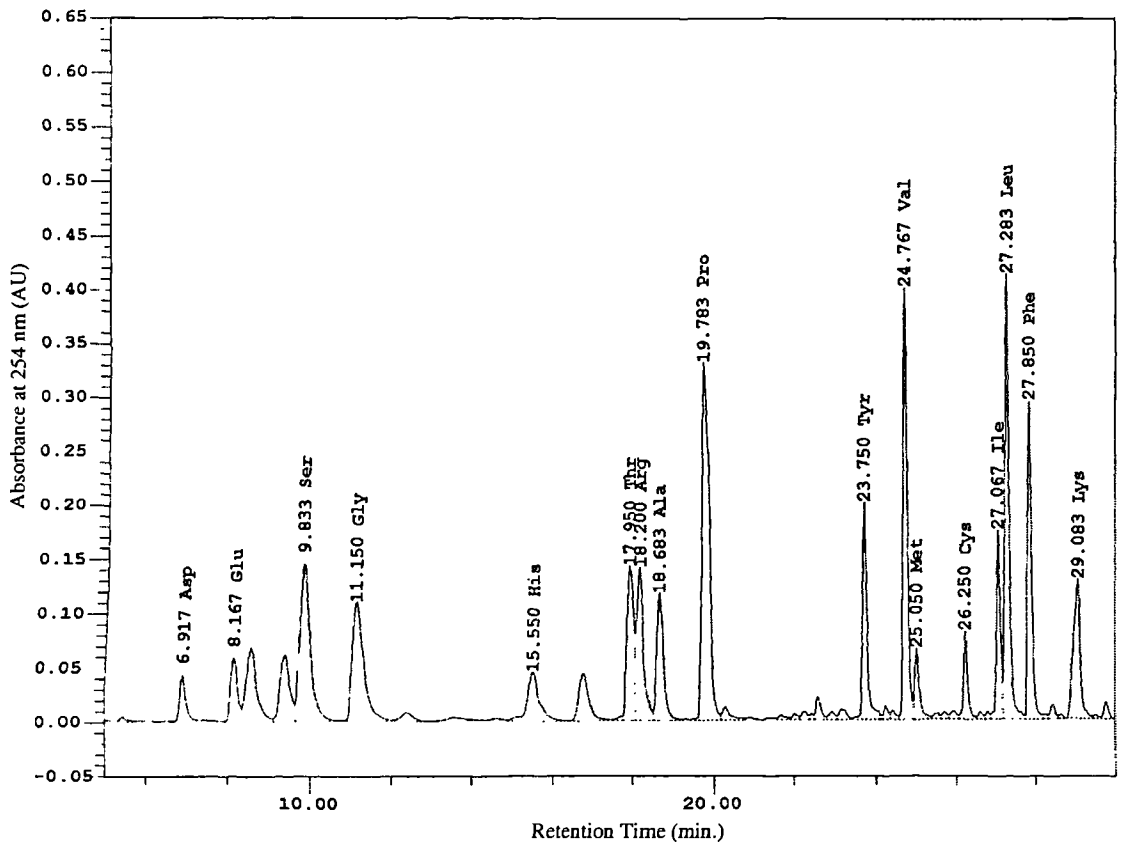

Figure 7.15 Chromatogram of the PTC derivatives of amino acids for *A. fuciphagus* nest constructed in April 1997 (marked nest S058).

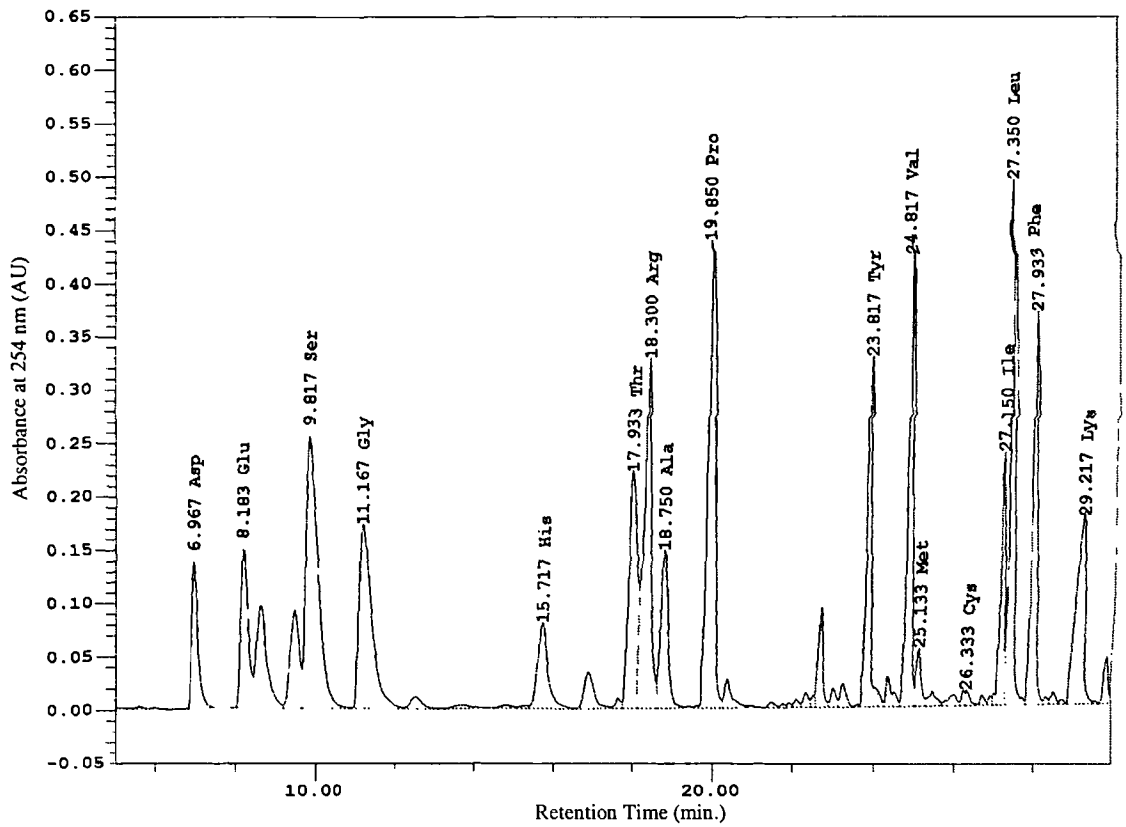

Figure 7.16 Chromatogram of the PTC derivatives of amino acids for *A. fuciphagus* nest constructed in June during the heavy moulting period (unmarked nest).

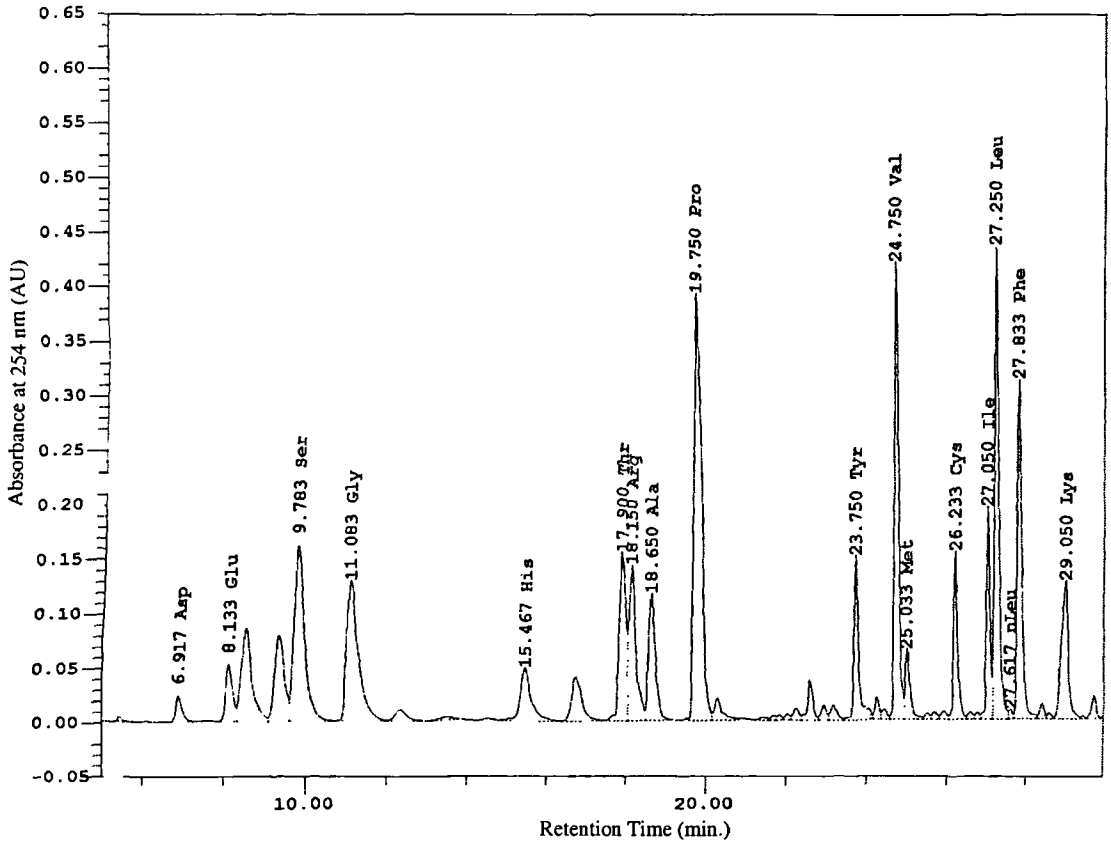

Figure 7.17 Chromatogram of the PTC derivatives of amino acids for *A. fuciphagus* nest constructed in July 1997 (marked nest S058).

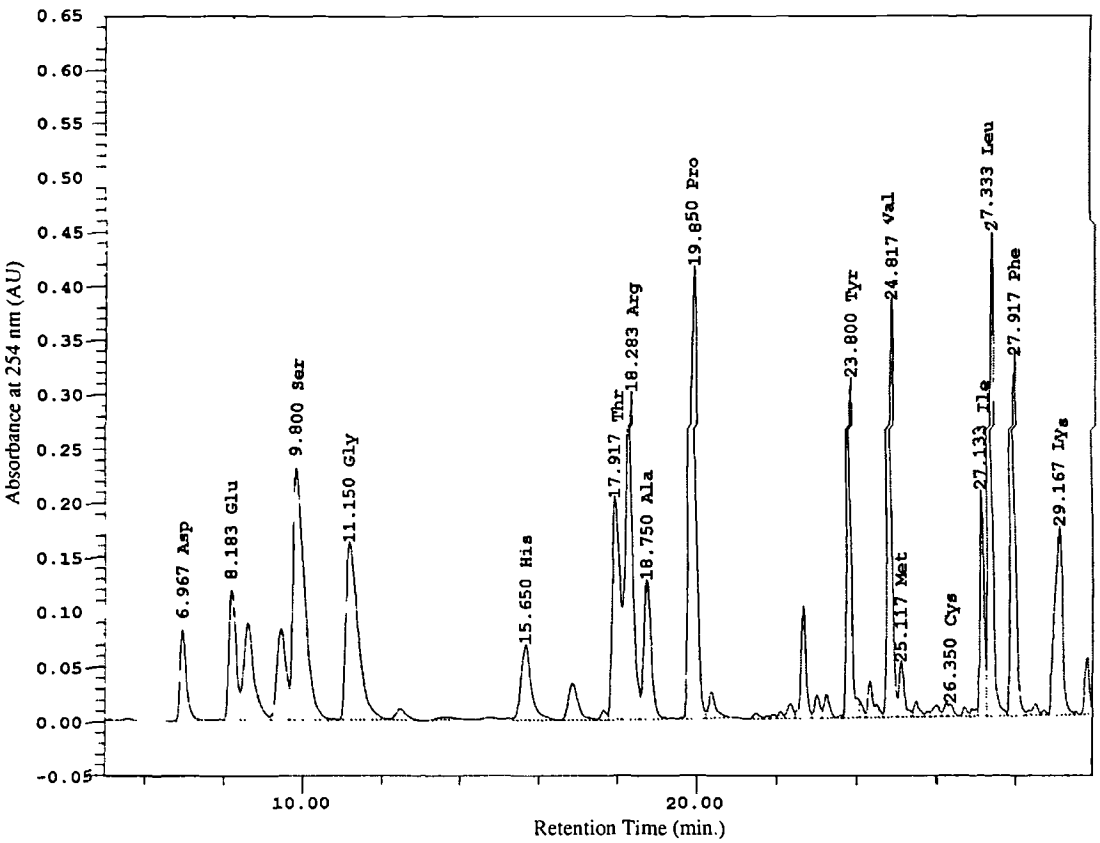

Figure 7.18 Chromatogram of the PTC derivatives of amino acids for *A. fuciphagus* nest constructed in August 1997 (marked nest S058).

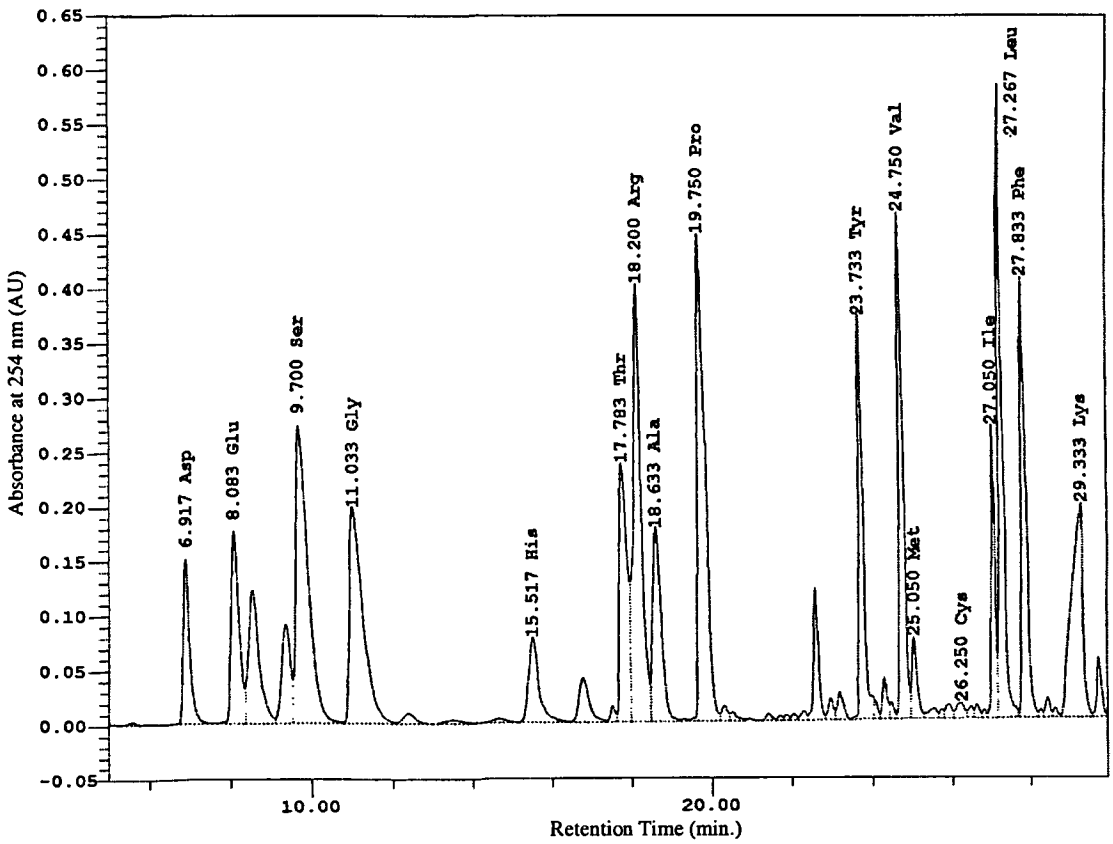

Figure 7. 19 Chromatogram of the PTC derivatives of amino acids for *A. maximus* nest.

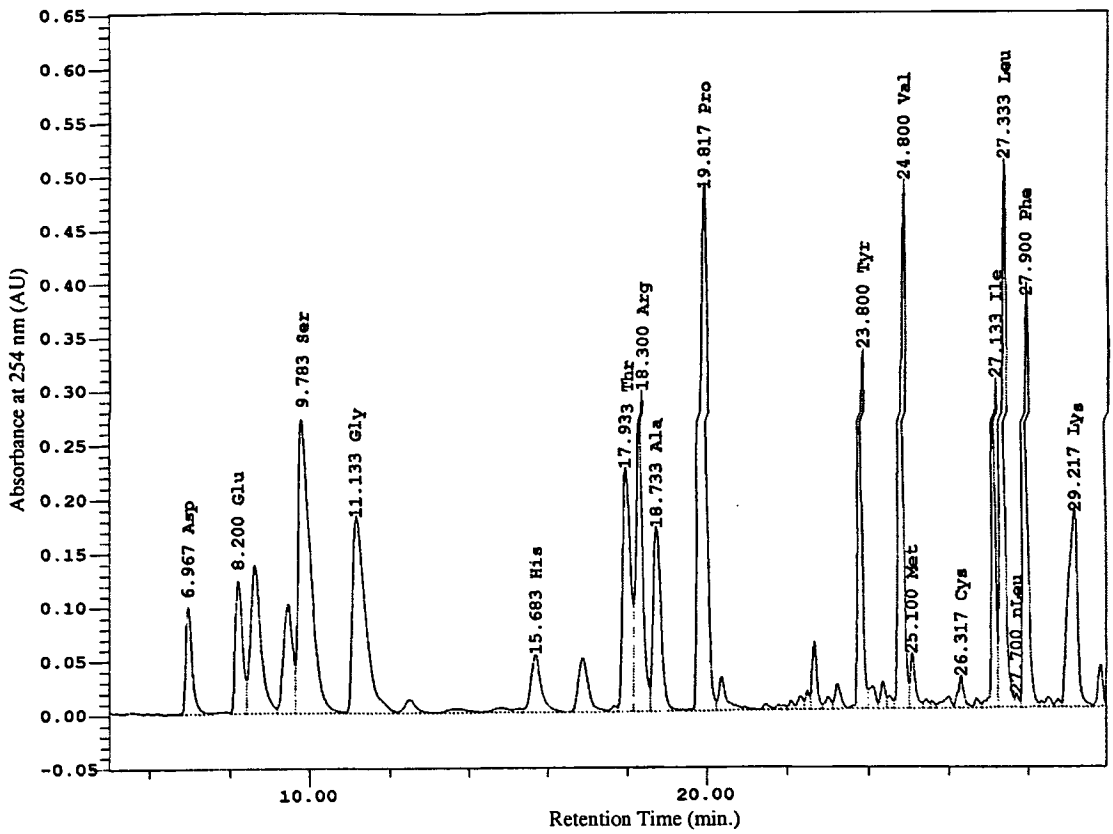

Figure 7.20 Chromatogram of the PTC derivatives of amino acids for *C. esculenta* nest.

Serine, proline, threonine, leucine, valine and glycine occurred in high concentration in the nests of *A. fuciphagus*, *A. maximus* and *C. esculenta*. This result suggested that these were the most common amino acid residues in the polypeptide backbone in good agreement with the observations made by Kathan and Weeks (1969).

Table 7.8 Inter-specific comparison of the concentration of various amino acids from nest of three species of swiftlets (shown as mean ± SE with the percentage of total in parenthesis).

Amino acid	Concentration (nmol per mg of dried nest)		
	A. fuciphagus (n=22)	*A. maximus* (n = 5)	*C. esculenta* (n = 3)
Aspartic acid (Asp)	40.2 ±17.9 (2.5%)	38.7 ±17.5 (3.8%)	14.8 ±10.5 (2.1%)
Glutamic acid (Glu)	62.2 ±22.1 (4.2%)	56.1 ±15.4 (5.6%)	20.9 ±16.0 (2.9%)
Serine (Ser)	155.2 ±47.6 (10.8%)	112.7 ±12.9 (11.5%)	58.9 ±31.6 (8.8%)
Glycine (Gly)	110.4 ±30.0 (8.1%)	82.5 ± 6.8 (8.4%)	48.4 ±18.2 (7.6%)
Histidine (His)	77.3 ±27.5 (4.9%)	42.3 ± 5.8 (4.3%)	15.3 ± 7.9 (2.3%)
Threonine (Thr)	112.6 ±28.4 (8.5%)	89.6 ± 6.7 (9.2%)	41.5 ±22.7 (6.2%)
Arginine (Arg)	77.8 ±24.0 (5.5%)	70.6 ±13.2 (7.2%)	31.0 ±14.8 (4.7%)
Alanine (Ala)	52.9 ±12.8 (4.4%)	46.2 ± 4.6 (4.7%)	32.2 ± 7.0 (5.3%)
Proline (Pro)	119.4 ±26.5 (9.5%)	86.6 ± 5.9 (8.9%)	77.2 ± 7.5 (13.2%)
Tyrosine (Tyr)	54.5 ±16.9 (4.2%)	51.2 ± 4.1 (5.3%)	17.1 ±17.2 (2.2%)
Valine (Val)	109.1 ±26.9 (8.4%)	72.0 ± 6.6 (7.4%)	60.5 ± 7.0 (10.2%)
Methionine (Met)	12.7 ± 3.0 (1.0%)	9.2 ± 1.0 (0.9%)	6.1 ± 0.3 (1.1%)
Cystine (Cys)	48.7 ±15.8 (5.8%)	6.8 ± 5.8 (0.6%)	38.1 ±15.6 (7.3%)
Isoleucine (Ile)	55.7 ±15.7 (4.0%)	37.7 ± 3.5 (3.9%)	31.2 ± 6.4 (5.1%)
Leucine (Leu)	117.7 ±30.3 (8.9%)	84.9 ± 7.1 (8.8%)	57.5 ±10.1 (9.6%)
Phenylalanine (Phe)	85.5 ±21.4 (6.6%)	61.3 ± 4.8 (6.3%)	41.7 ± 9.9 (6.8%)
Lysine (Lys)	25.2 ± 1.5 (2.7%)	31.6 ± 3.4 (3.2%)	22.5 ± 5.0 (4.6%)

7.3 SEASONAL INTRA-SPECIES VARIATIONS

Within the same species, nests produced by *A. fuciphagus* in May and July contained a relatively higher number of feathers and are characterised by a small nest crest. in contrast, nests produced in the so-called "good" season between September and February, are comprised mainly of pure whitish saliva, or at most with only few down feathers adhering between the salivary laminae. Similarly, nests produced by *A. maximus* between May and July are traditionally considered of the lowest quality because of a higher content of feathers. Good quality nests are built between September and February where there is clearly a higher saliva content that appears as white patches between strips of fluffy feathers. This is the traditional view. In this study, results of the chemical composition of nest were presented.

Of all the seventeen amino acids, one sialic acid, two hexosamine, three hexoses and one deoxyhexose identified in the nest samples of *A. fuciphagus*, only few constituents exhibited any seasonal variations. These comprised lysine, galactosamine and mannose, in which lysine only constituted 2.7% of the total amino acids content while mannose made up of a mere 0.3% of the total neutral and amino sugars. Even then, such variations were not confined to nest constructed at any particular season but occurred among different batches of nests. For instance, the concentrations of galactosamine were highest in August. Nevertheless, it appears that successive nests constructed at different times of the year did not show major differences.

Variations between one nest from another are expected because the genetic make-up of each individual within a colony habours some heterogeneity. Unlike the synthesis of protein where the genes control the assemblage of amino acids into polypeptides by accurate template mechanism, the synthesis of polysaccharide is controlled by a non-template multi-enzyme mechanism involving a large variety of glycosyltransferases (Sharon, 1975; Kleene & Berger, 1993). Nevertheless, these enzymes are themselves genetically controlled in their synthesis (Hughes, 1983). The protein structure itself is believed to exert secondary constraints to the glycosylation machinery, or in the extreme provides recognition portions for glycosyltransferases that act on the protein or class of proteins (Kornfeld & Kornfeld, 1985). In principle, the biosynthesis pathway leading to the production of mature glycoprotein is complex, involving various kinds of glycosyltransferases, glycosidases, and carbohydrate-modifying enzymes. In addition, proteins that mediate the transport of sugar nucleotides across the membranes of the endoplasmic reticulum and the Golgi apparatus has been discovered (Hirschberg & Snider, 1987). Consequently, more than one carbohydrate unit is often present, attached at different positions of the polypeptide chain. Each attachment site frequently accommodates different glycans, resulting in microheterogeneity of the whole molecule or the formation of glycoforms. Therefore, glycosylation of a polypeptide usually generates a set of glycoforms, all of which share an identical backbone but are dissimilar either in the structure or

disposition of their carbohydrate units (Lis & Sharon, 1993). This hypothesis would explain the uniformity observed in the analysis of the amino acid residues of all samples as compared to the more variable nature of the monosaccharide product.

7.4 INTER-SPECIES VARIATIONS

There are distinctive morphological differences between the nests constructed by *A. fuciphagus*, *A. maximus* and *C. esculenta* (e.g. Medway, 1966; Medway & Pye, 1977). However, there has been no previous investigation of the composition of the translucent salivary cement produced by different species (Cranbrook *et al.*, 1996). Although no comparative study has ever been carried out to investigate the inter-specific chemical constituents of the nest, bit and pieces of information could be gathered from research that required the preparation of extract from edible nest, particularly collocalia mucoid.

Fucose was not detected in the collocalia mucoid preparation for investigation of myxovirus neuraminidase (Howe *et al.*, 1961). The origins of the nest materials or the species that produce them were not identified, but generally referred as "oriental or Chinese edible nest swiftlets". In addition, Biddle and Belyavin (1963) reported that crude bird nest purchased from dealers came in two grade of materials where the second graded nest had an obvious different appearance, somewhat darker and contaminated with feathers and other extra extraneous matter. Comparative tests in the haemagglutination inhibitory activity of these nests showed that there was a considerable difference in yield between the two grades of nest. This variation was attributed to the difference in the concentration of released sialic acids after mild acid hydrolysis. These results indicated there are some variations in the composition in the chemical constituents of different nest material. Furthermore, molecular studies of nine enzyme systems of two species of swiftlets (Lim, 1993) and cytochrome *b* mitochondrial DNA (Lee *et al.*, 1996) indicate that member of *Collocalia* and *Aerodramus* are unlikely to be monophyletic. Hence, this genetic difference would be reflected in the composition of the salivary secretion.

Results from this study showed that the carbohydrate composition exhibits more variation than do the protein constituents. There is more disparity in the monosaccharides content between the nests of *C. esculenta* and *A.fuciphagus*, or *A. maximus*, than between *A. fuciphagus* and *A. maximus*. Sialic acid concentrations are notably less but the concentrations of galactose are higher in *C. esculenta*, but no differences were observed between *A. fuciphagus* and *A. maximus*. Another important difference is the absence of fucose in the nest of *A. maximus*, but it is present at high concentration in the other two species, with higher concentration in *C. esculenta* nestthan in the nest of *A. fuciphagus*.

Studies have shown that different types of glycoprotein can be produced on the same "assembly line" and it was suggested that the probable control lies in the enzyme that incorporates the sugar into the terminal peptide-linked polysaccharide side chain (Sharon, 1975; Candy, 1980). For example, two independently processed types of *O*-linked glycosylation have been identified in the cellular slime mould, *Dictyostelium discoideum* (Champion *et al.*, 1991). In the context of this study, the "assembly line" would imply the organelles within the columnar epithelial cells of the salivary glands. The primary basis for determining the structures of the sugar chains produced by a cell lies in the specificity of the enzyme for the donor and acceptor substrates (Paulson & Colley, 1989). Species-specific glycosylation and selective expression of certain glycosyltransferases also plays an important role in the appearance of oligosaccharide patterns (Rademacher *et al.*, 1988). An example of a species-dependent glycosylation is the occurrence of terminal α-D-galactosyl residues that comprise approximately 23% of total galactose in the calf, but was completely absent in humans (Spiro & Bhoyroo, 1984).

Furthermore, spatio-temporal expression of glycosyltransferases appears to be regulated at the level of transcription, although it may be subjected to tissue- and cell-type specific regulation and post-translational modification (Kleene & Berger, 1993; Harduin-Leper *et al.*, 1995; Colley, 1997). The carbohydrate mioety of plasma and cellular fibronectin, a type of glycoprotein present on the cell surface of fibroblasts, is distinctively different with respect to the linkage of sialic acid, the degree of sialylation and the absence or presence of fucose (Fukuda & Hakomori, 1979; Fukuda *et al.*, 1984). All these findings offer some potential explanations for the variations observed in the composition of sialic acid and the other monosaccharides in the glycoprotein of edible nests.

In the case of *C. esculenta* nests having significantly less sialic acid and more galactose than nests of the other two species, it is hypothesised that *C. esculenta* has a higher level of galactosyltransferase and less sialyltransferase. Sialic acid are glycosidically linked to either the 3- or 6-hydroxyl groups of galactose residue, or to the 6-hydroxyl group of *N*-acetylglucosamine or *N*-acetylgalactosamine residues, and can form polysialic chains (Harduin-Leper *et al.*, 1995). When the terminal end of the peptide-linked polysaccharide is substituted by sialic acid, this would then prevent further incorporation of the galactose (Blanken & Van de Eijnden, 1985). In the Golgi apparatus of the rat liver cells, there is significant overlap in the functional co-localisation of sialyl- and galactosyltransferase. It has been postulated that if two glycosyltransferases are co-localised, they will compete for the limited concentration of transported donor (Etchison & Freeze, 1996). In a more recent study, Smilovich *et al.* (1998) showed that competition reaction occurs *in vivo* between α-2,6-sialyltransferase and α1,3-galactosyltransferase where the absence of sialylation results in an increased of galactosylation.

By inference, in the other two species, a higher concentration of sialyltransferase would increase the rate of sialic acid incorporation, resulting in the difference observed in this study.

The low concentration of glucose and mannose detected could be because they were transformed into galactose and fucose during the biosynthesis of glycoprotein (Candy, 1980), or that mannose is cleaved before the mature glycoprotein process is attained (Kornfeld & Kornfeld, 1985). The most common inter-conversion of nucleoside diphosphate sugars is by the reaction of epimerisation. For instance, L-fucose is formed from mannose via the nucleotide-linked sugar GDP-Man (guanosine diphosphomannose) after epimerisation reaction that involves two stages of transformation. The first stage results in the formation of a nucleotide-linked 4-keto-6-deoxy intermediate, which is later converted into GDP-L-fucose by enzymes generally referred to as oxidoreductases (Sharon, 1975). Similarly, the sugar donor UDP-glucose (uridine diphosphoglucose) is converted to UDP-galactose (uridine diphospho-galactose) catalysed by the enzyme UDP-gluco 4-epimerase (Candy, 1980).

In mammalian cells, mannose for glycoprotein synthesis is assumed to originate mostly, if not entirely, from intracellular glucose. A mannose-specific transporter responsible for delivering mannose to cells for glycoprotein synthesis has also been identified (Panneerselvam & Freeze, 1996; Panneerselvam *et al.*, 1997). However, mannose metabolism may be much more complex since all the metabolic intermediates (Man-6-P, Man-1-P, GDP-Man, GDP-Fucose, Dolichol-p-Man etc) ultimately lead to protein glycosylation. Therefore, the absence of fucose in *A. maximus* nest strongly suggests that one or more of the many classes of enzymes responsible for mannose metabolism or its conversion to fucose, is lacking. Alternatively, another possible hypothesis is that one class of enzyme, i.e. fucosyltransferases (Breton *et al.*, 1998); responsible for transporting fucose from the donor GDP-fucose to the receptor is perhaps absent in *A. maximus*. This would have resulted in the failure to incorporate fucose in the glycosylation.

7.5 CONCLUSIONS

This study represents the first ever undertaking to elucidate the seasonal variations in the chemical constituents of nests produced by *A. fuciphagus*, and to investigate inter-specific differences in the nests of *A. fuciphagus*, *A. maximus* and the basal attachment of *C. esculenta* nests.

Results from this study showed that apart from few constituents, batches of nests from *A. fuciphagus* constructed at different times of the year did not differ significantly in the chemical composition. The only sialic acid identified is *N*-acetylneuraminic acid. The rest of

the monosaccharides comprised two hexosamines, three hexoses and one deoxyhexose. The hexosamines, the most abundant of all sugars, are glucosamine and galactosamine. The hexoses are galactose, mannose and glucose, but the concentration of mannose and glucose is approximately 2.2% of the total neutral and amino sugar. The only deoxyhexose identified is fucose. For the protein composition, seventeen amino acids occur in various quantities. These are aspartic acid, glutamic acid, serine, glycine, histidine, threonine, arginine, alanine, proline, tyrosine, valine, methionine, cystine, isoleucine, leucine, phenylalanine and lysine. Furthermore, serine, proline and threonine are the three most abundant amino acids found in the nest of *A. fuciphagus*.

Identical monosaccharides and amino acids are identified in the nest cement of *C. esculenta* and *A. maximus*, except that fucose is absence in the latter species. Results show that *C. esculenta* has significantly lower concentration of sialic acid but a greater concentration of galactose as compared to *A. fuciphagus* or *A. maximus*. These differences are not observed among the latter two species. However, fucose is absent in the nest of *A. maximus*, as manifested by the absence of a corresponding peak in the chromatogram, but occurs in substantial concentrations in *A. fuciphagus* and *C. esculenta*. There is also slightly more fucose per unit weight of dried nest in *A. fuciphagus* and *C. esculenta*. The actual glycosylation process that produces the observed differences is not determined in this study.

Differences detected in the elution profile of the chromatogram would theoretically offer a diagnostic tool for the identification of edible nests of unknown origin. This is useful when there is a need to monitor and regulate the trade or movement of marketable edible nests from the source country. In addition, it is commonly accepted that fake or adulterated edible nests have found their way into the market. In this study, all samples were analysed using high performance liquid chromatography, a highly sensitive and accurate piece of apparatus. Because this diagnostic procedure requires only a minute concentration of sample, usually within the range of 50 to 200 μg (1 g = 1,000,000 μg) of nest sample, a single strain of salivary material separated from a whole nest is sufficient for repeated analysis. Nevertheless, more tests are need for finer characterisation. In addition, nests from different geographical regions or recognised subspecies, which were not covered in this study, ought to be analysed to complement and build up databases of standard diagnostic criteria.

Finally, since there are no major differences in the chemical composition of nest constructed in different season, the only argument for the grading of nest material must be based on the morphological appearance, particularly the size of the nest crest as well as the concentration of feathers incorporated in the nest. In this respect, traditional standards based on the cleanliness and the amount of feathers incorporated in the nest is very important. Although the essence of this criterion is very subjective, it will still be applied and accepted in the future, exactly as it has been during the past few decades. Therefore, any recommendation on the

sustainable harvest of this natural produce will have to adhere to this rule and the additional findings from the biological study of the swiftlets. Ultimately, the recruitment rate of swiftlets should not be compromised in long run for the exploitation of their nests and the wish to generate maximum profit from each harvest.

Chapter 8
Sustainable Management

8.1 INTRODUCTION

Sustainability is a mutually enchancing relationship between dynamic human economic systems and more slowly changing ecological systems, such that human activities do not destroy the integrity of self-organising systems that provide the environmental context (Norton, 1992). Accordingly, sustainable management of the edible nest swiftlets requires balancing the repetitive harvesting of the edible nests to sustain a lucrative industry, while maintaining the viability and productivity of the swiftlet colonies. Unlike other wildlife resources, edible nest swiftlets can be sustainably managed with relative ease because a product of the species is harvested rather than the species itself. Provided the reproductive rate is not severely undermined or disturbed by exploitation, a swiftlet colony should to be able to maintain or increase its population.

Easy as this may sound, the reality is usually the opposite when humans are involved. Conflicts of interest among various communities or individuals usually hinder any effective management. Lack of proper knowledge on the swiftlets' breeding biology results in over-exploitation of the nests. Furthermore, escalating consumer demand also pushes up market prices, which results in an increased frequency of harvesting for short-term gain, and poaching activities. Exploitation pressures have increased tremendously and in many areas harvesting may continue year round, with eggs and nestlings being destroyed at each collection (Cranbrook, 1984; Valli & Summers, 1990). With this onslaught, successful fledging at each breeding season is reduced, depleting the population's breeding capacity and suppressing the rate of recruitment.

Therefore, the ultimate aim of this study was to produce a sustainable harvesting strategy based on sound scientific knowledge that would be both acceptable to the local communities and endorsed by relevant government institutions. Co-operation from the local communities who are entrusted with the rights to harvest the edible bird nest is of the utmost importance. They need to comprehend the basic principles behind the harvesting regimes in relation to the swiftlets' breeding biology and to be convinced of the beneficial outcome in long run. The relevant government institution, namely the Sarawak Forest Department has the jurisdiction to oversee the implementation of the recommended management plan, as well as to protect the swiftlets' feeding ground and nesting habitats.

This chapter describes the factors that caused the decline in the edible nest swiftlets populations in Sarawak and the needs for their conservation. Three major factors and one potential problem are described in Section 8.2.1, while Section 8.2.2 gives the current population size of *A. fuciphagus* in middle Baram, and the *A. maximus* colonies in Bau and Kakus. Details of the recommended sustainable management plan for edible nest swiftlets are presented in Section 8.3. Finally, an integrated approach to swiftlet conservation is presented in Section 8.4. It comprises the establishment of nature reserves to protect the wild swiftlets colonies and the introduction of "swiftlets house farming" as a new approach to an interactive management.

8.2 PROBLEMS AND NEEDS FOR SWIFTLETS CONSERVATION

8.2.1 Declining Yield

8.2.1.1 Over-harvesting

Over the past five decades, annual production of edible nest has fallen dramatically because of a sharp decline in wild swiftlet populations (Good & Wong, 1989). Throughout Sarawak, the declining yield could be attributed to one major problem, the over collection of nests. It was evident that the interval between each harvest was too short to permit any substantial number of nestlings to fledge. There are several factors that drive the current patterns of exploitation, but the nest collectors and the owners are the main cause of this problem. However, many have repeatedly rejected this responsibility, blaming it on poachers, or at most reluctantly admitted to it.

Improvements in the standard of living and a change in lifestyle has made money an essential part of daily life, not only in major towns, but also in the interior part of the State. With limited opportunities and job employment, the consequence is that the edible swiftlets' nests are being harvested more often, sometimes as frequently as every thirty days. Unless this issue is addressed and rectified by the cave owner, there is no hope of maintaining the existing swiftlet populations in Sarawak. Some far-sighted owners, who have wisely recognised and corrected this mistake, have adopted harvesting strategies that are friendlier to the swiftlets.

The other factor is the profit motive among nest traders. Many caves are contracted out for a limited period of time by the rightful owners. Therefore, the contractors' only concern is to reap as much profit as possible during these tenure years. This practice has been in existence for years in many nest-yielding caves, most notably at Niah Cave. In an extreme case, the use of unethical tactics by a few irresponsible businessmen, and in some caves even the involvement of gangsters, was partly to blame. The rightful owners are deprived of management control, more often forcefully rather than willingly. Consequently, harvesting is

being carried out as frequently as the new owner desired, while the rightful owners are only given a portion of the profit from the sale of nests.

8.2.1.2 Poaching

Nest theft or poaching has always been a conveniently blamed for declining yields by most cave owners. If this was true, then it would be an unprecedented miracle for a group of people to bring down a population of 1.7 millions swiftlets at Niah (Good, 1993) to a mere 300,000 to 400,000 individuals by poaching alone. Nevertheless, nest theft remains a serious threat to cave management, especially when nests are left inside a cave for several months to allow successful breeding.

There are few ideal caves that have both a substantial yield and only one or two entrances, like those found in middle Baram. Most limestone outcrops have ramifying cave systems with multiple entrances or openings, principally those caves producing the black-nests. Many caves such as those in Bau and Bukit Sarang are so scattered among limestone karst and have such low production of nests that they are uneconomical if not totally impossible to guard.

When a cave can not be guarded efficiently, the owners have no choice but to harvest the nests frequently to avoid suffering any losses from poaching. This contributes to the increased frequency of harvest. For communal caves, guarding is completely out of question. The occurrence of nest theft is impossible to control or stop because it usually involves the same people from the villages who have rights to the cave. Such a state of affairs is referred to in Malay language as "*musuh dalam kelambu*" which means "enemy within a mosquito net".

Passive guarding by gating and blocking off unnecessary or secondary openings might be the only solution. However, a proper gate must not obstruct the inward and outward flight of the swiftlets or other cave inhabitants. For this purpose, horizontally placed metal bars are more suitable than vertical ones. At the same time, they should allow a free flow of air to avoid altering the cave microclimate. Unfortunately, not many owners can afford the high construction costs, especially when dealing with numerous small isolated caves or caves with multiple entrances.

8.2.1.3 Habitat Loss

The impact of habitat loss on the edible nest swiftlet populations in Sarawak has never been assessed. To a certain degree, the clearing of large tracts of prime forest must have some impact by reducing the insect abundance and swiftlet food availability, thus lowering the natural carrying capacity for swiftles populations. However, its importance is probably less severe than over-harvesting of nests, since selectively-logged forest still has reasonable

populations and varieties of insects (Thiollay, 1997). This is further supported by the fact that well established colonies of swiftlets are known to occur in populated towns or cities with much less vegetation. In addition, the ratio of *A. maximus* to mossy nest swiftlets (*A. salanganus* and *C. esculenta*) at Niah Cave was estimated to be about 5:1 in 1987 (Leh, 1987; Good, 1993), but this had reversed to 1:3 in 1996 (Leh, per. comm.), indicating the pressure from frequent harvest is greater than habitat loss.

In most areas, logging is the main cause of habitat loss but selectively logged forest still has considerable vegetation coverage that is able to support substantial insect fauna. On average, logging in tropical forest destroys up to 63% of the canopy coverage and 38% of the undergrowth, which is then invaded by dense re-growth. Exactly how the swiftlets adapt to these changes remain unclear. However, upper canopy bird species, particularly small insectivores, do not seem to be significantly reduced by such clearance (Thiollay, 1997). The air space above the forest canopy is the foraging habitat for swiftlets and because they utilise the outer part of the vegetation, and they are thus not greatly influenced by the inner structure of the forest.

Commercial plantations and land conversion contribute to habitat loss with more acute consequences. Plantations totally replace selectively logged forest, or any regenerated secondary forest, with a monoculture of crops with less heterogeneity. The impact of such conversion is obvious at the initial stage of planting when the land is cleared of all vegetation, leaving vast expanse of bare earth. In Sarawak, the total land area converted into oil palm (*Elaeis guineensis*) plantation was about 146,000 hectares in 1999 and this is estimated to increase to 300,000 hectares by the year 2000 (Sarawak Online, 1999). Vast areas within the foraging range of swiftlets near to Niah Cave and the Baram basin have been cleared and planted with oil palms. Elsewhere around Bukit Sarang, trees of the *Acacia* species are planted instead for a proposed paper and pulp mill nearby.

Limestone quarrying is another threat to the swiftlet cave, especially those located in the middle Baram. For example, Lubang Sepayang is located within the boundary of a quary concession. The effect quarrying is direct and evident, and results in the total destruction of the roosting and breeding caves for the swiftlets. Quarry activities in Baram started around 1986 at Batu Gading, and have since demolished several major limestone blocks, some containing nest caves. Now it is threatening the adjacent blocks that house the few remaining major colonies of *A. fuciphagus* in Sarawak.

8.2.1.4 Potential Threat

Accumulated pesticides, particularly DDT, not only kill birds directly but also interfere with eggshell production and cause nesting failure. However, it was only in the mid-1960s that

reliable reporting and an understanding of the lethal levels of various organochlorine pesticides in wild vertebrate populations were available (Little & Crowe, 1997).

DDT or 1,1,1-trichloro-2,2-bis(*P*-chlorophenly) ethane and 1,1-dichloro-2,2-bis(*P*-cholorophenyl) ethylene (DDE) pesticides affect normal eggshell formation by increasing magnesium and phosphate levels, with fatal consequences caused by denting and development failure. These pesticides were responsible for widespread eggshell thinning and reproductive failure of a variety of raptors such as *Haliaeetus leucocephalus* or the Bald Eagles (Grier, 1982; Gill, 1990) and other species such as the cuckoo-shrike (Safford & Jones, 1997).

Swiftlets and other insectivorous birds are also especially susceptible to pesticide poisoning. Insects exposed to low dosage of insecticides are not killed immediately. Instead, they may be swept by prevailing winds into the air and fed upon since they are easy prey. In Sarawak, the use of DDT is restricted to the control of malaria. Even then, its use is only permitted for residual spraying in an event of outbreaks and this practice is gradually being phased out (Malaysian Ministry of Health, 1999). Aerial DDT spraying is forbidden. As such, the immediate threat in near future appears to come from extensive use of pesticides in agriculture, or in commercial plantations. Similarly, in Java, Indonesia, concern about effects of pesticide use in the agriculture sector has been raised (Wahyu, 1995).

The expansion of oil palm plantations in the state is very rapid. Nevertheless, the only pesticides permitted for aerial spraying in large plantations comprise the groups with less persistent active ingredient (Malaysian Ministry of Agriculture, 1999). Those normally used in oil palm plantations include organophosphate pesticides such as acephate, chlorpyrifos and trichlorfon or other chemical classes such as propoxur (carbamate-based), diflubenzuron (benzoylphenylurea class) and chlorothalonil (chloronitrile-class). Pesticides of the organophosphate class are considered moderately to highly toxic to bird (Hudson *et al.*, 1984; Briggs, 1992) while diflubenzuron and chlorothalonil are practically non-toxic to birds (Kidd & James, 1991).

8.2.2 Current Population Size

8.2.2.1 Primary Study Site At Lubang Salai

A direct count of swiftlets was carried out only at Lubang Salai because of its single entrance that could be easily monitored and the small population of *A. fuciphagus* contained within. This census placed the swiftlet population within this cave at around 3,053 to 3,663 individuals with an average of 3,296 birds (Table 8.1). It was difficult to differentiate *A. fuciphagus* from *C. esculenta* in the streams of emerging flight and the latter was therefore

included in the count. Nevertheless, the *C. esculenta* population was estimated at only 100 to 120 individuals, based on the number of nests counted inside the cave. Depending on the season, this single-chambered cave of moderate height yielded between 915 to 1,398 nests per harvest (Table 8.2), with an average of 1,217 nests between April 1997 and February 1998. This translates to an average number of sexually productive swiftlets of 2,434 birds within this colony, or 73.8% of the whole population.

Table 8.1 Population censuses of *A. fuciphagus* in Lubang Salai during April and May 1997.

Date	6 April	9 April	10 April	17 April	17 May
Number of individuals	3,053	3, 353	3,146	3,663	3,269

Table 8.2 Total numbers of nests inside Lubang Salai including nests left for breeding and marked nests used in this study, and calculated numbers of breeding swiftlets based on two birds per nest.

Date	April 97	September 97	November 97	December 97	February 98
Total nests	915	1,240	1,398	1,176	1,357
Number of sexually productive swiftlets	1,830	2,480	2,796	2,352	2,714

In April 1997, the *A. fuciphagus* colony at Lubang Beruang produced 840 nests, which suggested a breeding population of 1,680 birds (Table 8.3). Lubang Tuking produced approximately 1,800 nests (or 3,600 sexually productive individuals). Further downriver, Lubang Sepayang was reported to produce a combined yield of 4,000 nests while Lubang Mering Jau Sing had about 800 nests. This is equivalent to 8,000 and 1,600 sexually productive individuals, respectively. Based on this information, the sexually productive population of *A. fuciphagus* including those from Lubang Salai is roughly 17,314 individuals. Results from Lubang Salai showed that as much as 73.8% of a colony comprised sexually productive individuals. Therefore, the whole population of *A. fuciphagus* in middle Baram is extrapolated to be 23,500 birds, inclusive immature and sexually unproductive individuals.

Table 8.3 Estimated numbers of nests, and sexually productive individuals, of *A. fuciphagus* from major caves in middle Baram.

Name of Cave	Total nests	Number of sexually productive birds
Lubang Beruang	840	1,680
Lubang Tuking	1,800	3,600
Lubang Sepayang	4,000	8,000
Lubang Mering Jau Sing	800	1,600
TOTAL	7,440	14,880

8.2.2.2 Other Sites

The brief studies at Bau and Kakus generated some information of the nest yield of *A. maximus* from other swiftlet caves. Lubang Poyang at Bau contained not more than 20 nests at the time of the study in April 1997. In addition, accounts from the cave owners revealed that Lubang Merasuk and Lubang Tupak produced roughly 670 and 780 nests, respectively from a harvest in May 1997. This placed the *A. maximus* population in Bau at no less than 2,940 individuals, because there were other larger caves where nest production data were not available. At Bukit Sarang in Kakus, the population of sexually productive individuals of *A. maximus* was estimated to range from 4,962 to 5,456 individuals as shown in Table 8.4.

Table 8.4 Estimated numbers of nests, and sexually productive individuals, of *A. maximus* from caves around Bukit Sarang, Kakus.

Name of Cave	Total nest	Number of sexually productive birds
Lubang Rusa	392	784
Lubang Up-Parong	30 – 35	60 – 70
Lubang Tujuh	93	186
Lubang Nunok	100	200
Lubang Galuk Ujek	85	170
Lubang Akek-lai	117 – 156	234 – 312
Lubang Dangon	8	16
Lubang Talitai & Gelan	100	200
Lubang Me	9 –11	18 – 22
Lubang Laliang	100	200
Lubang Padung Hantu	93	186
Lubang Up-bila	47	94
Lubang Air	234	458
Lubang Medawak	179	358
Lubang Perintah	171	342
Lubang Ludang	62 – 80	124 – 160
Lubang Danum Salop	< 50	< 100
Lubang Lobong	5 – 10	10 – 20
Lubang Danum Sepilut	78 – 156	156 – 312
Lubang Jelan Kekayau	< 80	< 160
Lubang Kanarut	60 – 160	120 – 320
Lubang Towtuang	10	20
Lubang Keepiak-Iliang	5	10
Lubang Perbin	20	40
Lubang Batu Kerkop	5	10
Lubang Out-Ayuk	78	156
Lubang Berkurung Tuguang	40	80
Lubang Batu Isuit	20	40
Lubang Tanokpula	10	20
Lubang Benuyang	39	78
Lubang Seneiling	62	124
Lubang Pu-u-nunok	39	78
Lubang Parit	60	120
TOTAL	≈ 2,481 – 2,728	≈ 4,962 – 5,456

8.3 RECOMMENDED SUSTAINABLE HARVESTING STRATEGIES

Results from the analysis of the chemical constituents of *A. fuciphagus* nests constructed at different months of the year showed little seasonal variation (section 7.3). Therefore, it is unnecessary to take into consideration the chemical properties of the nest as determinant of harvesting date when drafting a management plan. However, important decisions in designing optimal harvesting strategies rest upon the morphological appearance of the nests and the breeding productivity of swiftlets.

Under natural conditions, without any exploitation of nests, *A. fuciphagus* has a minimum of two annual breeding bouts, while a small proportion of the population is capable of producing a third brood. Nevertheless, current harvesting practises do not give swiftlets any chance to breed because of the short interval between successive harvests. Therefore, it was concluded that at least one bout of breeding should be set aside for raising the young. Hence, the important question is when is the most suitable and productive time for breeding?

From a biological stand point, the Aug-Nov or Dec-Mac breeding bouts should be selected in preference to the Apr-Jul breeding bout, because more swiftlets can produce a clutch during this period (Tables 4.1 and 4.8). Hence, more young swiftlets are produced for the same opportunity cost of a missed harvest.

The productivity from the Aug-Nov and Dec-Mac breeding bouts did not differ much. The RI value for Lubang Salai is 1.32 and 0.97 for the Aug-Nov and Dec-Mac breeding bout, respectively, representing a small difference of 0.35 nestling raised per adult pair. Similarly, the corresponding value recorded in Lubang Beruang is 1.28 and 1.03, showing a difference of 0.25 nestling raised per adult pair. However, the Aug-Nov breeding bout witnessed a faster and more active nest building period (Table 5.31), with cleaner, heavier and bigger nests (Table 5.42 & Table 5.43). Nests of such quality can also fetch the highest selling price. Therefore, it is advisable to harvest nests of this season from an economic standpoint. This establishes a clear compromise point between nest exploitation and conservation. Furthermore, all nests are rebuilt if this batch of nests is harvested (Table 5.35). In effective, the consequence of nest harvesting based on this recommendation is that it only reduces by approximately half the natural breeding capacity of the swiftlets.

It is recommended that the batch of nests built after the Aug-Nov breeding bout, and the major moulting season, be harvested as shown schematically in Figure 8.1. Assuming nest building of the year begins sometime in mid-August, this harvest will be carried out in mid-October. Most of these nests will contain eggs or even very young nestlings, and these have to be destroyed. It has been observed that the adult swiftlets are able to absorb such abuse and make repeated attempts at breeding. Because *A. fuciphagus* employs a multi-brooded breeding strategy, the overall success of reproduction is not determined by any one single bout of

Date	Action	Interval	
Early August			
Mid August	Onset of nest building		
Late August			
		30 days	
Early September			60 days
Mid September	Nest completed		
Late September	First egg appears		
Early October			
Mid October	**FIRST HARVEST**		
Late October		10 – 14 days	
Early November	Expected redeposition		≈ 47 ± 6 days
Mid November			
Late November		30 days	
Early December	**SECOND HARVEST**		
Mid December	Re-deposition	immediately	
Late December			
		30 days	
Early January	Replacement nest		
Mid January	Eggs appear		
Late January		≈ 25 days	
Early February	First hatching		≈ 110 – 120 days (BREEDING PERIOD)
Mid February			
Late February			
		≈ 45 days	
Early March			
Mid March			
Late March	Fledging		
Early April	**THIRD HARVEST** or "cave cleaning"		
Mid April			
Late April			
		≈ 47 ± 6 days	
Early May			
Mid May	Expected subsequent clutch		
Late May			
Early June	**FOURTH HARVEST** or "cave cleaning"		
Mid June			
Late June			
Early July			
Mid July	**FIFTH HARVEST**		
Late July			

Figure 8.1 The recommended sustainable harvesting schemes for *A. fuciphagus* in Sarawak.

breeding but by the cumulative total of several attempts. Therefore, the destruction of one batch of eggs or nestlings does not hold up the swiftlet for another attempt.

After the first harvest of the year in October, new replacement nests are anticipated to be deposited within 10 to 14 days, and nests will approach their maximum size in approximately another 30 days. The second recommended harvest should be carried out before any eggs are laid so that the salivary glands are still active. Hence, nest rebuilding will begin immediately, usually within two days after removal (section 5.2.2). Thereafter, the nests should be left undisturbed, allowing the swiftlets to raise their young in a period that coincides with the Dec-Mac breeding bout.

The next harvest, which is the third of the year, can be done as soon as the nestlings have fledged in early April the following year, approximately four months after the previous harvest. This interval is sufficient for one successful bout of breeding that comprises 30 days for nest construction, 25 days for incubation (Table 4.10), 45 days for brooding (Table 4.11) and an additional 20 days to allow for variations. A similar minimum interval of 130 to 135 days between harvest was proposed by Kang *et al.* (1991) to achieve sustainable harvest. After the nestlings have fledged, a small portion of the colony will probably continue breeding. Results from this study have shown that the Apr-Jul breeding bout is the least productive (Table 4.8). Consequently, it is best to prevent this by constantly removing the nest until the onset of the heavy moult in May and June (Table 4.22 & Figure 4.9) to conserve resources and energy that would otherwise be invested in the least productive breeding attempt of the year. This allows the swiftlets to condition themselves, building up lipid or protein storage and have a better start in the subsequent bout of breeding starting in August.

As the major moult is approaching, nest building activity will decrease accordingly. Not many nests are rebuilt (Table 4.2), or at most small token nests are constructed from apparently degenerating salivary glands. In this study, it has been observed that many of these nests fall before the start of the following breeding bout (section 5.4). Therefore, it is advisable to harvest all the nests constructed during this period and allow the entire colony a clean start with a better uniformity in the size of nest. Such practise has been carried out traditionally and is generally referred as "cave cleaning". This can be carried out twice as recommended and the second "cave cleaning" should be done in late July.

Finally, behavioural studies have revealed that swiftlets leave the cave to forage during the day and only return in the evening (section 4.7.1). Therefore, nest harvesting should be carried out during the day, preferably between 1000 and 1400 hours, while the swiftlets are away. This will minimise the disturbance to the swiftlets. In addition, incubating swiftlets are very sensitive to abrupt outbursts of sound and easily startled. During the period allocated for breeding, it is recommended that the swiftlets be disturbed as little as possible. If there is a need to enter the cave, it is advisable to forewarn the incubating swiftlets in order to avoid a frenzied departure

that might throw the eggs off the nest (section 4.7.2). This could be done by clapping, or coughing outside the cave, and allowing time for the swiftlets to leave their nest cautiously.

8.4 AN INTEGRATED APPROACH TO SWIFTLET CONSERVATION

8.4.1 Participation Of Local Communities

The management of swiftlets should incorporate careful consideration of the biological, social, economic and legal parameters. Community participation, customary tenure systems and traditional practices must be respected and built upon in designing or implementing any conservation plan (McNeely, 1994). Sankaran (1998) concluded that a sustainable harvest regime could only exist in the Andaman and Nicobar islands, India, if some form of cave ownership exists. In Sarawak, the local communities or individuals are given the rights to harvest the nests although the Edible Birds' Nest Rules, 1998, states that all edible nest yielding caves are state property. In this respect, there needs to be more transparency on the licensing of harvesting rights. In addition, the registrar of licensees needs to be updated regularly and more efforts are needed to ascertain that every licensee complies with the recommendations for sustainable management. Successful implementation of the recommended plan not only requires commitment on the part of the State government, but also depends on the support and involvement of cave owners. In Sarawak, most of the nest yielding caves are located in remote areas and widely scattered, making enforcement extremely difficult and not feasible in many areas. Therefore, the participation and co-operation of the cave owners is critical importance.

8.4.2 Establishment Of Nature Reserves

Swiftlets roost in caves but forage far away from their roosting caves. Observation has shown that swiftlets of the genus *Aerodramus* can fly up to 25 km one way from known nest caves to feed (Cranbrook, 1984; Francis, 1987b). Ideally, a large tract of forest, preferably primary forest surrounding the caves, should be reserved as the main feeding ground for the swiftlets. Conversely, swiftlets might be able to tolerate some degradation of habitat around their roosting cave if there are other suitable feeding grounds nearby. In Baram, *A. fuciphagus* has been observed feeding above regenerating forest left for approximately 15 years after being selectively logged. Further to the west, *A. maximus* and two other species of swiftlets were observed feeding above oil palm plantation.

It has been proposed that substantial expanses of land should be gazetted around all the swiftlets caves as nature reserves. Beside maintaining the integrity of the environment inside or around the caves, this area should provide an adequate supply of food for swiftlets, especially

when they need to forage closer to their roosting cave when raising young. In future, these reserves would be the only remaining areas with high quality feeding grounds, when adjacent areas have been cleared for agriculture or development.

8.4.3 Interactive Management — Swiftlets House Farming

Interactive management is a strategy of species preservation that relies upon co-ordination of a "metapopulation" that includes populations living in the wild and in captivity (Conway, 1995). Given the current trend of habitat fragmentation and conversion, species conservation over the long term will require management to reduce extinction risk, and thus may include *ex situ* populations (Mallinson, 1995). As a secondary measure to conserve the edible nest swiftlets, this strategy could be used to increase their survival prospects with the integrated support of subpopulations established in "swiftlets houses". However, unlike traditional zoos or other captive breeding programs, the swiftlets are free to forage outside and only return to roost and nest. "Swiftlet farming" can be defined as a production system of edible swiftlets nest by preparing special designs and construction of building to allow swiftlets to nest (Wirjoatmodjo & Samedi, 1996). It could be likened to apiculture, but instead of a hive, a specially constructed building imitating a cave-liked environment provides alternative or additional roosting places.

This idea is not new. The practise of farming the edible nest swiftlets has been in existence for some time in Java, Indonesia. It is believed that the first of such houses originated from Sedayu in East Java in 1880 (Marzuki, 1987). The initial approach was passive and colonisation of such buildings by the swiftlets was a matter of pure luck. Little was done to improve the conditions within these houses to attract the swiftlets. It was only in the post-war decades that techniques of house farming experienced some improvements and flourished in Java, and more recently spread to Sumatra (Nugroho & Whendrate, 1996; Mardiastuti, 1996). Currently, there is an estimated 6,000– 7,500 swiftlet houses in Java (Pakpahan & Soehartono, 1994).

In Java, houses occupied by *C. esculenta* have been used extensively to convert into edible nest swiftlets houses through a of cross-fostering programme where eggs of *A. fuciphagus* are swapped into nests of *C. esculenta.* As the new *A. fuciphagus* establish themselves, the light intensity within the building is reduced to 2Ef or less by sealing and reconstructing all large openings into small window apertures (Marzuki, 1987). Another approach is to construct buildings that emulate cave-liked conditions. Parallel wooden beams spaced at regular interval are fixed onto the ceiling to provide nesting sites (Kuncoro, 1995). To lure the swiftlet, recording of swiftlets roosting vocalisation is repeatedly played at dusk from

many loud speakers distributed in the buildings. In all cases, water in pots and pans are placed on the ground to maintain a relative humidity of 80 – 90% and temperature at 24 to 26°C (Whendarto & Madyana, 1988; Wahyu, 1995).

This practice is not known to occur in Sarawak. Successful establishment of such "swiftlets houses" in Sarawak would require a thorough understanding of the seasonal breeding patterns of *A. fucipahgus*, *A. maximus* and *C. esculenta*, as well as of their distribution. There is still no sign of a swiftlet house, or any attempt to establish one in Sarawak thirty-eight years after Medway's (1961) article on swiftlets house farming was published in the Sarawak Gazette. Nevertheless, any such undertakings in the future will require the approval of the State authorities, e.g. the Forest Department or the Biodiversity Council. Compared to the free-enterprise system in Indonesia, somewhat open to abuse, an opportunity exists for careful state planning with sustainable management and species conservation to forefront in the process. There is ample scope for both species of edible nest swiftlets to be sustainably managed. Because the white-nest species has now been comprehensively studied, there is now a pressing need to acquire a better understanding of the breeding periodicity of *A. maximus* that have a wider distribution range in Sarawak.

8.5 CONCLUSIONS

This study has despelled any doubt that there is little hope for the conservation of edible nest swiftlets if their nests are too frequently harvested and their eggs and nestlings are destroyed. Because edible nest swiftlets employ a multi-brooded reproductive strategy, they nevertheless have a high tolerance to nest or brood destruction during their breeding season.

A sustainable management plan is recommended, based on sound scientific data from a full year of comprehensive study of *A. fuciphagus* in middle Baram. It has been shown that *A. fuciphagus* normally produce two broods annually, although a small percentage can produce a third brood. Therefore, in order to maintain or to gradually increase the population size of a colony, at least one bout of breeding bout should be permitted each year. After evaluating all the biological results and taking into consideration the social and economical aspects, it was concluded that conservation efforts should focus on the breeding bout between December and March. This would enable two batches of good quality nest to be harvested before allowing the swiftlets to breed. Furthermore, the reproductive vigour of the swiftlets during this period is not seriously decreased and a considerable number of young swiftlets can be produced from the same opportunity cost of foregoing a harvest.

However, there are still several difficulties that need to be resolved. First and foremost is the breakdown of traditional custom, and resulting disunity, among the local communities. This

would seriously hinder the implementation of the recommended management plan in communal caves. An associated issue is the increase in poaching activities. Poaching could effectively be eliminated in caves with single or few openings by gating or positioning cave guards. Immediate problems arise when the people entrusted with harvesting rights became the poachers. Surprisingly, this is an open secret in almost all communal caves. Lastly, there is a need to have more transparency in the regulation and licensing of the harvesting rights. Although all caves in Sarawak are the property of the State, harvesting rights should be granted in a form of renewable license to those enjoying the customary ownership. Transparency and an updated register of owners would legally remove any potential disputes in time to come.

The traditional paradigm of conserving and protecting a species for the sole purpose of species survival and perpetuating biodiversity is obsolete. The practicality and meaning of the word "conservation" needs to be redefined to suite evolving social and economic needs. The conservation of edible nest swiftlets in the next millennium is not as simple as safeguarding the remaining wild populations but requires facing the challenge of a new yet old concept — the commercialisation of "swiftlet farming". The consequences are evident in Indonesia and Vietnam. Unfortunately, Sarawak is lagging behind its neighbours in "swiftlets farming". However, with the recommendations from this study and a recently adopted Wild Life Master Plan, Sarawak is set to benefit from the introduction of "swiftlets farming" and at the same time ensuring the long term survival of the wild populations. A three-pronged strategy, of a sustainable management plan based on sound scientific findings, consolidated conservation policies and an efficient mass production technique, should give the state of Sarawak the supremacy it needs to reclaim its reputation as the centre for the bird nest industry and a role model for a new conservation paradigm in this region.

Finally, there is a need to monitor the success of the recommended sustainable management plan, and can only be considered a success if there is an increase in the nest yields. The caves in middle Baram are most suitable for this purpose because there is currently a reliable scientific record of the total nest yield from all the major nest producing caves. In addition, future work should concentrate on *A. maximus* because this species has a wider distribution in Sarawak, but information on their breeding biology is incomplete compared to *A. fuciphagus*.

REFERENCES

Ali, S. & Ripley, S. D. (1983) *The handbook of the birds of India and Pakistan.* Oxford University Press, Delhi.

Anon. (1994) *Resolution of the conference of the parties.* Convention on International Trade in Endangered Species of Wild Fauna and Flora, Ninth Meeting of the Conference of the Parties. Fort Lauderdale (United States of America), 7 – 18 November 1994. http://www.wcmc.org.uk/CITES/english/eresol911.htr.

Anon. (1996) Reports on the proceeding of the Technical Workshop on Conservation Priorities and Actions For Edible-Nest Swiftlets (Pursuant to Resolution Conference 9.15). Surabaya, Indonesia, 4 – 7 November 1996.

Astheimer, L. B., W. A. Buttemer & J. C. Wingfield. (1995) Seasonal and acute changes in adrenocortical responsiveness in an arctic-breeding bird. *Hormones and Behavior.*, 29 : 442 – 457.

Banks, E. (1935) Notes on Birds in Sarwak with a list of native names. *Sarawak Mus. Jour.*, 4 (3) No.14 : 267 – 326.

Banks, E. (1937) Seasonal variation in the "white" edible birds' nests. *Sarawak Mus. Jour.*, 4 : 519 – 522.

Banks, E. (1986) A note on edible birds' nests. *Brunei Mus. Jour.*, 6 (2) : 209 – 210.

Barrett-Lennard, L. G., J. K. Ford & K. A. Heise. (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Anim. Behav.*, 51 : 553 – 565.

Basir, M. M., F. Gombek, L. Ambu, S. H. Yatim & L. K. Sim. (1996) *Biology, distribution and management of swiftlets in Malaysia with special reference to Collocalia fuciphaga & C. maxima.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Bauchau, V. & Seinen, I. (1997) Clutch desertion and re-nesting in pied flycatchers: an experiment with progressive clutch removal. *Anim. Behav.*, 54 : 153 – 161.

Becking, J. H. (1985) Swift. Pages 572 – 575. In *A Dictionary of Birds* (ed. B. Cambell and E. Lack). Poyser, Calton.

Beeley, J. G. (1985) *Glycoprotein and proteoglycan techniques, Vol 16.* In Laboratory techniques in biochemistry and molecular biology (ed. R. H. Burdon & P. H. van Knippenberg). Elsevier, Amsterdam.

Bennett, E. L., T. G. Melvin, J. G. Robinson & A. R. Rabinowitz. (1996) A master plan for wildlife in Sarawak. *Wildlife Conservation Society and Sarawak Forestry Department* : 116 – 124.

Biddle, F. & Belyavin, G. (1963) The haemagglutination inhibitor in edible bird-nest: its biological and physical properties. *J. gen. Microbiol.*, 31 : 31 – 44.

Birkhead, T. R. & Møller, A. P. (1992) *Sperm competition in birds: Evolutionary causes and consequences.* Academic Press, London.

Birkhead, T. R. & Møller, A. P. (1993) Why do male birds stop copulating while their partners are still fertile. *Anim. Behav.*, 45 : 105 – 118.

Blanken, W. M. & Van den Eijnden, D. H. (1985) Biosyhthesis of terminal Gal1,3Galß1,4GlcNAc-R oligosaccharide sequences on glycoconjugates. *J. Biol. Chem.*, 260 : 12927 – 12934.

Boersma, P. D. (1982) Why some birds take so long to hatch. *Amer. Natur.*, 120 (6) : 733 – 750.

Bradbury, B. & Blakey, J. K. (1998) Diet, maternal condition, and offspring sex ratio in zebra finches, *Poephila guttata. Proc. R. Soc. Lond.*, B 265 : 895 – 899.

Braun, B. M. & Hunt, G. L. Jr. (1983) Brood reduction in black-legged kittiwakes. *Auk*, 100 : 469 – 476.

Breton, C., R. Oriol & A. Imberty. (1998) Conserved structural features in eukaryotic and prokaryotic fucosyltransferases. *Glycobiology*, 8 : 87 – 94.

Briggs, S. A. (1992) *Basic guide to pesticides: their characteristics and hazards.* Hemisphere Publishing Corp., Washington, Philadelphia, London.

Brinkhof, M. W. G. & Cavé, A. J. (1997) Food supply and seasonal variation in breeding success: an experiment in the European Coot. *Proc. R. Soc. Lond.*, B 264 : 291 – 296.

Broad, S. (1987) Swiftlets' spit in the soup. *TRAFFIC Bull.*, 9 : 45 – 56.

Broad, S. (1995) Swiftlet nest: feeding a booming market. *IUCN Bull.*, 26 (1) : 22.

Brooke, R. K. (1970a) Geographical variation and distribution in *Apus barbatus, A. bradfieldi* and *A. niansae.* (Aves: Apodidae). *Durban Ms. Novitates.*, 8 (19) : 363 – 374.

Brooke, R. K. (1970b) Taxonomic and evolutionary notes on the subfamilies, tribes, genera and subgenera of the Swifts (Aves: Apodidae). *Durban Mus. Novitates.*, 9 (2) : 13 – 24.

Brooke, R. K. (1972) Generic limits in old world Apodidae and Hirundinidae. *Bul. Brit. Ornit. Club.*, 92 : 53 – 57.

Brown, C. R. & Brown, M. B. (1986) Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). *Ecology*, 67 : 1206 – 1218.

Brown, C. R., M. B. Brown & M. L. Shaffer. (1991) Food-sharing signals among socially foraging cliff swallows. *Anim. Behav.*, 42 : 551 – 564.

Bruggeman, V., E. D'Hondt., L. Berghman, O. Onagbesan., D. Vanmontfort., F. Vandesande & E. Decuypere. (1998) The effect of food intake from 2 to 24 weeks of age on LHRH-I content in the median eminence and gonadotrophin levels in pituitary and plasma in female broiler breeder chickens. *Gen. Comp. Endocrinol.*, 112 (2) : 200 – 209.

Bryant, D. M. & Tatner, P. (1990) Hatching asynchrony, sibling competition and siblicide in nesting birds: studies of swiftlets and bee-eater. *Anim. Behav.*, 39 : 657 – 671.

Buonomo, F.C., P. Griminger & C. G. Scanes. (1982) Effects of gradation in protein-calorie restriction on the hypothalamic pituitary-gonadal axis in young domestic fowl. *Poult. Sci.*, 61 : 800.

Burder, J. R. N. (1961) The birds' nest caves at Gomantong, North Borneo. *Mal. Nat. Jour.*, 21st Anniv. Special Issue : 172 – 177.

Burke, W. H. & Dennison, D. T. (1980) Prolactin and luteinizing hormone levels in female turkeys (*Meleagris gallopavo*) during a photoinduced reproductive cycle and broodiness. *Gen. Comp. Endocrinol.*, 41 : 92.

Callaghan, D. A., J. S. Kirby, & B. Hughes. (1997) The effect of recreational waterfowl hunting on biodiversity – implication for sustainability. In *Harvesting wild species: Implication for biodiversity conservation* (ed. C. H. Freese). The John Hopkins University Press, Baltimore and London.

Candy, D. J. (1980) *Biological functions of carbohydrates.* Blackie, Galsgow and London.

Carraway, K. L. & Hull, S. R. (1991) Cell surface mucin-type glycoproteins and mucin-like domains. *Glycobiology*, 1 : 131 – 138.

Cate, C. T. & Hilbers, J. (1991) Effects of brood size on inter-clutch intervals, offspring development and male-female interactions in the ring dove (*Streptopelia risoria*). *Anim. Behav.*, 41 : 27 – 36.

Champion, A., A. A. Gooley, M. Callahgan, M. I. Carrin, R. L. Bernstein, E. Smith & K. L. Williams. (1991) Immunodominant carbohydrate determinants in the multicellular stages of *Dictyostelium discoideum. J. Gen. Microbiol.*, 137 : 2431 —2438.

Chantler, P. & Driessens, G. (1995) *Swifts, a guide to the swifts and treeswifts of the world.* Pica Press, Sussex.

Chêng, T.-K. (1969) *Archaeology in Sarawak.* W. Heffer & Sons Ltd., Cambridge.

Colley, K. J. (1997) Golgi localization of glycosyltransferases: more questions than answer. *Glycobiology*, 7 : 1 – 13.

Conway, M. (1995) Wild and zoo animal interactive management and habitat conservation. *Biodiversity and Conservation*, 4 : 573 – 595.

Corpuz, L. B. & Leon, J. L. (1996) *Harvesting of edible nests and national policies governing edible nest swiftlets in the Philippines.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Cranbrook, Earl of [IV] & Lord Medway. (1965) Lack of ultrasonic frequencies in the calls of swiftlets. *Ibis*, 107 : 258.

Cranbrook, Earl of (1984) Report on the birds' nest industry in the Baram District and at Niah, Sarawak. *Sarawak Mus. Jour.*, 33 (54) : 145 -170.

Cranbrook, Earl of [V], S. Somadikarta & S. N. Kartikasari. (1996) *Swiftlets (Aves, Apodidae, "Collocaliini"): An annotated bibliography prepared for the Depatment of the Environment.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Cresswell, W. (1997) Nest predation: a relative effects of nest characteristics, clutch size and parental behaviour. *Anim. Behav.*, 53 : 93 – 103.

Crick, Q. P., D. W. Gibbons & R. D. Magrath. (1993) Seasonal changes in clutch size in British birds. *J. Anim. Ecol.*, 62 : 263 – 273.

De Groot, R. A. (1983) On the trail of bird's nest soup : caves, climbs and high stakes. *Smithsonian.*, 14 (6) : 66 – 74.

Dhondt, A. A. (1989) The effect of old age on the reproduction of Great Tits *Parus major* and Blue Tits *P. caeruleus*. *Ibis*, 131 : 268 – 280.

Dickinson, E. C. (1989) A review of smaller Philippine swiftlets of the genus *Collocalia*. *Forktail*, 5 : 23 – 34.

Duckworth, W. & Kelsh, R. (1988) A bird inventory of Similajau National Park. *International Council For Bird Preservation, Cambridge.*

El Halawani, M. E., W. H. Burke & P. T. Dennison. (1980) Effect of nest deprivation on serum prolactin level in resting female turkey. *Biol. Reprod.*, 23 : 118.

Er, K. B. H., M. J. Vardon, M. T. Tanton, C. R. Tidemann & G. J. W. Webb. (1995) *Edible birds' nest swiftlets and CITES: A review of the evidence of population decline and nest harvesting effects.* Working paper 1995/3. Centre for Resource and Environmental Sciences, Australian National University.

Etchison, J. R. & Freeze, H. H. (1996) A new approach to mapping co-localization of multiple glycosyl transferases in functional Golgi preparations. *Glycobiology*, 6 : 177 – 189.

Eu, H. K. (1996) *Elixir of the Empress Dowanger.* New Straits Times, Tue., 9 July 1996.

Fan, Z. & He, F. (1996) *The status and trade of Edible-nest Swiftlets genus Collocalia in China.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Farner, D. S. (1960) *Digestion and the digestive system. In* Biology and comparative physiology of birds (A. J. Marshall eds.). Academic Press, New York and London.

Fogden, M. P. L. (1972) The seasonality and population dynamics of equatorial forest bird in Sarawak. *Ibis*, 114 (3) : 307 – 342.

Fodgen, M. P. L. & Fodgen, P. M. (1979) The role of fat and protein reserves in the annual cycle of the Grey-backed camaroptera in Uganda (Aves: Sylvidae). *J. Zool. Lond.*, 189 : 233 – 258.

Follett, B. K. (1976) Plasma follicle-stimulating hormone during photoperiodically induced sexual maturation in male Japanese quail. *J. Endocrinol.*, 69 : 117.

Francis, C. M. (1987a) Hatching asynchrony and egg-size variation in White-bellied Swiftlets (*Collocalia esculenta*). Unpubl. MSc. thesis. Queen's University, Kingston, Ontario, Canada.

Francis, C. M. (1987b) The management of edible bird's nest caves in Sabah. *Sabah Forest Department* : 1 – 217.

Freese, C. H. (1997) The "use it or lost it" debate. In *Harvesting wild species: Implication for biodiversity conservation* (ed. C. H. Freese). The John Hopkins University Press, Baltimore and London.

Fukuda, M. & Hakomori, S. (1979) Carbohydrate structure of galactoprotein, a major transformation-sensitive glycoprotein released from Hamster embryo fibroblast. *J. Biol. Chem.*, 254 : 5451 – 5457.

Fukuda, M., S. B. Levery & S. Hakomori. (1984) Carbohydrate structure of Hamster plasma fibronectin. *J. Biol. Chem.*, 257 : 6856 – 6860.

Fullard, J. H., R. M. R. Barclay & D. W. Thomas. (1993) Echolocation in Free-flying Atiu Swiftlets (*Aerodramus sawtelli*). *Biotropica*, 25 (3) : 334 – 339.

Furr, B. J. A., R. C. Bonney, R. J. England & F. J. Cunningham. (1973) Luteinizing hormone and progesterone in peripheral blood during the ovulatory cycle of the hen (*Gallus domesticus*). *J. Endocrinol.*, 57 : 159.

Gibson-Hill, C. A. (1952) The apparent breeding seasons of land birds in North Borneo and Malaya. *Bull. Raffles Mus.*, 24 : 270 – 294.

Gill, F. B. (1990) *Ornithology*. W.H. Freeman and Company, New York.

Good, L. K. (1993) The status of the Black Nest Swiftlets in Niah. *Tiger Paper.*, 20 (1) : 15 - 18.

Good, L. K. & Wong, P. M. H. (1989) *Birds' nest industry and swiftlet conservation in Sarawak*. In proceedings of the Pan Malaysian Forestry Conference, Kuantan, July 1989.

Grier, J. W. (1982) Ban on DDT and subsequent recovery of reproduction in Bald Eagles. *Science*, 218 : 1232 – 1235.

Griffin, D. R. (1958) *Listening in the dark; the acoustic orientation of bats and men*. Yale Univ. Press., New Haven.

Griffin, D. R. & Thompson, D. (1982) Echolocation by cave swiftlets. *Behav. Ecol. Sociobiol.*, 10 : 119 – 123.

Gunawardena, J. (1997) The collection of the Indian Swiftlet *Collocalia unicolor* for the bird-nest trade in Sri Lanka. *Oriental Club Bulletin*, 26 : 23 – 25.

Hails, C. J. & Turner, A. K. (1985) The role of fat and protein during breeding in the White-bellied Swiftlet (*Collocalia esculenta*). *J. Zool. Lond.*, 206 (A) : 469 – 484.

Hammond, R. W., W. H. Burke & F. Hertelendy. (1981) Influence of follicular maturation of pregesterone release in chicken granulosa cells in respone to turkey and ovine gonadotrophins. *Biol. Reprod.*, 24 : 1048.

Hara, S., M. Yamaguchi, Y. Takemori, K. Furuhata, H. Ogura, & M. Nakamura. (1989) Determination of Mono-*O*-acetylated *N*-Acetylmeuraminic acids in human and rat sera by fluorometric High-performance Liquid Chromatography. *Anal. Biochem.*, 179 : 162 – 166.

Harduin-Leper, A., M.-A. Recchi & P. Delannoy. (1995) 1994: the year of sialyltransferases. *Glycobiology*, 5 : 741 – 758.

Harrisson, T. (1959) New archaeological and ethnological results from Niah caves, Sarawak. *Man 1* : 1 – 18.

Harrisson, T. (1966) Onset of echo-location clicking in *Collocalia* Swiftlets. *Nature, Lond.*, 212 : 530 – 531.

Harrisson, T. (1974) The food of *Collocalia* swiftlets (Aves, Apodidae) at Niah Great Cave in Borneo. *J. Bombay Nat. Hist.*, 71 : 376 – 393.

Harvey, S., C. G. Scanes & K. I. Brown. (1986) Adrenals. In *Avian Physiology* (ed. P. D. Sturkie). Springer-Verlag, New York.

Hau, M., M. Wikelski & J. C. Wingfield. (1998) A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proc. R. Soc. Lond.*, B 265 : 89 – 95.

Heaney, V. & Monagham, P. (1995) A within-clutch trade-off between production and rearing in birds. *Proc. R. Soc. Lond.*, B 261 : 361 – 365.

Hector, J. A., J. P. Croxall & B. K. Follett. (1986) Reproductive endocrinology of the Wandering Albatross *Diomedea exulans* in relation to biennial breeding and deferred sexual maturity. *Ibis*, 128 : 9 – 22.

Hirschberg, C. B. & Snider, M. D. (1987) Topography of glucosylation in the rough endoplasmic reticulum and Golgi apparatus. *Ann. Rev. Biochem.*, 56 : 63 – 87.

Höhn, E. O. (1961) Endocrine glands, thymus and pineal body. In *Biology and comparative physiology of birds. Vol. II* (ed. A. J. Marshall). Academic Press, New York and London.

Honda, S., T. Konishi, S. Suzuki, M. Takahashi, K. Kakehi, & S. Ganno. (1983) Automated analysis of hexosamines by High-performance Liquid Chromatography with photometric and fluorimetric postcolumn labelling using 2-cyanoacetamide. *Anal. Biochem.*, 134 : 483 – 488.

Hopkins, C. D. & Bass, A. H. (1981) Temporal coding of species recognition signals in an electric fish. *Science*, 212 : 85 – 87.

Hose, C. (1926) *Natural man: A record from Borneo*. Reprinted Oxford University Press, Singapore, 1988.

Hose, C. (1927) *Fifty years of romance and research*. pp. 98, 186, 190,192. Hutchinson & Co. Ltd., London.

Hose, C. & McDougall, W. (1912) *The pagan tribes of Borneo* (1st ed.). Vol. 2. Reprinted Frank Cass & Co. Ltd., London, 1966.

Houston, D. C., D. Donan & P. Jones. (1995a) The source of nutrients required for egg production in zebra finches. *J. Zool. Lond.*, 235 : 469 – 484.

Houston, D. C., D. Donan, P. Jones, I. D. Hamilton & D. Osborne. (1995b) Changes in the muscle condition of female zebra finches *Poephila guttata* during egg laying and the role of protein storage in bird skeletal muscle. *Ibis*, 137 : 322 – 329.

Howe, C., L. T. Lee & H. M. Rose. (1960) Influenza virus sialidase. *Nature*, 188 : 251 – 252.

Howe, C., L. T. Lee & H. M. Rose. (1961) *Collocalia* mucoid : A substrate for Myxovirus Neuraminidase, *Arch. Biochem. Biophys.*, 95 : 512 – 520.

Huang, E. S.-R., K. J. Kao & A. V. Nalbandow. (1979) Synthesis of sex steroids by cellular components of chicken follicles. *Biol. Reprod.*, 20 : 454.

Hudson, R. H., R. K. Tucker & M. A. Haegele. (1984) *Handbook of toxicology of pesticides to wildlife.* Resource Publication 153. U. S. Department of Interior, Fish and Wildlife Service, Washington, D.C.

Hughes, R. C. (1983) *Glycoprotein.* Chapman and Hall, London.

Imai, K., K. Tanaka & S. Nakajo. (1972) Gonadotrophic activities of anterior pituitary and of blood plasma and ovarian respone to exogenous gonadotropin in moulting hens. *J. Reprod. Fert.*, 30 : 433.

Inskipp, T., N. Lindsey & W. Duckworth. (1996) An anntated checklist of the birds of the oriental region. *Oriental Bird Club, U.K.*

Johnson, A. L. (1986) Reproduction in female. In *Avian Physiology* (ed. P. D. Sturkie). Springer-Verlag, New York.

Johnston, D. W. (1958) Sex and age characters and salivary glands of the chimney swift. *Condor*, 60 : 73 – 84.

Kang, N. & Lee, P. G. (1991) The Edible-nest swiftlets *Aerodramus spp. Nature Malaysiana*, 16 : 44 - 51.

Kang, N. & Lee, P. G. (1993) Bird's nest soup: Panacea or ill? *Nature Watch*, Singapore., 1 (1) : 15 – 18.

Kang, H., C. Hail & J. Sigurdsson. (1991) Nest construction and egg-laying in the Edible-nest swiftlets (*Aerodramus spp.*) and the implications for harvesting. *Ibis*, 133 : 170 - 177.

Kathan, R. H. & Weeks, D. I. (1969) Structure studies of collocalia mucoid. I. Carbohydrate and amino acid composition. *Arch. Biochem. Biophys.*, 134 : 572 – 576.

Kellogg, W. N. (1958) Echo ranging in the porpoise. *Science*, 128 : 982 – 988.

Kendeigh, S. C., V. R. Dol'nik & V. M. Gavrilov. (1977) Avian energetics. In *Granivorous birds in ecosystems* (ed. J. Pinowski and S. C. Kendeigh). Cambridge University Press, London.

Kidd, H. & D. R. James. (1991) *The agrochemicals handbook* (3rd eds.). Royal Society of Chemistry Information Services, Cambridge, UK.

Klatchko, J. (1994) Little birds, big business. *Asia Inc.*, 80 – 91.

Kleene, R. & Berger, E. G. (1993) The molecular and cell biology of glycosyltransferases. *Biochim. Biophys. Acta*, 1154 : 283 – 325.

Koncoro, S. (1995) *Studi preferensi persarangan burung walet (*Collocalia fuciphaga*) terhadap jenis kayu dan posisi lagur tempat bersarang pada rumah budidaya sarang burung*. Unpubl. thesis, Universitas Airlangga, Surabaya, Indonesia.

Kong, Y. C., W. M. Keung, T. T. Tip, K. M. Ko, S. W. Tsao & M. H. Ng. (1987) Evidence that epidermal growth factor is present in swiftlet's (*Collocalia*) nest. *Comp. Biochem. Physiol.*, 87 B (2) : 221 – 226.

Kornfeld, R. & Konfeld, S. (1985) Assembly of asparagine-linked oligosaccharides. *Annu. Rev. Biochem.*, 54 : 631 – 664.

Krapu, G. L. (1981) The role of nutrient reserves in mallard reproduction. *Auk*, 98 : 29 – 38.

Lack, D. 1964. Swift. Pages 793 – 795. In *A New Dictionary of Birds* (ed. A. L. Thomson). Nelson, London.

Lack, D. & Lack, E. (1951) The breeding biology of the swift (*Apus apus*). *Ibis*, 93 : 501 – 546.

Landsman, R. E. (1993) Sex differences in external morphology and electric organ discharges in imported *Gnathonemus petersii* (Mormyriformes). *Anim. Behav.*, 46 : 417 – 429.

Langham, N. (1980) Breeding biology of the Edible-nest Swiftlet *Aerodramus fuciphagus*. *Ibis.*, 122 (4) : 447 – 461.

Lau, A. S. M. & Melville, D. S. (1994) International trade in swiftlet nests with special reference to Hong Kong. *TRAFFIC International, Cambridge.*

Lee, P. G. & Kang, N. (1994) The reproductive strategies of edible-nest swiftlets (*Aerodramus spp.*). *Bull. British Ornithologiest' Club*, 114 (2) : 106 – 112.

Lee, P. L. M., D. H. Clayton, R. Griffiths & R. D. M. Page. (1996) Does behaviour reflect molecular phylogeny in cave swiftlets (Aves: Apodidae)? A test using cytochrome *b* mitochondrial DNA sequences. *Proc. Natl. Acad. Sci. USA*, 93 : 7091 – 7096.

Leh, C. M. U. (1987) *A status report on the swiftlets and Bats of Niah Cave*. The Sarawak Museum.

Leh, C. M. U. (1993) *A guide to birds' nest caves and birds' nest of Sarawak.* The Sarawak Museum.

Lim, C. K. (1993) *Variasi protein dan systematik burung layang-layang perut putih (White-bellied Swiftlets).* Unpubl. thesis. Zool. Dept., Univeristy of Malaya, Kuala Lumpur.

Lindström, Å., G. H. Visser & S. Daan. (1993) The energetic cost of feather synthesis is porportional to basal metabolic rate. *Physiol. Zool.*, 66 : 490 – 510.

Linström, Å, S. Daan & G. H. Visser. (1994) The conflict between moult and migratory fat deposition: a photoperiodic experiment with bluethroats. *Anim. Behav.*, 48 : 1171 – 1181.

Lis, H. & Sharon, N. (1993) Protein glycosylation: structural and functunal aspects. *Glycobiology*, 218 : 1 – 27.

Little, R. M. (1996) Conference report - South African Wildlife Management Association Conference on the Sustainable Use of Wildlife (9 – 11 April, 1996). *S. Afr. J. Wildl. Res.*, 26 (4) : 99.

Little, R. M. & Crowe, T. M. (1997) Pesticide residues in helmeted guineafowl *Numida meleagris* livers collected on deciduous fruits farms in the Western Cape province, South Africa. *S. Afr. J. Wildl. Res.*, 27 (1) : 1 – 4.

Lotem, A. (1998) Brood reduction and begging behaviour in the Swift *Apus apus*; no evidence that large nestlings restrict parental choice. *Ibis*, 140 : 507 – 511.

Lourie, S. A. & Tompkins, D. M. (1998) The diets of Malaysian swiftlets (in press).

Low, H. (1848) *Sarawak: Its inhabitants and productions* (1st ed.). p. 378. Reprinted Frank Cass & Co. Ltd., London (1968).

Ludvig, E., L. Vanisek, J. Torok, & T. Csorgo. (1995) Seasonal variation of clutch size in the European blackbird *Turdus meruda*: a new ultimate explanation. *J. Anim. Ecol.*, 64 : 85 – 94.

Mainka, S. A. & Mills, J. A. (1995) Wildlife and traditional Chinese medicine – supply and demand for wildlife species. *Jour. Zoo & Wildl. Medicine.*, 26 : 193 – 200.

Malaysian Ministry of Agriculture (1999) Guidelines on the arial application of pesticides. http://agrolink.moa.my/doa/english/laws/aa_anex2.htm

Malaysian Ministry of Health (1999) Malaria Control. http://dph.gov.my/Division/dcd/Verktor/malaria.htm#MALARIA

Mallinson, J. J. C. (1995) Conservation breeding programmes: an important ingredient for species survival. *Biodiversity and Conservation*, 4 : 617 – 635.

Manual, C. G. (1937) Beneficial swiftlets and edible birds' nest industry in Bacuit, Palawan. *Philippine J. Sci.*, 62 (3) : 379 – 391.

Mardiastuti, A. (1996) *Distribution of swiftlet houses in Java and Madura.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Mardiastuti, A. & Mranata, B. (1996) *Biology and Distribution of Indonesian swiftlets with a special reference to Collocalia fuciphaga and Collocalia maxima.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Marshall, A. J. (1961) Breeding seasons and migration. In *Biology and Comparative Physiology of Birds. Vol. II.* (ed. A. J. Marshall). Academic Press, New York & London.

Marshall, A. J. & Folley, S. J. (1956) The origin of nest-cement in edible-nest swiftlets (*Collocalia sp.*). *Proc. Zool. Soc. Lond.*, 126 : 383 – 389.

Marzuki, H. A. (1987) Prinsip-prinsip budidaya pemeliharaan burung walet. *Biro Pusat Rehabilitasi Sarang Burung.*

McNeely, J. A. (1994) Protected areas for the 21st century: working to provide benefits to society. *Biodiversity and Conservation*, 3 : 390 – 405.

Medway, Lord. (1957) Birds' Nest Collecting. *Sarawak Mus. Jour.*, 8 (10) N.S. : 252 – 260.

Medway, Lord. (1958) Birds' nesting among the Land Dayaks. *Sarawak Mus. Jour.*, 8 (11) N. S. : 465 – 469.

Medway, Lord. (1959) Echo-location among *Collocalia. Nature, Lond.*, 184 : 1352 – 1535.

Medway, Lord. (1960) Cave Swiftlets. *In:* Smythies, B. E. *The Birds of Borneo.* Oliver & Boyd, Edinburgh.

Medway, Lord. *(1961a)* Birds' nest businessmen. *The Sarawak Gazette*, 28 Febuary 1961, 19 – 20.

Medway, Lord. (1961b) The identity of *Collocalia fuciphaga* (Thunberg). *Ibis*, 103a : 625 – 626.

Medway, Lord. (1962a) The relationship between the reproductive cycle, moult and changes in the sublingual salivary glands of the swiftlet *Collocalia Maxima* Hume. *Proc. Zool. Soc. Lond.*, 138 (2) : 305 – 315.

Medway, Lord. (1962b) The swiftlets (*Collocalia*) of Niah Cave, Sarawak. Part I. Breeding Biology. *Ibis*, 104 : 45 - 66.

Medway, Lord. (1962c) The swiftlets (*Collocalia*) of Niah Cave, Sarawak. Part II. Ecology and the regulation of breeding. *Ibis*, 104 : 228 - 245.

Medway, Lord. (1963) The antiquity of trade in edible birds'-nest. *Fed. Mus. J.*, N.S. 8 : 36 - 47.

Medway, Lord. (1966) Field characters as a guide to the specific relations of swiftlets. *Proc. Linn. Soc. Lond.*, 177 (2) : 151 - 177.

Medway, Lord. (1967) The function of echonavigation among swiftlets. *Anim. Behav.*, 15 : 416 – 420.

Medway, Lord. (1969) Studies on the biology of the edible-nest swiftlets of South-east Asia. *Malay. Nat. J.*, 22 (2) : 57 – 63.

Medway, Lord, J. R. D. Wall & G. E. Wilford. (1967) Unusual features on the walls of limestone caves at Bau, West Sarawak, Malaysia. *Z. Geomorph*, NF 11 (2) : 161 – 168.

Medway, Lord & Pye, J. D. (1977) Echolocation and the Systematics of Swiftlets. (pp. 225 – 238). In *Evolutionary Ecology* (ed. B. Stonehouse and C. Perrins). Macmillan, London.

Mills, J. A. & Jackson, P. (1994) Killed for a cure: A review of the world-wide trade in tiger bone. *TRAFFIC International, Cambridge.*

Milner-Gulland, E. J. & Beddington, J. R. (1993) The exploitation of elephants for the ivory trade: an historical perspective. *Proc. R. Soc. Lond.*, B 252 : 29 – 37.

Monaghan, P., M. Bolton & D. C. houston. (1995) Egg production constraints and evolution of avian clutch size. *Proc. R. Soc. Lond.*, B 259 : 189 – 191.

Moreau, R. E. & Moreau, W. M. (1940) Incubation and fledging periods of African birds. *Auk*, 57 : 313 - 325.

Morton, G. A. & Morton, M. L. (1990) Dynamics of postnuptial molt in free-living mountain white-crowned sparrows. *Condor*, 92 : 813 – 828.

Ng, M. H., K. H. Chan & Y. C. Kong. (1986) Potentiation of mitogenic response by extracts of the swiftlet's (*Collocalia*) nest. Biochem. International, 13 (3) : 521 – 531.

Nguyen Quang, P. (1990) Discovery of the Black-nest swiftlet *Collocalia maxima* Hume in Vietnam and preliminary observation of its biology. *Manuscript due to be sent to the Bulletin du Museum (Zoologie).*

Nguyen Quang, P. (1993) *The biological basis of sustainability of harvesting, conservation and development the resource of Edible-nest Swiftlet* Collocalia fuciphaga germani *Oustalet in Vietnam.* Unpubl. PhD. thesis, University of Hanoi.

Nguyen Quang, P. (1994) Breeding and moult in the Edible-nest swiftlets *Collocalia fuciphaga germani* in Vietnam. *Alauda*, 62 (2) : 107 - 115.

Nguyen Quang, P. (1996) *Some major factors influencing the breeding success of white-nest swiftlets Collocalia fuciphaga germani Oustalet in Vietnam.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Nguyen Quang, P. (1998) Influence of cave structure, microclimate and nest harvesting on the breeding of the White-nest Swiftlet *Collocalia fuciphaga germani* in Vietnam. *Ibis*, 140 : 257 – 264.

Nilsson, J.-Å. (1993) Bisexual incubation facilitates hatching asynchrony. *Amer. Natur.*, 142 (4) : 712 – 717.

Norton, B. G. (1992) A new paradigm for environmental management. In *Ecosystem health: New goals for environmental management.* (ed. R. Costanza, B. G. Norton, and B. D. Haskell). Island Press, Washington, D. C.

Novick. A. (1959) Acoustic orientation in the cave swiftlet (*Collocalia brevirostris unicolor*). *Biol. Bull. Mar. Ins. Lab. Wood Hole*, 117 : 497 – 503.

Nugroho, E. & Whendrato, I. W. (1994) The farming of Edible-nest Swiftlets, *Aerodramus fuciphagus*, in Indonesia. *Indonesian Swiftlet Lovers Association, Semarang.*

Nugroho, E., I. Whendrato & I. M. Madyana. (1994) Merubah rumah seriti menjadi rumah walet. *Eka Offset, Semarang.*

Nugroho, E. & Whendrate, I. (1996) *The farming of Edible-nest swiftlets in Indonesia.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Oberholser, H. C. (1906) A monograph of the genus *Collocalia. Proc. Acad. Nat. Sci. Philadelphia*, 58 : 177 – 212.

Orolfo, P. (1961) Discovery of Bird's Nest Caves in North Borneo. *Sarawak Mus. Jour.*, 10 : 270 – 273.

Pakpahan, A. M. & Soehartono, T. R. (1994) *Current Situation of the Edible-nest Swiftlets in Indonesia.* In proceedings of the 1994 Convention of the Parties to CITES meeting in Florida, U.S.A.

Panneerselvam, K. & Freeze, H. H. (1996) Mannose enters mammalian cells using a specific transporter that is insensitive to glucose. *J. Biol. Chem.*, 271 : 9417 – 9421.

Panneerselvam, K., J. R. Etchison, F. Skovby and H. H. Freeze. (1997) Abnormal metabolism of mannose in families with Carbohydrate-deficient Glycoprotein Syndrome Type 1. *Biochem. Mol. Med.*, 61 : 161 – 167.

Paulson, J. C. & Colley, K. J. (1989) Glycosyltransferases: structure, localization, and control of cell type-specific glycosylation. *J. Biol. Chem.*, 264 (30) : 17615 – 17618.

Payne, R. B. (1972) Mechanisms and control of molt. In *Avian Biology, Vol. II* (ed. D. S. Farner and J. R. King). Academic Press, London and New York.

Perrins, C. M. (1970) The timing of birds' breeding season. *Ibis*, 112 : 242 – 255.

Perrins, C. M. & McCleery, R. H. (1985) The effect of age and pair bond on the breeding success of Great Tits *Parus major.* Ibis, 127 : 306 – 315.

Peters, J. L. (1940) *Check-list of birds of the World.* Vol. 4 : 220 – 259. Harvard University Press, Cambridge.

Pozsgay, V., H. Jennings & D. L. Kasper. (1987) 4,8-Anhydro-N-acetylneuraminic acid isolation from edible bird's nest and structure determination. *Eur. J. Biochem.*, 162 : 445 – 450.

Price, L. (1996) The Gomantong Caves. *Malayan Naturalist*, 49 (3) : 22 – 27.

Pye, J. D. (1980) Echolocation signals and echoes in air. pages 309 – 353. In *Animal sonar systems* (ed. R-G. Busnel and J. F. Fish. Pleunum Publishing Corp., New York, New York.

Rademacher, T. W., R. B. Parekh & R. A. Dwek. (1988) Glycobiology. *Annu. Rev. Biochem.*, 57 : 785 – 838.

Raharjo, Y.C., A. Hoo, S. Wiryoatmodjo & M. Subrata. (1996) *Nest production and management systems of cave-inhabiting Collocalia fuciphaga and C. maxima from some known areas in Indonesia.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Rawles, W. E. (1960) The integumentary system. In *Biology and comparative physiology of birds. Vol. I* (ed. A. J. Marshall). Academic Press, New York and London.

Richner, H., A. Oppliger & P. Christe. (1993) Effect of an ectoparasite on reproduction in great tits. *J. Anim. Behav.*, 62 : 703 – 710.

Rodriguez-Gironés, M. A. (1996) Siblicide: the evolutionary blackmail. *Amer. Natur.*, 148 (1) : 101 – 122.

Rowe, L., D. Ludwig & D. Schluter. (1994) Time, condition and the seasonal decline of avian clutch size. *The Amer. Natur.*, 143 (4) : 698 – 722.

Safford, R. J. & C. G. Jones. (1997) Did organochlorine pesticide use cause declines in Mauritian forest birds? *Biodiversity and Conservation*, 6 : 1445 – 1451.

Sales, G. & Pye, D. (1974) *Ultrasonic communication by animals.* Chapman and Hall, London.

Salomonsen, F. (1983) Revision of the Melanesian Swiftlets (Apodes, Aves) and their Conspecific forms in the Indo-Australian and Polynesian Region. *Biol. Skr. Dan. Vid. Selsk.*, 23 (5) : 1 – 112.

Salwasser, H. (1990) Conserving biological diversity: A perspective on scope and approaches. *Forest Ecology and Management*, 35 : 75 – 90.

Sankaran, R. (1995) Impact assessment of nest collection on the Edible-nest Swiftlet in the Nicobar islands (SACON Occasional Report 1). *Salim Ali Centre for Ornithoilogy & Natural History* : 1 – 26.

Sankaran, R. (1998) The impact of nest collection on the Edible-nest Swiftlet *Collocalia fuciphaga* in the Andaman & Nicobar Islands. *Salim Ali Centre for Ornithoilogy & Natural History* : 1 – 41.

Sarawak Online (1999) Commercial agriculture — major crops (settled agriculture). http://www.sarawak.gov.my/sarawak_online/comm_agr/crops.htm.

Sas-Rolfes, M. T. (1995) *Rhino: Conservation, economics and trade-off.* IEA Environment Unit, London.

Scanes, C. G., P. J. Sharp, S. Harvey, P. M. M. Godden, A. Chadwick & W. S. Newcomer. (1979) Variation in plasma prolactin, thyroid hormones, gonadal steriods and growth hormone in turkeys during the induction of egg laying and mult by different photoperiods. *Br. Poult. Sci.*, 20 : 143.

Scanes, C. G. (1986) Pituutary gland. . In *Avian Physiology* (ed. P. D. Sturkie). Springer-Verlag, New York.

Schoech, S. J., R. L. Mumme & J. C. Wingfield. (1996) Prolactin and helping behaviour in the cooperatively breeding Florida scrub-jay, *Aphelocoma c. coerulescens. Anim. Behav.*, 52 : 445 – 456.

Selman, R. G. & Houston, D. C. (1996) The effect of prebreeding diet on reproductive output in zebra finches. *Proc. R. Soc. Lond.*, B 263 : 1585 – 1588.

Sharon, N. (1975) *Complex carbohydrates: Their chemistry, biosynthesis, and functions.* Addison-Wesley Publishing Company, London.

Sharp, P. J., C. G. Scanes, J. B. Williams, S. Harvey & A. Chadwick. (1979) Variations in concentrations of prolactin, luteinzing hormone, growth hormone and progesterone in the plasma of broody bantams (*Gallus domesticus*). *J. Endocrinol.*, 80 : 51.

Sibley, C. G. & Monroe, B. L. (1990) *Distribution and Taxonomy of Birds of the World.* Yale University Press, New Haven & London.

Silverin, B., M. Kikuchi & S. Ishii. (1997) Seasonal changes in follicle-stimulating hormone in free-living Great Tits. *Gen. Comp. Endocrinol.*, 108 : 366 – 373.

Sim, B. K. (1994) *A town built on bird's saliva.* The Star, Tuesday, 17 November 1994.

Skutch, A. F. (1945) Incubations and nestling periods of central American birds. *Auk*, 62 : 8 - 37.

Smilovich, D., N. Malagolini, C. Fagioli, C. Lalla, R. Sitia & F. Serafini-Cessi. (1998) Differential expression of Galα1,3Gal epitope in polymeric and monomeric IgM secreted by mouse myeloma cells deficient in α2,6-sialyltransferase. *Glycobiology*, 8 : 841 – 848.

Smyth, D. M. & Roberts, J. R. (1983) The sensitivity of echolocation by the Grey Swiftlet (*Aerodramus spodiopygius*). *Ibis*, 125 : 339 – 345.

Smythies, B. E. (1960) *The Birds of Borneo*. Oliver and Boyd, London.

Soehartono, T. & Mardiastuti, A. (1996) *Searching to the conservation of swiftlets: A case of Indonesia.* In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Spiro, R. G. & Bhoyroo, V. D. (1984) Occurance of α-D-galactosyl residues in the thyroglobulins from several species. *J. Biol. Chem.*, 259 : 9858 – 9866.

Sreekumar, K. & Sharp, P. (1998) Effect of photostimulation on concentrations of plasma prolactin in castrated batams (*Gallus domesticus*). *J. Neuroendocrinology*, 10 (2) : 147 – 154.

St. John, S. (1862) *Life in the forests of the Far East.* Vol. 1. Reprinted Oxford University Press, Kuala Lumpur, 1974.

St. John, S. (1879) *The life of Sir James Brooke: Rajah of Sarawak.* p. 404. William Blackwood & Sons, Edinburgh.

Strydom, D. J. & Cohen, S. A. (1994) Comparison of amino acid analyses by Phenylisothiocyanate and 6-Aminoquinolyl-*N*-hydroxysuccinimidyl Carbamate *precolumn derivatization. Anal. Biochem.*, 222 : 19 – 28.

Sturkie, P. D. (1965) Reproduction in the female and egg production. In *Avian Physiology* (2nd ed.). Cornell University Press, Ithaca.

Suthers, R. A. & Hector, D. H. (1982) Mechanisms for the reproduction of echolocating clicks by the Grey Swiftlet, *Collocalia spodiopygia. J. Comp. Physiol.*, 148 (4) : 457 – 470.

Svensson, E. (1995) Avian reproductive timing: when shuld parents be prudent? *Anim. Behav.*, 49 : 1569 – 1575.

Swaddle, J. P. & Witter, M. S. (1994) Food, feathers and fluctuating asymmetries. *Proc. R. Soc. Lond.*, B 255 : 147 – 152.

Tarburton, M. K. (1986a) The reproductivelife of the White-rumped Swiftlet in Fiji. *Emu*, 86 : 214 – 227.

Tarburton, M. K. (1986b) The food of the White-rumped Swiftlet (*Aerodramus spodiopygius*) in Fiji. *Notornis* 33 (1) : 1 – 16.

Tarburton, M. K. (1987) An experimental manipulation of clutch and brood size of White-rumped Swiftlets *Aerodramus spodiopygius* of Fiji. *Ibis*, 129 (1) : 107 – 114.

Then, S. (1997) *Ban on harvesting birds nests lifted.* The Star, 28 February 1997.

Thiollay, J.-M. (1997) Disturbance, selective logging and bird diversity: A Neotropical forest study. *Biodiversity and Conservation*, 6 : 1155 – 1174.

Tompkins, D. M. (1997) Impact of nest-harvesting on swiftlet reproduction. *J. Wildl. Res.*, 2 (2) : 102 – 106.

Valli, E. & Summers, D. (1990) Nest gatherers of Tiger cave. *Nat. Geogr. Mag.*, 117 (1) : 107 – 133.

Varki, A. & Diaz, S. (1984) The release and purification of sialic acids from glycoconjugates: Methods to minimise the loss and migration of O-Acetyl groups. *Anal. Biochem.*, 137 : 236 – 247.

Varki, A. (1992) Biosynthesis and function of *N*- and *O*-substituted sialic acids. *Glycobiology*, 12 : 25 – 40.

Verboven, N. & Verhulst, S. (1996) Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis. *J. Anim. Ecol.*, 65 : 264 – 273.

Wahyu, D. W. (1995) *Mengembangkan populasi walet lewat penangkaran.* Pancaraba, Mitra Lingkungan (Kemaran) : 88 –95.

Wang, C. C. (1921) The composition of Chinese edible bird's nest and the nature of their proteins. *J. Biol. Chem. Baltimore.*, 49 : 429 – 439.

Ward, P. (1969a) The annual cycle of the Yellow-vented bulbul *Pycnonotus goiavier* in a humid equatorial environment. *J. Zool. Lond.*, 157 : 25 – 45.

Ward, P. (1969b) Seasonal and diurnal changes in the fat content of an equatorial bird. *Physiol. Zool.*, 42 : 85 – 95.

Waugh, D. R. & Hail, C. J. (1983) Foraging ecology of a tropical aerial feeding bird guide. *Ibis*, 125 (2) : 200 – 217.

Whendarto, I. & Madyana, M. (1988) *Budidaya burung walet.* Eka Offset, Semarang.

Whittow, C. C. (1986) Energy metabolism. In *Avian Physiology* (ed. P. D. Sturkie). Springer-Verlag, New York.

Wilford, G. E. (1964) The geology of Sarawak and Sabah caves. *Geological Survey Borneo Region, Malaysia.*, Bull. 6 : 1 – 177.

Wilson, S. C. & Cunningham, F. J. (1980) Modification by metyrapone of the open period for pre-ovulatory LH release in the hen. *Br. Poult. Sci.*, 21 : 351.

Wingfield, J. C., T. P. Hahn, R. Levin & P. Honey. (1992) Environmental predictability and control of gonadal cycles in birds. *J. Exp. Zool.*, 261 : 214 – 231.

Wingfield, J. C. & Farner, D. S. (1993) Endocrinology of reproduction in wild species. In *Avian biology IX* (ed. D. S. Farner, J. R. King & K. C. Parkes), pp. 163 – 327. Academic Press.

Wirjoatmodjo, S. & Samedi. (1996) Sustainable management programme of Indonesian swiftlet nest prodction (revised). In proceedings of the CITES Technical Workshop on Conservation Priorities and Acitons on Edible Bird's Nest, 4 – 7 Nov 1996, Surabaya, Indonesia.

Wyndham, E. (1986) Length of birds' breeding seasons. *Amer. Natur.*, 128 (2) : 155 – 164.

Young, J. Z. (1981) *The life of vertebrates.* (3rd eds.) p 352. Oxford Univ. Press., New York.

The plates below were taken using flash photography. Without it the photographs would be completely pitch black. Always bear in mind species of the genus *Aerodramus* are able to roost and nest in **TOTAL DARKNESS!**

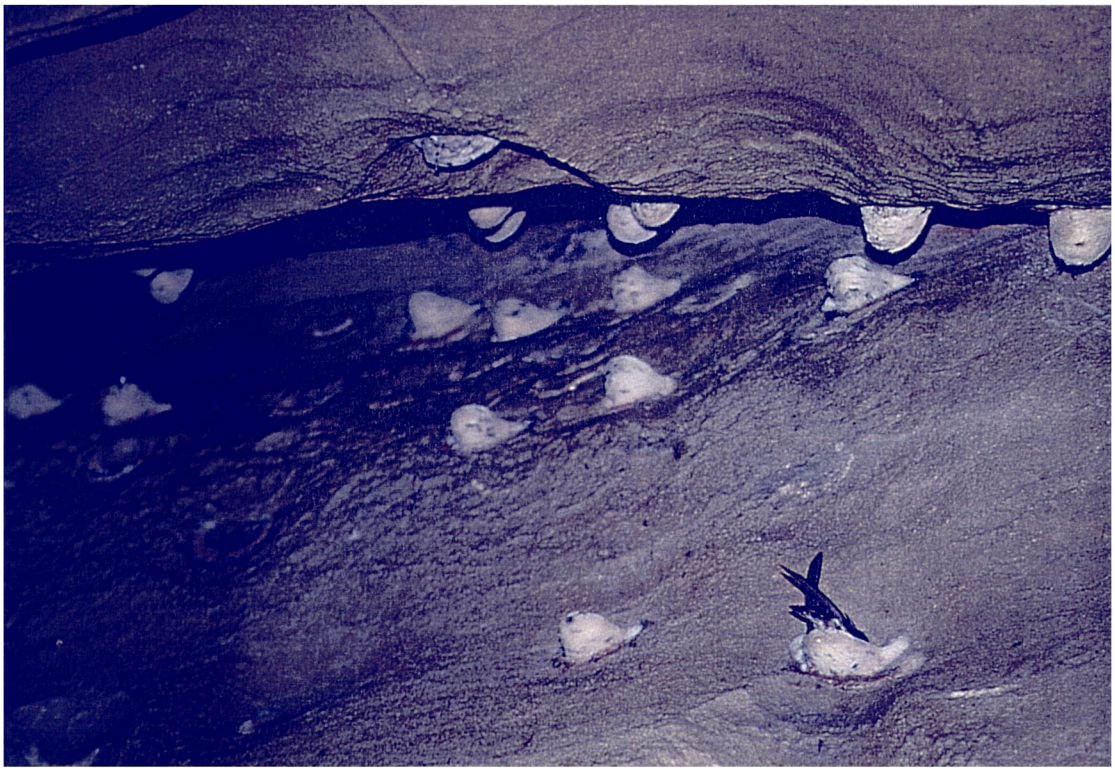

Plate 1. White-nest Swiftlets (*Aerodramus fuciphagus*) nesting on near vertical surfaces of a narrow cavern in Lubang Tuking, middle Baram (1997).

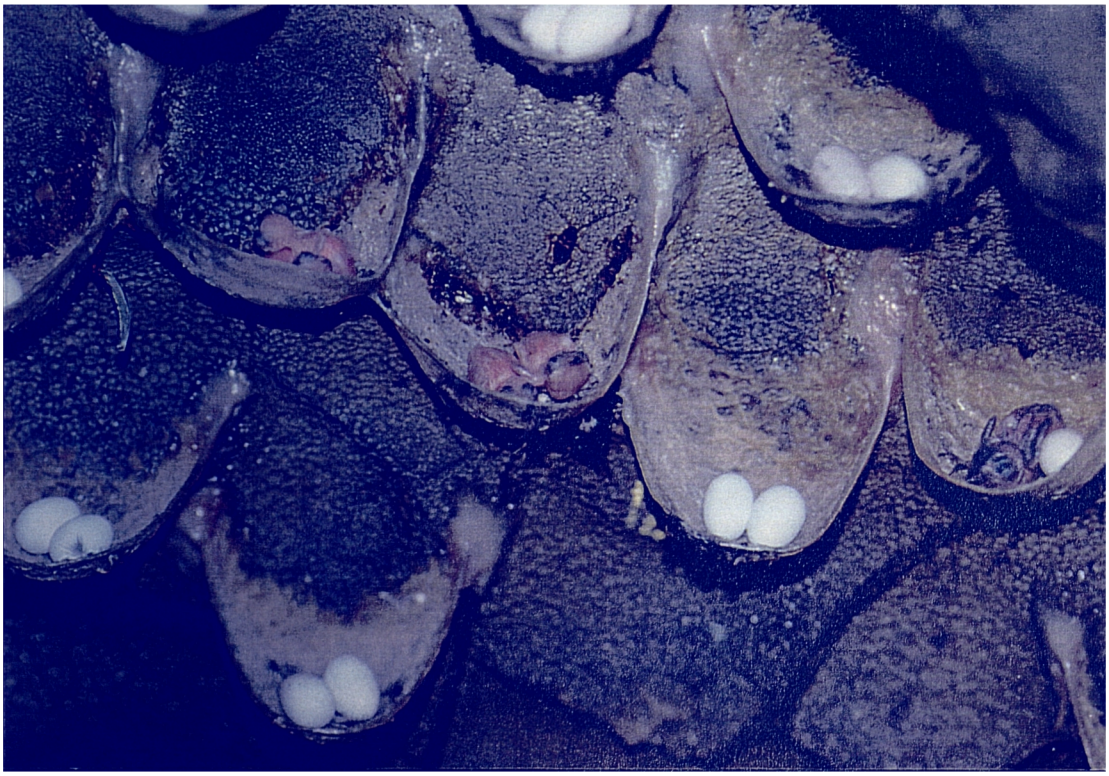

Plate 2. Eggs and nestlings of *A. fuciphagus*; the naked pinkish ones are stage-1 nestlings of about 1 to 6 days old; to the right is a stage-2 nestling (L. Salai, 1997).

Plate 3. Two stage-2 *A. fuciphagus* nestlings of approximately 7 to 13 days old; note the minute feather sheath on the main feather tracks (L. Salai, 1997).

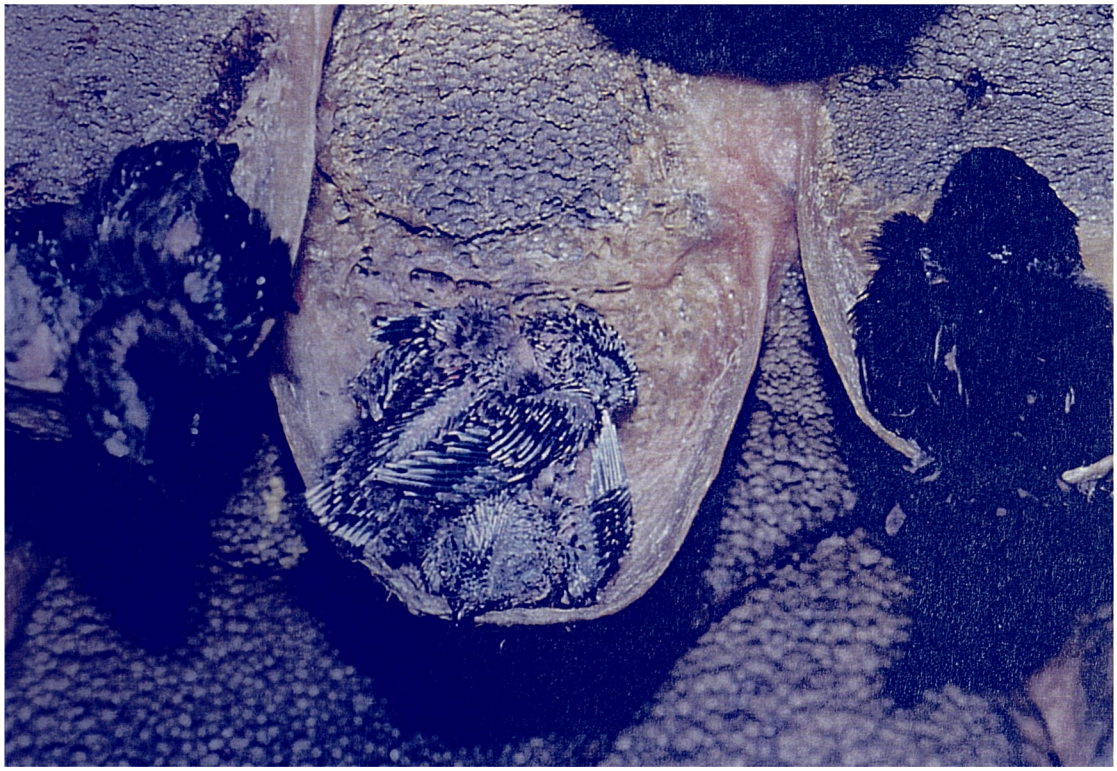

Plate 4. Stage-3 or porcupine-liked nestling of *A. fuciphagus* (≈ 14 – 20 days old); note the erupted feather sheaths; the nestling to the right is roughly a week older or stage-4 (L. Salai, 1997).

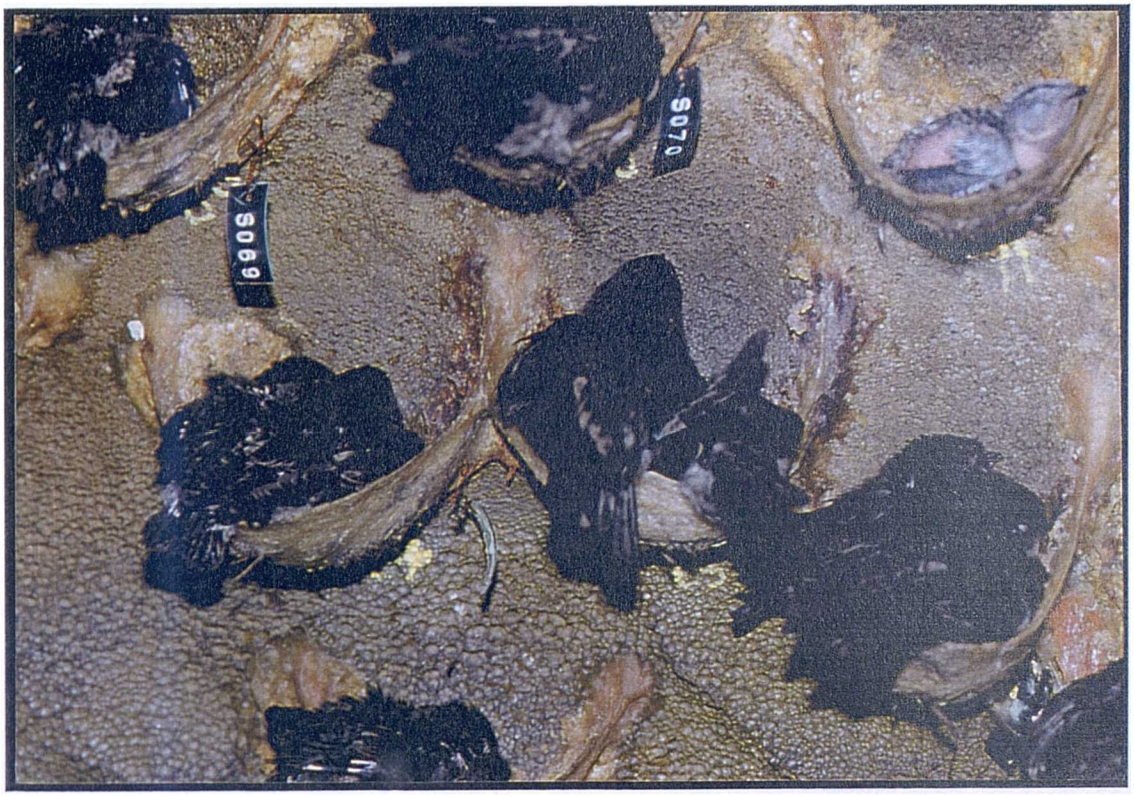

Plate 5. Two stage-4 nestling of *A. fuciphagus* between 21 – 27 days old (middle left); to the right are stage-5 nestling (≈ 28 – 35 days old) with well developed primary feathers but not over-shooting the tip of the rectrices (L. Salai, 1997).

Plate 6. Many stage-7 or near fledging nestling of *A. fuciphagus* (≈ 45 days old); their wings are fully grown and they spend most of the time hanging by the crest of the nest (L. Salai, 1997).

Plate 7. Nestling of *A. fuciphagus*, showing various stages of growth; the one to the extreme right is stage-6 nestling of 36 – 40 days old (L. Salai, 1997).

Plate 8. Multi-nest incident occurs exclusively after a successful breeding attempt; it is very likely that the pair responsible for the construction is the offspring(s) from the precursor nest (L. Salai, 1997).

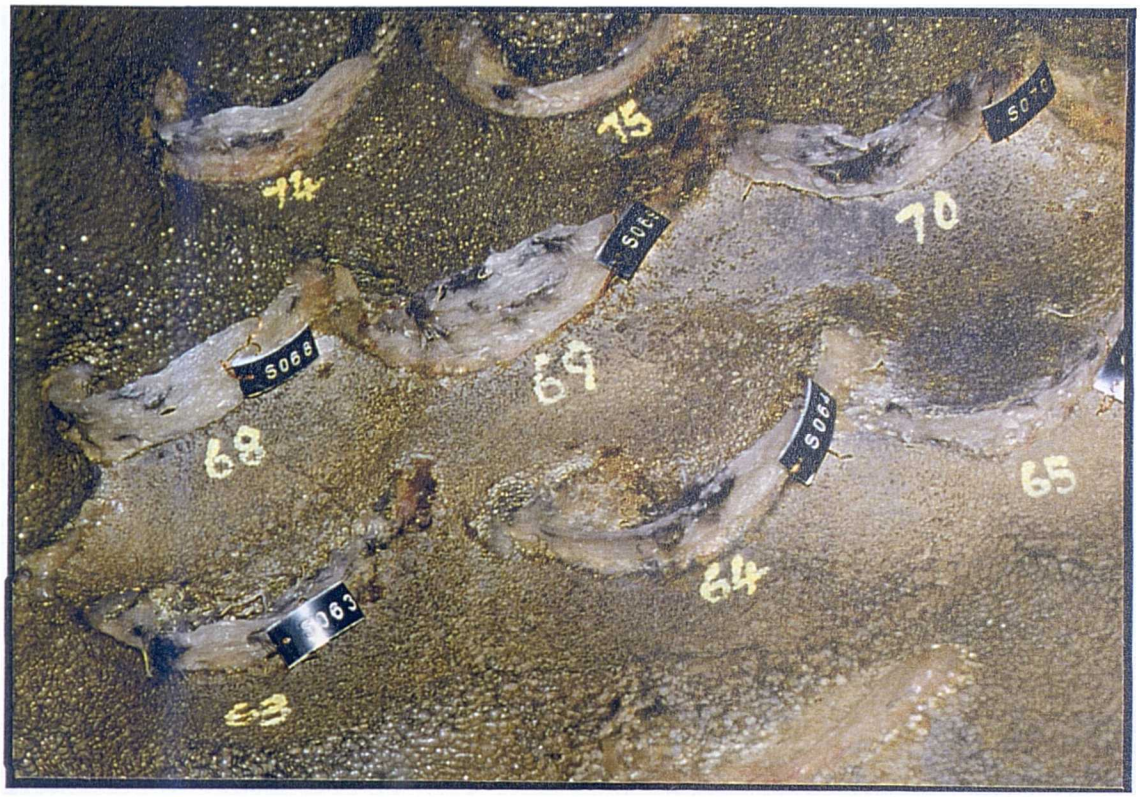

Plate 9. Marked nest of *A. fuciphagus* used in this study; parametric measurements, i.e. D, R, & P, were obtained from these nests; the nest crest is beginning to form (L. Salai, 1997).

Plate 10. After a breeding attempt, deteriorated nest was restored, usually with addition of new salivary nest cement as clearly shown in this photograph; the brownish old nest has been in the cave for about five months (L. Beruang, 1997).

Appendix 1. Systematic list of cave swiftlets of the genus *Hydrochous*, *Collocalia* and *Aerodramus*. *

Species	Common Name	Distribution
Genus *Hydrochous* Brooke		
Hydrochous gigas	Giant Swiftlet	Java; Sumatra; Peninsular Malaysia; Borneo.
Genus *Collocalia* Gray		
Collocalia esculenta	White-bellied Swiftlet	Extensive range in SE Asia; Greater Sundas (mainland and satellite islands); throughout Andaman and Nicobar Is.; Myanmar; Peninsular Thailand; Malaysia; Borneo; Phillipines; New Guinea;
Collocalia linchi	Linchi Swiftlet	Endemic to Sundaic regions; throughout Java; localised in Sumatra and Mount Kinabalu in Borneo.
Collocalia troglodytes	Pygmy Swiftlet	Endemic to Philippine.
Genus *Aerodramus* Oberholser		
Aerodramus elaphra	Seychelles Swiftlet	Endemic to the Seychelles.
Aerodramus francica	Grey-rumped Swiftlet	Endemic to Mascarene islands of Mauritius and Réunion.
Aerodramus unicolor	Indian Edible-nest Swiftlet	Endemic to South India and Sri Lanka.
Aerodramus mearnsi	Philippine Grey Swiftlet	Endemic to Philippines
Aerodramus infuscata	Moluccan Swiftlet	Endemic to SE Sulawesi and Moluccan Islands.
Aerodramus hirundinacea	Mountain Swiftlet	Endemic to New Guinea
Aerodramus spodiopygius	White-rumped Swiftlet	Extensive range on islands on Papuasia, Melanesia and Polynesia.
Aerodramus terraereginae	Australian swiftlet	NE Australia (Queensland)
Aerodramus brevirostris	Himalayan Swiftlet	Extensive S and SE Asian range; Himalaya; Nepal; Bhutan; NE India; uplands of Bangladesh; SW China; N Loas; Myanmar; W Thailand.
Aerodramus whiteheadi	Whitehead's Swiftlet	Endemic to the Philippines.

Species	Common Name	Distribution
Genus *Aerodramus* (continuation)		
Aerodramus nuditarsus	Bare-legged Swiftlet	S and SE New Guinea.
Aerodramus orientalis	Mayr's Swiftlet	Two locations on Melanesian Islands.
Aerodramus salanganus	Mossy-nest Swiftlet	Endemic to Greater Sundas (Sumatra; Java; Borneo).
Aerodramus vanikorensis	Uniform Swiftlet	Philippines; E Indonesia; New Guinea; Melanesia.
Aerodramus pelewensis	Palau Swiftlet	Endemic to Palau Islands.
Aerodramus bartschi	Guam Swiftlet	Endemic to S Mariana Islands.
Aerodramus inquietus	Caroline Swiftlet	Endemic to Caroline Islands.
Aerodramus sawtelli	Sawtell's Swiftlet	Endemic to Atiu Islands in Cook Archipelago.
Aerodramus leucophaeus	Polynesian Swiftlet	Endemic to the Polynesian Islands.
Aerodramus maximus	Black-nest Swiftlet	Wide ranging in SE Asia and throughout the sundas; Myanmar; Thai Peninsula; Peninsular Malaysia; Sumatra; W Java; Borneo;
Aerodramus fuciphagus	White-nest Swiftlet	Extensive though separated SE Asian and Indonesian range; Andaman and Nicobar Islands; coastal SE Asia; SE Hainan coast; Vietnam; Cambodia; Thailand; offshores islands of Peninsular Malaysia; Sumatra; Java; Borneo; Phillipines.
Aerodramus papuensis	Papuan Swiftlet	Endemic to New Guinea.

* **Sources**

1. Cranbrook [V], Earl of, Somadikarta, S. & Kartikasari, S. N. (1996) Swiftlets (Aves, Apodidae, "Collocaliini"): An annotated bibliography prepared for the Depatment of the Environment. *Paper presented in Workshop on the Conservation of the Edible Birdnest of the genus* Collocalia., *4 - 7 Nov 1996, Surabaya, Indonesia.*

2. Chantler, P. & Driessens, G. (1995) *Swifts, a guide to the swifts and treeswifts of the world.* Pica Press, Sussex.

Appendix 2. The date of the lay of the first egg and the fledging of the last nestling for marked nests inside Lubang Salai from April 1997 to March 1998, showing the breeding capability of each pair in every breeding cycle.

Nest	April-July		August-November		December-March	
	Egg	Fledged	Egg	Fledged	Egg	Fledged
S 001	11 May	12 Jul	? 8 Sep	1 Nov (‡) 1 Nov (‡)	5 Jan	18 Mac
S 002	6 Jun	—	23 Sep 27 Sep	? 6 Dec	5 Jan 24 Jan	— ?
S 003	30 May	23 Jul	? 13 Sep	20 Nov 20 Nov	20 Jan 23 Jan	26 Mac 26 Mac
S 004 †	5 May	—	empty		empty	
S 005	6 Jun	?	? 29 Sep	6 Dec *	23 Jan 26 Jan	2 Apr —
S 006	20 Jun	16 Aug	18 Sep 13 Oct	— 15 Dec	20 Jan 23 Jan 19 Feb	— — ?
S 007	abandoned		18 Sep	26 Nov	5 Jan 9 Jan	14 Mac —
S 008	11 May 15 May	17 Jul 23 Jul	7 Oct	—	23 Jan 6 Feb 9 Feb	— ? —
S 009	adandoned		empty		26 Feb	?
S 010	16 Apr	—	13 Sep 30 Sep 3 Oct	— 6 Dec 7 Dec	5 Jan 8 Jan	18 Mac 18 Mac
S 011	5 May	—	23 Sep 25 Sep	— —	9 Feb	—
S 012	?	23 Jul	18 Sep 26 Sep	— 12 Dec	15 Jan 18 Jan	— —
S 013	5 May	8 Jul	13 Sep 30 Sep 3 Oct	— 6 Dec 6 Dec	? 20 Jan	29 Mac 29 Mac
S 014	empty		19 Sep	26 Nov	? 5 Jan	15 Mac 15 Mac
S 015 †	11 May	6 Jun	? 1 Nov	5 Jan 5 Jan	? 16 Jan	25 Mac 25 Mac
S 016	adandoned		empty		30 Jan	9 Apr
S 017	16 Apr 19 Apr	— 23 Jun	10 Oct 13 Oct	2 Jan 2 Jan	? 15 Jan	21 Mac 21 Mac
S 018	16 Apr 21 Apr	— 25 Jun	30 Sep 4 Sep	12 Dec —	? 20 Jan	29 Mac 29 Mac
S 019	11 May	—	20 Sep 23 Sep	— —	20 Jan 9 Feb	— ?
S 020	19 Apr 22 Apr	— —	? 18 Sep	26 Nov 26 Nov	? 15 Jan	— 26 Mac
S 021	10 Apr 14 Apr	19 Jun 20 Jun	8 Sep 11 Sep	20 Nov 20 Nov	? 15 Dec	— 19 Feb
S 022	27 Apr 1 May	10 Jul 10 Jul	26 Sep 28 Sep	4 Dec 4 Dec	? 5 Jan 26 Feb	— — ?
S 023	21 Apr	5 Jul	13 Sep 16 Sep	26 Nov *	5 Jan 7 Jan	14 Mac 14 Mac

(continuation of Appendix 2)

Nest	April-July		August-November		December-March	
	Egg	Fledged	Egg	Fledged	Egg	Fledged
S 024	3 May	12 Jul	? 13 Sep 22 Sep	— — —	? 5 Jan	19 Mac 19 Mac
S 025	3 May	12 Jul	18 Sep	26 Nov	6 Feb 9 Feb	— 21 Apr
S 026	empty		? 13 Sep	21 Nov 21 Nov	20 Jan 23 Jan 19 Feb	— — ?
S 027	adandoned		? 26 Sep	— 5 Jan	? 15 Jan	1 Apr 1 Apr
S 028	adandoned		30 Sep 2 Nov	— —	15 Jan 18 Jan	24 Mac *
S 029	?	23 Jul	27 Oct	—	8 Jan 12 Jan	18 Mac —
S 030	3 May	—	13 Oct 17 Oct	— —	20 Jan 24 Jan 9 Feb	— — —
S 031†	adandoned		27 Oct	—	23 Jan 26 Jan	— —
S 032	adandoned		30 Sep	6 Dec	2 Jan 5 Jan	19 Mac 19 Mac
S 033	5 May	?	23 Oct 27 Oct	5 Jan —	21 Jan 23 Jan	2 Apr 2 Apr
S 034 †	?	24 Jul	16 Oct 20 Oct	— —	15 Jan 19 Jan	24 Mac 24 Mac
S 035 †	3 May	—	27 Oct 30 Nov	— —	? 23 Jan	30 Mac 30 Mac
S 036	26 Apr 30 Apr	8 Jul 8 Jul	1 Nov 5 Nov	5 Jan 5 Jan	empty	
S 037	11 May 13 May	23 Jul —	? 11 Nov	? 12 Jan	30 Jan 2 Feb	— —
S 038	9 May	—	24 Oct 27 Oct	— —	15 Jan 17 Jan 9 Feb	— — —
S 039	empty		13 Oct 16 Oct	26 Dec 5 Jan	21 Jan 23 Jan	28 Mac 28 Mac
S 040 †	adandoned		22 Oct 26 Oct	6 Jan 6 Jan	empty	
S 041	5 May	12 Jul	13 Sep 15 Sep	— 20 Nov	? 2 Feb	? —
S 042	removed		13 Oct 27 Oct	— 5 Jan	empty	
S 043	removed		13 Sep 15 Sep	22 Nov 22 Nov	empty	
S 044 †	removed		27 Oct 1 Nov	5 Jan 5 Jan	4 Feb 8 Feb	? ?
S 045 †	abandoned		empty		9 Feb	?
S 046	removed		empty		empty	
S 047	abandoned		? 29 Aug	4 Nov 4 Nov	2 Dec 6 Dec	— 14 Feb

(continuation of Appendix 2)

Nest	April-July		August-November		December-March	
	Egg	Fledged	Egg	Fledged	Egg	Fledged
S 048	removed		13 Oct 16 Oct	? 2 Jan	? 9 Feb	— —
S 049	removed		? 8 Sep 1 Nov	— — —	empty	
S 050	removed		24 Aug 29 Aug 11 Nov	— 1 Nov —	9 Feb ?	? ?
S 051	removed		1 Nov 26 Nov	— —	26 Feb	?
S 052	removed		24 Aug 28 Aug 20 Nov 24 Nov	4 Nov 4 Nov 1 Feb 1 Feb	26 Feb	?
S 053	3 May 5 May	— —	30 Aug 3 Sep	4 Nov 4 Nov	9 Feb ?	? ?
S 054 †	empty		1 Nov	—	? 2 Feb	? ?
S 055	11 May	—	8 Sep 11 Sep	20 Nov 20 Nov	9 Feb 13 Feb	— —
S 056 †	22 Apr	5 Jul	? 11 Nov	12 Jan 12 Jan	9 Feb 13 Feb	— ?
S 057 †	empty		15 Oct 18 Oct	* *	26 Feb	?
S 058 †	empty		15 Oct 18 Oct	5 Jan 5 Jan	26 Feb	?
S 059	19 Apr 21 Apr	— —	23 Se 25 Sep	6 Dec 6 Dec	7Feb 9 Feb	— —
S 060	22 Apr	5 Jul	? 8 Sep 30 Sep 20 Oct	— — — 28 Dec	9 Feb	—
S 061	5 May 8 May	* 15 Jul	18 Sep 20 Oct 24 Oct	— 5 Jan 5 Jan	19 Feb 23 Feb	? ?
S 062 †	11 May	—	20 Oct	25 Dec	17 Jan 20 Jan	— 30 Mac
S 063	empty		29 Aug 2 Sep	4 Nov —	empty	
S 064	empty		24 Aug 27 Aug	4 Nov 4 Nov	empty	
S 065	empty		30 Jul 16 Aug 19 Aug	— ‡ 4 Nov	5 Jan	16 Mac
S 066	abandoned		16 Aug 19 Aug	27 Oct 1 Nov	3 Jan 5 Jan	20 Mac 20 Mac
S 067	empty		9 Aug ?	20 Oct —	3 Jan	18 Mac
S 068	empty		? 8 Sep 7 Oct	— — —	? 9 Feb	? ?

(continuation of Appendix 2)

Nest	April-July		August-November		December-March	
	Egg	Fledged	Egg	Fledged	Egg	Fledged
S 069	empty		24 Aug 27 Aug	4 Nov 4 Nov	? 3 Feb	? ?
S 070	empty		19 Aug 23 Aug	1 Nov 4 Nov	5 Jan	—
S 071	removed		3 Sep ?	20 Nov —	? 4 Jan	— —
S 072	removed		24 Aug 26 Aug	— —	5 Jan 26 Feb	— ?
S 073	abandoned		8 Sep 11 Sep	20 Nov 20 Nov	22 Jan	?
S 074	removed		24 Aug 26 Aug 27 Oct 1 Nov	— — — —	9 Feb	—
S 075	removed		empty		empty	

Note : a "—" sign denotes the loss of egg before hatching, a " * " means lost of nestling; some of the fledging dates are estimates, a "‡" denotes prematured fledged nestling, a "†" are nests removed on 13 September 1997.

Appendix 3. The value of parameter P and R when the first egg was laid in each of the three breeding cycles from April 1997 to March 1998.

Nest	April-July		August-November		December-March	
	P (cm)	R (cm)	P (cm)	R (cm)	P (cm)	R (cm)
S 001	13.9	6.1	14.3	7.0	14.8	6.8
S 002	13.0	3.1	13.0	5.1	13.0	5.1
S 003	13.1	5.0	13.7	5.1	13.7	5.0
S 004	13.3	6.0	empty		empty	
S 005	12.2	4.4	13.7	6.3	13.7	6.3
S 006	16.4	7.3	14.2	7.6	13.7	8.1
S 007	abandoned		11.2	3.4	12.0	3.2
S 008	14.0	6.5	14.0	7.4	11.4	7.5
S 009	adandoned		empty		14.0	3.8
S 010	15.4	3.0	15.2	3.9	15.2	3.7
S 011	14.3	3.6	16.2	4.2	15.8	4.4
S 012	15.3	8.1	14.5	8.3	15.7	9.2
S 013	14.1	6.8	12.2	7.4	12.3	7.0
S 014	empty		14.8	9.2	14.6	9.0
S 015	15.4	7.5	15.4	7.3	15.4	7.7
S 016	adandoned		empty		11.7	1.9
S 017	13.0	5.4	12.4	5.4	12.4	5.4
S 018	15.3	6.2	14.4	8.1	14.4	6.1
S 019	14.0	5.8	14.8	6.0	14.8	6.0
S 020	16.9	8.2	14.5	8.7	14.3	8.4
S 021	12.5	3.6	13.1	4.1	13.4	4.1
S 022	14.9	3.6	15.9	4.8	15.9	4.8
S 023	14.8	4.9	12.2	5.5	12.8	5.3
S 024	11.9	2.6	12.9	3.1	14.0	3.7
S 025	13.3	5.3	13.9	5.6	14.0	5.4
S 026	empty		15.7	7.7	15.2	7.7
S 027	adandoned		14.0	7.3	14.4	8.0
S 028	adandoned		13.1	6.8	13.0	7.2
S 029	13.1	6.8	15.3	7.5	15.4	7.7
S 030	13.0	7.1	13.7	7.4	13.5	7.7
S 031	adandoned		14.1	6.7	13.7	6.5
S 032	adandoned		13.8	6.8	13.6	6.8
S 033	15.4	8.6	15.0	7.5	14.9	8.3
S 034			13.0	6.0	13.5	6.8
S 035	14.3	5.1	14.0	5.3	13.7	5.0
S 036	14.5	7.1	14.2	7.7	empty	
S 037	13.9	7.3	13.8	7.2	13.8	7.2
S 038	13.6	6.4	14.4	6.6	13.7	6.5
S 039	empty		14.9	8.0	14.9	8.0
S 040	adandoned		12.0	6.1	empty	
S 041	13.9	5.6	13.3	6.0	13.2	5.8

continuation of Appendix 3

Nest	April-July		August-November		December-March	
	P (cm)	R (cm)	P (cm)	R (cm)	P (cm)	R (cm)
S 042	removed		13.4	5.8	empty	
S 043	removed		14.0	5.5	empty	
S 044	removed		14.1	5.6	14.5	5.5
S 045	abandoned		empty		13.2	4.7
S 046	removed		empty		empty	
S 047	abandoned		11.9	8.5	11.5	7.8
S 048	removed		13.1	6.8	13.5	7.1
S 049	removed		15.7	3.7	empty	
S 050	removed		13.2	4.6	13.7	5.0
S 051	removed		14.9	2.6	14.9	3.4
S 052	removed		16.7	5.9	16.8	5.7
S 053	12.1	6.5	12.7	6.9	12.7	6.7
S 054	empty		13.4	8.3	13.3	8.7
S 055	12.4	4.5	14.3	4.5	14.6	4.6
S 056	11.8	5.7	11.5	5.9	11.3	6.0
S 057	empty		12.5	5.4	12.5	5.3
S 058	empty		13.3	3.9	14.2	4.2
S 059	14.5	3.6	14.1	5.2	14.8	4.8
S 060	12.8	6.1	12.6	6.4	12.2	6.3
S 061	15.7	8.7	15.1	8.3	15.5	8.3
S 062	14.4	8.7	12.8	7.8	12.1	7.7
S 063	empty		14.7	6.9	empty	
S 064	empty		15.1	5.5	empty	
S 065	empty		14.5	5.1	15.0	5.1
S 066	abandoned		13.7	5.0	14.6	5.9
S 067	empty		13.6	5.8	14.0	6.0
S 068	empty		13.2	5.3	14.0	5.3
S 069	empty		13.6	5.7	15.7	5.9
S 070	empty		14.6	6.0	15.5	6.0
S 071	removed		14.1	4.6	14.2	4.6
S 072	removed		11.8	6.2	12.1	6.3
S 073	abandoned		13.9	6.0	14.3	5.9
S 074	removed		12.8	6.0	13.2	5.4
S 075	removed		empty		empty	

Appendix 4. Typical daily activities inside Lubang Salai during the brooding period of *A. fuciphagus* and the nature of a returning swiftlet locating its roosting site.

Hours — Activities [Notes]

0900 — about 10 birds from the marked site (S001 – S 062) flew off when alarmed.

0920 — 2 birds flew in. One settled quite fast, flew in directly to the nest and alight on it. Then flutter to nearby nest, inspecting it but flew back.

— the other made 6 attempts before landing. Each trial, fluttering near nest site, emitting a rapid continuos clicking. After failing to land for 5 – 10 seconds, it flew off and circled in the cave (clicking reduced to a short 2 –3 second interval) before making another attempt. The same bird was restless and flew off in less then 10 minute. It seemed to be trying very hard to locate its nest. Of the total of 6 attempts, 4 were made starting from the better lit outer chamber. [NOTE : usually a bird will fly to the outer chamber and re-entering it, presumably a better lighting enable them to regain their sense of direction].

0940 — Feeding (nest S 123); 3 incubating birds (S013, S019 & S025) and one clinging outside (S 018).

0950 — Feeding (S003).

0955 — Feeding (S064).

0957 — Feeding (S103), then sit in nest. [NOTE : brooding parents were prompted to fly off with a slight movement of my body then incubating ones].

1010 — Feeding (S123); feeding unmarked nest below S071. [NOTE : nestling seemed to response and squeaking as soon as the clicking of returning adult were heard (sometimes not their parents)].

1020 — Feeding (S003 & S123).

1030 — One bird made 10 revolving rounds inside cave before landing. In the meantime, it made 4 checking (with very rapid clicking, usually near the cave wall) on one site and another 2 more checking on the opposite site of the cave. Finally it settled on the 2nd one (with 2 checking).

1045 — Feeding, unmarked nest beside S074.

1110 — One bird flew in and circled for 7 – 8 rounds inside cave before landing.

1115 — the one clinging outside S018 moved inside and incubating.

1125 — one bird flew in straight to its nest (unmarked), clean and smooth without circling.

1130 — Feeding (S050).

1135 — Feeding (S121).

1140 — Feeding (S102 & T5).

1145 — Feeding (S064).

1146 — one bird returned to nest S019, landed after 4 attempts. It flew directly to the nest site but flutter and rapidly clicking trying to land but back off after just as it was about to get a foot hold. Repeated this for 3 times, without circling inside the cave.

1150 — one bird flew in straight to its nests and settled. Flew off when beamed with infra-red scope and settled at the far side of the cave for a short while before leaving the cave. [NOTE : seemed like the bird are alerted and can detect the infra-red light from the scope].

1200 — 10 birds in marked nests (S001 to S 062).

1205 — S014 flew straight to its nest, very smooth and no circling.

1245 — Feeding (S065, S066 & S123).

1250 — Feeding (S064).

1325 — Feeding (T5).

1330 — Feeding (S003).

1335 — Feeding (S121).

— one bird was circling (about 50 cycles) inside cave and made 6 attempts to land but failed. Checking at 2 different site with rapid clicks and finally settled in nest S002.

1345 — one bird flew in, settled on the cave surface above some nests for few seconds before flying a short distance down to nest S020.

1400 — Feeding (S063 & S121).

— 10 birds were still around marked site, S043 and S 019 flew off after being alarmed. Both have been inside cave since last night. (Check the next day showed that S043 have newly hatched chicks).

1425 — Feeding (S026 & S121); nest S014 was joined by its partner (i.e 2 birds in one nest).

1430 — 13 birds in marked site S001 to S 062.

— a bird (from S020) returned but landed in nest S025 which was already occupied. Some squeaking followed and the newly arrived bird immediately flew off and finally settled in nest S020.

1435 — S018 was joined by its partner.

— a bird landed in nest S013 with another bird sitting in it (I thought it was the partner). Then it flew off squeaking and finally settled in S010. The owner of S013 did not fight back in the whole event.

1445 — Feeding (S001 & S 064); 22 birds were around the marked site. [NOTE : some birds are beginning to return].

1520 — Owner of S038 flew in straight to an unoccupied nest (S034), then moved to another one a short distance away (S037), and then flew back to the nest it first landed. Few second later, it again moved to a 3rd nest (S038) located above the first one and finally settled down. [NOTE : another example that the swiftlets can not locate precisely its nest at the first instant they returned].

1535 — Feeding (T5).

1600 — 27 birds at marked site (S001 – S037, most with eggs or young) had returned while only 2 birds at marked site (S037-S062, mostly empty) returned.

	Site S001 – S034	Site S037 – S062
4:00 pm	27	2
4:30 pm	35	5
5:00 pm	40	10

1645 — Feeding by both parents at T5; Feeding (S102). [NOTE: most birds will circle inside cave as more bird entering it. A lot of commotions and squeaking at this time].

1745 — 2 birds were seen fighting for a nest; the new comer landed beside another bird sitting in its nest. Then the 2 began squeaking, pecking each other and flapping their wing at the same time. Somehow, their legs got inter-locked and both fell off the nest in the process. [NOTE : Stage 4 nestling in S065 was clinging on the nest crest, flexing and flapping its wings].

Appendix 5. The amount of released *N*-acetylneuraminic acid from hydrolysed edible nest samples quantified using high-performance liquid chromatography.

Nest	Month (Code)	Sample (mg)	Ret. time (min)	Area (µV x sec.)	Height (µV)	Area (%)	Height (%)	Amount (pmol/50µl)	% Amount
	Apr (A040)	0.2	8.733	11312529	528379	91.56	93.52	337.22	97.27
S040	Jul (Au40)	0.3	8.750	2030649	96839	84.19	87.78	61.80	100.00
	Aug (Se040)	0.3	8.783	8916173	428322	93.26	94.67	273.36	98.68
	Apr (A045)	0.3	8.450	5115183	233368	88.61	90.71	149.76	98.69
S045	Jul (Au045)	0.2	8.300	5072185	257298	84.64	89.80	167.65	98.91
	Aug (Se045)	0.3	8.567	4560403	224784	84.73	88.48	144.25	98.33
	Apr (A056)	0.4	8.283	4846861	246394	88.30	91.28	160.54	98.75
S056	Jul (Au056)	0.2	8.467	14457335	721199	91.27	92.99	462.81	98.20
	Aug (Se056)	0.2	8.633	4846072	236717	86.26	89.63	151.91	98.36
	Apr (A057)	0.3	8.467	7106358	352869	89.03	91.61	226.44	98.41
S057	Jul (Au057)	0.2	8.433	6068721	303731	88.33	91.13	194.91	98.33
	Aug (Se057)	0.2	8.617	2941600	145449	86.12	89.67	94.77	99.18
	Apr (A058)	0.2	8.517	5371470	256264	86.98	90.00	164.45	98.40
S058	Jul (Au058)	0.3	8.483	4337167	215366	86.18	89.39	138.21	98.40
	Aug (Se058)	0.3	8.667	8802788	423422	89.48	91.72	271.72	97.79
	Apr (A062)	0.2	8.733	4929143	236587	90.86	92.96	150.99	98.82
S062	Jul (Au062)	0.3	8.717	360707	174178	88.98	91.60	111.16	99.23
	Aug (Se062)	0.2	8.783	2696895	130936	89.13	91.63	83.57	99.34
m 01	Jun	0.2	8.717	5469617	265760	91.66	93.52	169.61	98.74
m 02	Jun	0.3	8.850	5210058	249466	91.23	93.05	159.21	99.13
m 03	Jun	0.2	8.783	11613009	559506	94.60	95.76	357.09	98.64
m 04	Jun	0.3	8.517	6911364	340116	88.72	91.36	218.26	98.10
bn 1	Sep	0.2	8.333	9357155	470842	91.95	94.25	306.79	99.45
bn 2	Sep	0.2	8.367	6390310	322259	90.36	93.29	209.98	98.83
bn 3	Sep	0.3	8.400	10896266	546034	92.78	94.72	355.78	99.28
bn 5	Sep	0.2	8.433	4180795	209857	87.69	90.84	136.74	97.73
bn 6	Sep	0.3	8.467	4640587	231859	87.11	90.71	151.07	98.01
e 1	Aug	0.2	8.517	159189	8039	36.25	45.41	5.24	100.00
e 2	Nov	0.3	8.533	584314	29427	61.95	70.59	19.17	100.00
e 3	Oct	0.3	8.567	2517846	124372	83.82	88.14	81.04	99.71
Standard, Neu5Gc			7.050	4246122	243865	19.12	25.50	27.32	22.96
			7.533	4795569	257514	20.19	26.47	27.32	22.96
			7.200	4625262	254048	19.24	25.69	27.32	22.96
Standard, Neu5Ac			8.467	5878617	288594	26.48	30.18	38.20	32.10
			9.133	6242901	299230	27.55	30.74	38.20	32.10
			8.700	6414495	297598	26.68	30.09	38.20	32.10
Standard, Neu5,7Ac2			9.083	730255	31394	3.29	3.28	4.49	3.77
			9.833	790727	30581	3.33	3.14	4.49	3.77
			9.350	758637	30977	3.16	3.13	4.49	3.77
Standard, Nue5Gc9Ac			9.833	1889685	75962	8.51	7.94	12.59	10.58
			10.667	2080660	76862	8.76	7.90	12.59	10.58
			10.150	1978409	75409	8.23	7.63	12.59	10.58
Standard, Neu5,9Ac2			12.533	4497344	165793	20.69	17.34	27.99	23.52
			13.717	4915071	167914	20.26	17.25	27.99	23.52
			13.033	4706806	163333	19.58	16.52	27.99	23.52
Standard, reagent			13.983	2525892	74109	11.38	7.75		
			15.050	2317503	70103	9.76	7.20	—	—
			14.517	3147263	93154	13.09	9.42		
Standard, Neu5,7(8),9Ac3			15.217	1564670	46280	7.05	4.84	8.42	7.08
			16.783	1437197	39950	6.05	4.10	8.42	7.08
			15.950	1492181	41412	6.21	4.19	8.42	7.08

Nest samples:
Aerodramus fuciphagus — S040, S045, S056, S057, S058, S062, m 01, m 02, m 03 & m 04.
Aerodramus maximus — bn 1, bn 2, bn3, bn 5 & bn 6.
Collocalia esculenta — e 1, e 2 & e 3.

Appendix 6. Data for the 2-AA labelled monosaccharides from hydrolysed edible nest samples separated using GlycoSep R column.

Nest	Month	Sample		GluN	GalN	Gal	Man	Glu	Fuc
S 040	April	0.4 mg	Ret. time (min.)	9.017	9.933	19.567	20.567	21.600	26.717
			Area (µV x sec.)	15764444	19278086	327986	20628	51348	63512
			Height (µV)	1015417	1017601	15254	699	1769	2948
			Area (%)	30.22	36.96	0.63	0.04	0.10	0.12
			Amount (nmol/200µl)	6.86	7.25	1.72	0.11	0.21	2.57
			% Amount	36.63	38.74	9.20	0.60	1.12	13.71
	July	0.5 mg	Ret. time (min.)	9.033	9.967	19.517	0	0	26.567
			Area (µV x sec.)	19566807	23856069	353931	0	0	77256
			Height (µV)	1015901	1016077	16774	0	0	3525
			Area (%)	40.20	49.01	0.73	0	0	0.16
			Amount (nmol/200µl)	10.63	12.03	2.54	0	0	8.48
			% Amount	31.54	35.73	7.55	0	0	25.19
	August	0.6 mg	Ret. time (min.)	9.450	10.467	20.650	0	0	28.433
			Area (µV x sec.)	13912289	17543718	163160	0	0	33725
			Height (µV)	998856	1016515	7558	0	0	614
			Area (%)	35.82	45.18	0.42	0	0	0.09
			Amount (nmol/200µl)	9.97	11.37	1.81	0	0	2.45
			% Amount	38.94	44.42	7.08	0	0	9.56
S 045	April	0.5 mg	Ret. time (min.)	9.067	9.983	19.650	20.650	21.417	26.883
			Area (µV x sec.)	3692298	8796509	1060302	51636	29456	30533
			Height (µV)	290533	622765	49647	2335	1586	1528
			Area (%)	23.01	57.82	6.61	0.32	0.18	0.19
			Amount (nmol/200µl)	1.61	3.31	5.57	0.28	0.12	1.23
			% Amount	13.26	27.31	45.95	2.32	0.99	10.18
	July	0.7 mg	Ret. time (min.)	9.167	10.117	19.817	0	21.667	27.250
			Area (µV x sec.)	16886193	20886341	232022	0	30088	29872
			Height (µV)	1014914	1016530	11063	0	658	1439
			Area (%)	23.21	28.71	0.32	0	0.04	0.04
			Amount (nmol/200µl)	7.35	7.86	1.22	0	0.12	1.21
			% Amount	41.38	44.26	6.87	0	0.69	6.80
	August	0.4 mg	Ret. time (min.)	9.533	10.550	20.733	0	0	28.100
			Area (µV x sec.)	5254007	7002560	31339	0	0	8292
			Height (µV)	396835	481784	1498	0	0	598
			Area (%)	33.80	15.05	0.20	0	0	0.03
			Amount (nmol/200µl)	3.76	4.54	0.35	0	0	0.4
			% Amount	41.54	50.16	3.87	0	0	4.42
S 056	April	0.3 mg	Ret. time (min.)	9.100	10.050	19.733	20.700	0	27.050
			Area (µV x sec.)	17945123	21844384	312600	13839	0	64237
			Height (µV)	1017771	1018509	14197	726	0	2857
			Area (%)	38.68	47.08	0.67	0.03	0	0.14
			Amount (nmol/200µl)	7.81	8.22	1.64	0.08	0	2.60
			% Amount	38.39	40.40	8.07	0.37	0	12.77
	July	0.4 mg	Ret. time (min.)	9.200	10.150	19.900	20.883	21.733	27.417
			Area (µV x sec.)	18934580	22780493	491471	17422	8336	73433
			Height (µV)	1017340	1017452	23112	947	524	3603
			Area (%)	24.44	29.40	0.63	0.02	0.01	0.09
			Amount (nmol/200µl)	8.24	8.57	2.58	0.09	0.03	2.97
			% Amount	36.63	38.11	11.48	0.42	0.15	13.20
	August	0.4 mg	Ret. time (min.)	9.533	10.550	20.717	0	0	28.100
			Area (µV x sec.)	6073927	7404319	100758	0	0	9288
			Height (µV)	456269	506409	4616	0	0	639
			Area (%)	29.38	35.82	0.49	0	0	0.04
			Amount (nmol/200µl)	4.35	4.80	1.12	0	0	0.45
			% Amount	40.58	44.70	10.40	0	0	4.1

Continuation of Appendix 6.

Nest	Month	Sample		GluN	GalN	Gal	Man	Glu	Fuc
S 057	April	0.6 mg	Ret. time (min.)	9.150	10.100	19.850	0	21.667	27.283
			Area (µV x sec.)	13961739	18628117	256172	0	24242	31621
			Height (µV)	1000330	1016029	12572	0	1321	1580
			Area (%)	18.05	24.08	0.33	0	0.03	0.04
			Amount (nmol/200µl)	6.08	7.01	1.35	0	0.10	1.28
			% Amount	38.43	44.34	8.52	0	0.63	8.09
	July	0.4 mg	Ret. time (min.)	9.250	10.217	20.050	21.100	21.867	27.700
			Area (µV x sec.)	13143449	15967110	330272	6784	11552	27414
			Height (µV)	978740	1006968	15685	518	771	1400
			Area (%)	18.58	22.57	0.47	0.01	0.02	0.04
			Amount (nmol/200µl)	5.72	6.01	1.73	0.04	0.05	1.11
			% Amount	39.03	41.00	11.84	0.25	0.32	7.56
	August	0.4 mg	Ret. time (min.)	9.483	10.483	20.167	0	21.683	28.400
			Area (µV x sec.)	10203501	11959466	129978	0	48347	6933
			Height (µV)	765156	807790	5342	0	448	502
			Area (%)	40.16	47.07	0.51	0	0.19	0.03
			Amount (nmol/200µl)	7.31	7.75	1.44	0	0.42	0.50
			% Amount	41.96	44.49	8.28	0	2.38	2.89
S 058	April	0.4 mg	Ret. time (min.)	8.983	9.900	19.517	0	0	27.150
			Area (µV x sec.)	8115647	9541455	178194	0	0	1993
			Height (µV)	634726	674652	8451	0	0	557
			Area (%)	41.11	43.34	0.90	0	0	0.01
			Amount (nmol/200µl)	3.53	3.59	0.94	0	0	0.08
			% Amount	43.39	44.11	11.50	0	0	1.00
	July	0.5 mg	Ret. time (min.)	9.117	10.050	19.917	0	0	27.950
			Area (µV x sec.)	5414705	7510257	55512	0	0	6298
			Height (µV)	422588	525303	2783	0	0	516
			Area (%)	35.70	49.51	0.37	0	0	0.03
			Amount (nmol/200µl)	3.88	4.87	0.62	0	0	0.30
			% Amount	40.12	50.36	6.42	0	0	3.10
	August	0.5 mg	Ret. time (min.)	9.317	10.300	20.350	0	21.750	27.883
			Area (µV x sec.)	11963406	15522717	92095	0	2668	9440
			Height (µV)	90173	1005301	4326	0	494	621
			Area (%)	39.75	51,58	0.31	0	0.01	0.03
			Amount (nmol/200µl)	8.57	10.06	1.02	0	0.02	0.68
			% Amount	42.10	49.40	5.02	0	0.11	3.36
S 062	April	0.5 mg	Ret. time (min.)	9.167	10.117	19.833	20.817	22.267	27.250
			Area (µV x sec.)	18231011	22103104	642279	32748	36978	107746
			Height (µV)	1016560	1017103	30076	1493	761	4625
			Area (%)	39.30	47.64	1.38	0.07	0.08	0.23
			Amount (nmol/200µl)	7.93	8.32	3.37	0.18	0.15	4.36
			% Amount	32.64	34.22	13.88	0.73	0.62	17.92
	July	0.3 mg	Ret. time (min.)	9.133	10.083	19.950	0	0	27.850
			Area (µV x sec.)	2995056	4166683	44537	0	0	2690
			Height (µV)	237416	302186	2007	0	0	364
			Area (%)	37.81	52.60	0.56	0	0	0.03
			Amount (nmol/200µl)	2.15	2.70	0.49	0	0	0.20
			% Amount	38.76	48.77	8.94	0	0	3.52
	August	0.5 mg	Ret. time (min.)	9.017	9.950	19.533	0	21.767	27.350
			Area (µV x sec.)	16769622	21201283	221092	0	9204	11681
			Height (µV)	1015731	1017030	10486	0	544	738
			Area (%)	31.89	40.32	0.42	0	0.02	0.04
			Amount (nmol/200µl)	9.10	10.69	1.59	0	0.04	0.57
			% Amount	41.38	48.61	7.23	0	0.20	2.59

Continuation of Appendix 6.

Nest	Month	Sample		GluN	GalN	Gal	Man	Glu	Fuc
m 01	June	0.5 mg	Ret. time (min.)	9.000	9.950	19.483	20.517	0	26.517
			Area (µV x sec.)	18168093	23522732	628809	15928	0	47778
			Height (µV)	1013941	1014729	29700	1057	0	2243
			Area (%)	38.04	49.25	1.32	0.03	0	0.10
			Amount (nmol/200µl)	9.86	11.86	4.51	0.11	0	5.24
			% Amount	31.21	37.54	14.29	0.36	0	16.60
m 02	June	0.6 mg	Ret. time (min.)	9.367	10.350	20.417	0	0	27.950
			Area (µV x sec.)	9510881	12837151	133267	0	0	13276
			Height (µV)	724132	870798	6175	0	0	803
			Area (%)	35.63	48.09	0.50	0	0	0.04
			Amount (nmol/200µl)	6.81	8.32	1.48	0	0	0.65
			% Amount	39.45	48.20	8.57	0	0	3.77
m 03	June	0.6 mg	Ret. time (min.)	9.400	10.383	20.483	0	0	28.200
			Area (µV x sec.)	6062238	8842934	77717	0	0	13873
			Height (µV)	462769	606503	3535	0	0	779
			Area (%)	18.25	26.62	0.23	0	0	0.04
			Amount (nmol/200µl)	4.34	5.73	0.86	0	0	1.01
			% Amount	36.36	47.98	7.23	0	0	8.43
m 04	June	0.6 mg	Ret. time (min.)	9.417	10.400	20.483	0	0	28.200
			Area (µV x sec.)	8274200	11182458	90953	0	0	24063
			Height (µV)	666894	772024	4209	0	0	1267
			Area (%)	38.77	52.39	0.43	0	0	0.11
			Amount (nmol/200µl)	5.93	7.25	1.01	0	0	1.75
			% Amount	37.21	45.49	6.34	0	0	10.96
bn 1	September	0.5 mg	Ret. time (min.)	9.000	9.950	19.533	0	21.767	0
			Area (µV x sec.)	10535914	17680064	145858	0	12992	0
			Height (µV)	811195	1014356	6890	0	748	0
			Area (%)	33.11	55.55	0.46	0	0.04	0
			Amount (nmol/200µl)	5.72	8.91	1.05	0	0.06	0
			% Amount	36.33	56.64	6.65	0	0.38	0
bn 2	September	0.5 mg	Ret. time (min.)	9.133	10.067	19.967	0	21.633	0
			Area (µV x sec.)	5970202	9099260	66322	0	12164	0
			Height (µV)	471321	646889	3244	0	368	0
			Area (%)	15.64	39.08	0.28	0	0.05	0
			Amount (nmol/200µl)	4.28	5.90	0.74	0	0.10	0
			% Amount	38.83	53.53	6.69	0	0.95	0
bn 3	September	0.5 mg	Ret. time (min.)	9.000	9.933	19.550	20.583	0	0
			Area (µV x sec.)	11166056	15628435	761867	10586	0	0
			Height (µV)	858556	1005716	35397	619	0	0
			Area (%)	35.17	49.22	2.40	0.03	0	0
			Amount (nmol/200µl)	6.06	7.88	5.47	0.08	0	0
			% Amount	31.10	40.44	28.07	0.39	0	0
bn 5	September	0.5 mg	Ret. time (min.)	8.967	9.917	19.467	20.483	0	0
			Area (µV x sec.)	13068435	17071187	449689	10786	0	0
			Height (µV)	987011	1014675	21059	565	0	0
			Area (%)	38.67	50.52	1.33	0.03	0	0
			Amount (nmol/200µl)	7.09	8.61	3.23	0.08	0	0
			% Amount	37.32	45.29	16.99	0.41	0	0
bn 6	September	0.6 mg	Ret. time (min.)	9.133	10.083	19.967	0	0	0
			Area (µV x sec.)	3458082	4451604	74850	0	0	0
			Height (µV)	271951	321583	3459	0	0	0
			Area (%)	13.27	17.08	0.29	0	0	0
			Amount (nmol/200µl)	2.48	2.88	0.83	0	0	0
			% Amount	40.00	46.58	13.42	0	0	0

Continuation of Appendix 6.

Nest	Month	Sample		GluN	GalN	Gal	Man	Glu	Fuc
e 1	August	0.5 mg	Ret. time (min.)	9.233	10.183	20.133	0	21.983	27.533
			Area (µV x sec.)	4640059	7525503	222413	0	16914	40479
			Height (µV)	361841	532383	10529	0	608	1780
			Area (%)	13.47	21.84	0.65	0	0.05	0.12
			Amount (nmol/200µl)	3.32	4.88	2.47	0	0.15	2.94
			% Amount	24.17	35.46	17.96	0	1.05	21.36
e 2	November	0.5 mg	Ret. time (min.)	9.300	10.367	20.283	0	0	27.817
			Area (µV x sec.)	3351670	7516349	410925	0	0	32988
			Height (µV)	360371	529413	19120	0	0	1612
			Area (%)	25.98	58.28	3.19	0	0	0.26
			Amount (nmol/200µl)	2.40	4.87	4.56	0	0	2.39
			% Amount	16.88	34.24	32.07	0	0	16.82
e 3	October	0.6 mg	Ret. time (min.)	9.317	10.317	20.350	0	0	27.933
			Area (µV x sec.)	12615433	18048864	89749	0	0	7574
			Height (µV)	929165	1016237	4324	0	0	470
			Area (%)	23.94	34.25	0.17	0	0	0.01
			Amount (nmol/200µl)	9.04	11.70	1.00	0	0	0.55
			% Amount	40.56	52.49	4.47	0	0	2.47

Note : Dilution factor for sample Au 040, Se 062, m 01, b1, b3 and b5 is 3X; samples A040, A 045, Au 045, A 056, Au 056, A 057, Au 057, A 058 and A 062 is 6X; samples Se 040, Se 045, Se 056, Se 057, Au 058, Se 058, Au 062, m 02, m 03, m 04, b2, b6, e1, e2, e3 is 12X.

Appendix 7. The amount of various amino acid from hydrolysed edible nest samples quantified using high-performance liquid chromotography.

Nest	Month	Sample		Asp	Glu	Ser	Gly	His	Thr	Arg	Ala	Pro	Tyr	Val	Met	Cys	Ile	Leu	Phe	Lys
S040	Apr (A040)	1.9 mg	Ret. time (min.)	6 950	8 183	9.817	11.133	15.550	17.917	18.183	18.650	19.767	23.750	24.767	25.033	26.250	27.067	27.267	27.833	29.117
			Area (µV x sec.)	481775	877955	3614361	3089158	1246169	2312099	2021951	1892017	5486956	1772002	3686525	619217	932617	1484654	3993224	2935318	2083855
			Height (µV)	47442	76121	192887	147949	64949	182889	178850	147367	416075	224393	494963	73210	127047	220988	511061	359924	148594
			Area (%)	1.07	1.95	8.02	6.85	2.76	5.13	4.49	4.20	12.17	3.93	8.18	1.37	2.07	3.29	8.86	6.51	4.62
			Amount(pmol/0.2ml)	932.43	1684 65	4911 63	3807.10	2178.07	4334.63	2132.82	2293.63	4600.58	1776.20	4351.75	567.16	6448.67	1842.73	4366.54	3216.65	1543.85
			% Amount	1.83	3.30	9 63	7.47	4.27	8 50	4.18	4.50	9.02	3.48	8.53	1.11	12.65	3.61	8.56	6.31	3.03
	Jul (Au040)	2.0 mg	Ret. time (min.)	6.933	8.167	9 783	11.100	15.550	17.900	18.200	183667	19.767	23.750	24.767	25.050	26.267	27.067	27.283	27.850	29.150
			Area (µV x sec.)	533336	1015888	3854078	3068066	1195763	2353387	2372334	1784445	5336695	2318294	3387106	612513	226920	1416180	3624557	2877128	2182459
			Height (µV)	49517	85586	201855	146961	64897	187464	194223	139533	405817	302160	459295	74124	26143	214463	481689	343201	151793
			Area (%)	1.20	2.29	8.69	6.92	2.70	5.31	5.35	4.02	12.03	5.23	7.64	1.38	0.51	3.19	8.17	6.49	4.92
			Amount(pmol/0.2ml)	968.83	1888.57	5136.48	3781.88	2176.47	4443.57	2315.93	2172.22	4486.90	2370.05	4043.07	573.38	1092.64	1791.15	4120.52	3071.82	1577.69
			% Amount	2.10	4.09	11.11	8.18	4.71	9.61	5.01	4.70	9.71	5.13	8.75	1.24	2.36	3.88	8.91	6.65	3.41
	Aug (Se040)	1.8 mg	Ret. time (min.)	6.950	8.150	9.767	11.117	15.600	17.883	18.250	18.717	19.833	23.800	24.800	25.100	26.317	27.117	27.317	27.883	29.167
			Area (µV x sec.)	978633	1641934	4850897	3672729	1441475	2912521	4114256	1822054	5535138	2572448	3497682	500121	205380	1457540	3838746	3183010	2603119
			Height (µV)	89730	128885	239861	167492	76673	215762	309962	135209	426920	329104	433039	52748	16362	233244	478518	361990	175031
			Area (%)	1.86	3.12	9.23	6.99	2.74	5.54	7.83	3.47	10.53	4.89	6.65	0.95	0.39	2.77	7.30	6.05	4.95
			Amount(pmol/0.2ml)	1757.24	2998.26	6004.08	4428.68	2398.94	4581.98	3545.82	2153.22	4822.63	2712.39	3997.14	423.52	547.55	1998.60	4361.97	3313.36	1781.07
			% Amount	3.39	5.79	11.58	8.55	4.63	8.84	6.84	4.15	9.31	5.23	7.71	0.82	1.06	3.86	8.42	6.39	3.44
S 045	Apr (A045)	1.9 mg	Ret. time (min.)	6.933	8.200	9.917	11.217	15.517	18.017	18.167	18.700	19.767	23.767	24.767	25.067	26.267	27.083	27.283	27.867	29.017
			Area (µV x sec.)	176062	218339	1124064	1256869	406732	574671	1007383	1011849	4419325	370453	2526019	372823	659591	1034938	2491618	1722015	1045865
			Height (µV)	13075	19408	69037	65588	19995	67669	90062	91044	331744	42637	348225	46254	96143	159458	339785	226773	105207
			Area (%)	0.74	0.92	4.72	5.28	1.71	2.41	4.23	4.25	18.56	1.56	10.61	1.57	2.77	4.35	10.46	7.23	4.39
			Amount(pmol/0.2ml)	329.56	462.80	1806.59	1704.89	776.30	1591.43	1075.34	1420.80	3666.05	388.27	3081.80	383.93	4808.26	1356.33	2931.93	2063.49	1084.96
			% Amount	1.13	1.59	6.19	5.84	2.66	5.45	3.69	4.87	12.57	1.33	10.56	1.32	16.48	4.65	10.05	7.07	3.72
	Jul (Au045)	1.9 mg	Ret. time (min.)	7.200	8.333	9.833	11.133	15.583	17.750	18.183	18.583	19.667	23.650	24.650	24.933	26.167	26.967	27.183	27.733	28.950
			Area (µV x sec.)	1322974	2401689	8860855	6631932	2684511	5477986	4836406	3705789	10414755	3901286	6923765	919133	811571	2810608	7070718	5702648	577751
			Height (µV)	128216	193816	384291	262973	147666	330910	427515	232124	633123	475351	730744	97926	116776	418504	845391	594615	82980
			Area (%)	1.40	2.54	9.37	7.01	2.84	5.79	5.11	3.92	11.01	4.12	7.32	0.97	0.86	2.97	7.47	6.03	0.61
			Amount(pmol/0.2ml)	2641.30	4620.94	11523.79	7699.13	6269.08	7664.73	5255.93	3737.26	7421.33	4231.37	7247.46	802.80	1467.12	3866.67	8072.16	5679.93	734.69
			% Amount	2.97	5.20	12.96	8.66	7.05	8.62	5.91	4.20	8.34	4.76	8.15	0.90	1.65	4.35	9.08	6.39	0.83
	Aug (Se045)	2.2 mg	Ret. time (min.)	7.150	8.250	9.750	11.067	15.533	17.633	18.167	18.533	19.633	23.650	24.633	24.917	26.250	26.967	27.183	27.733	28.950
			Area (µV x sec.)	3148857	4016893	10995512	7758870	3103796	1802128	6991005	4003527	10993413	5034721	7165171	1121198	597774	2896420	7581609	6223297	745006
			Height (µV)	279430	284361	453471	294533	166445	347372	579912	237000	664764	574716	737681	107648	47310	431838	861236	619198	99847
			Area (%)	2.81	3.59	9.82	6.93	2.77	1.61	6.24	3.57	9.82	4.50	6.40	1.00	0.53	2.59	6.77	5.56	0.67
			Amount(pmol/0.2ml)	5682.75	6767.49	13592.33	8621.79	7058.92	8045.20	7130.45	3815.50	7792.73	5112.11	7315.95	881.08	639.51	3988.50	8222.80	5912.90	875.31
			% Amount	5.60	6.67	13.40	8.50	6.96	7.93	7.03	3.76	7.68	5.04	7.21	0.87	0.63	3.93	8.10	5.83	0.86

continuation of Appendix 7

Nest	Month	Sample		Asp	Glu	Ser	Gly	His	Thr	Arg	Ala	Pro	Tyr	Val	Met	Cys	Ile	Leu	Phe	Lys
S 056	Apr (A056)	2.1 mg	Ret. time (min.)	7.250	8.450	9.950	11.233	15.683	17.833	18.217	18 600	19.667	23.667	24.650	24.933	26.183	26.983	27.200	27.750	28.950
			Area (µV x sec.)	737282	1060842	6691487	5817459	2346389	4765802	3982435	3967244	11559511	3608486	7749963	897830	778054	3063748	7712488	5859823	468569
			Height (µV)	72237	102798	313591	240434	136961	310861	377085	256055	679149	452941	765393	99085	109005	460931	878733	629795	74854
			Area (%)	0.85	1.22	7.68	6.68	2.69	5.47	4.57	4.55	13.27	4.14	8.89	1.03	0.98	3.51	8.85	6.73	0.54
			Amount(pmol/0.2ml)	1515.35	2463.19	9409.78	7040.18	5818.80	7201.39	4635.63	4121.31	7961.57	4032.74	7589.54	812.13	1374.54	4254.35	8389.13	6013.33	666.95
			% Amount	1.81	2.94	11.24	8.41	6.95	8.60	5.54	4.92	9.51	4.82	9.07	0 97	1.64	5.08	10.02	7.18	0.80
	Jul (Au056)	1.9 mg	Ret. time (min.)	6.917	8.150	9.783	11.083	15.467	17.883	18.150	18.633	19.750	23.733	24.750	25.033	26.250	27.050	27.267	27.817	29.083
			Area (µV x sec.)	348650	642882	3054279	2778571	1083242	2120520	2087647	1725823	5477214	2152195	3551793	584177	391680	1492932	3766627	2917492	1847377
			Height (µV)	32067	56656	169585	136978	59580	172960	171360	135250	410907	270977	481923	69683	48395	223434	492896	345836	139459
			Area (%)	0.83	1.53	7.27	6.61	2.58	5.05	4.97	4.11	13.03	5.12	8.45	1.39	0.93	3.55	8.96	6.94	4.40
			Amount(pmol/0.2ml)	662.71	1265.29	4327.44	3527.07	2010.66	4098.25	2043.62	2105.86	4543.30	2131.93	4238.90	543.19	2273.81	1862.07	4214.39	3094.64	1447.,4
			% Amount	1.49	2.84	9.70	7.90	4.51	9.18	4.58	4.72	10.18	4.78	9.50	1.22	5.10	4.17	9.45	6.94	3.24
	Aug (Se056)	1.9 mg	Ret. time (min.)	6.983	8.200	9.800	11.133	15.650	17.917	18.267	18.733	19.833	23.800	24.817	25.117	26.333	27.133	27.333	27.917	29.183
			Area (µV x sec.)	802932	1520057	4916895	3913650	1479905	3074539	3872075	1921912	5930626	2724212	3672001	518389	205036	1534115	4007833	3338958	2704753
			Height (µV)	76636	122803	244789	176736	81366	225789	301975	143714	451012	346383	445741	55281	17105	237788	496714	377032	179718
			Area (%)	1.49	2.82	9.11	7.25	2.74	5.69	7.17	3.56	10.98	5.05	6.80	0.96	0.38	2.84	7.42	6.18	5.01
			Amount(pmol/0.2ml)	1519.09	2860.26	6126.12	4673.65	2535.38	4796.07	3454.83	2287.81	5098.45	2854.51	4113.12	442.62	568.40	2036.35	4526.04	3450.99	1838.82
			% Amount	2.86	5.38	11.52	8.79	4.77	9.02	6.50	4.30	9.59	5.37	7.73	0.83	1.07	3.83	8.51	6.49	3.46
S 057	Apr (A057)	1.9 mg	Ret. time (min.)	6.933	8.183	9.833	11.150	15.567	17.933	18.217	18.683	19.783	23.750	24.767	25.050	26.250	27.067	27.283	27.850	29.067
			Area (µV x sec.)	292650	651187	3121711	2763310	944138	2075892	1955557	1728221	5772694	1242672	3657333	560344	1271853	1554309	3848930	2784865	1489845
			Height (µV)	28682	57347	170571	134334	52445	169833	171582	137547	431789	162555	494566	65952	176872	226673	506502	339722	126753
			Area (%)	0.69	1.54	7.37	6.53	2.23	4.90	4.62	4.08	13.64	2.94	8.64	1.32	3.00	3.67	9.09	6.58	3.52
			Amount(pmol/0.2ml)	603.33	1280.19	4352.17	3459.58	1788.17	4023.79	2046.27	2141.44	4774.71	1303.99	4348.32	517.83	9093.38	1887.68	4328.35	3041.70	1312.84
			% Amount	1.19	2.54	8.62	6.85	3.54	7.97	4.05	4.24	9.45	2.58	8.61	1.03	18.01	3.74	8.57	6.02	2.60
	Jul (Au057)	1.9 mg	Ret. time (min.)	7.183	8.333	9.850	11.167	15.550	17.767	18.167	18.600	19.667	23.667	24.667	24.933	26.167	26.967	27.183	27.733	28.950
			Area (µV x sec.)	914443	1810164	7287610	5633063	2317998	4499816	4221461	3103047	8980702	3203434	5962534	839636	830106	2473655	6160480	4992461	605626
			Height (µV)	89630	152355	332151	234394	123911	294792	365958	206795	576921	415796	695553	94730	119941	376717	762507	530504	86872
			Area (%)	1.14	2.25	9.05	7.00	2.88	5.59	5.24	3.85	11.15	3.98	7.41	1.04	1.03	3.07	7.65	6.20	0.75
			Amount(pmol/0.2ml)	1865.19	3638.04	9964.75	6863.62	5269.90	6830.02	4498.76	3330.75	6761.64	3703.49	6900.02	777.06	1504.83	3484.83	7284.24	5072.39	767.14
			% Amount	2.38	4.63	12.69	8.74	6.71	8.70	5.73	4.24	8.61	4.72	8.79	0.99	1.92	4.44	9.28	6.46	0.98
	Aug (Se057)	1.9 mg	Ret. time (min.)	7.150	8.250	9.750	11.083	15.567	17.617	18.200	18.550	19.650	23.650	24.650	24.917	26.183	26.967	27.183	27.733	28.950
			Area (µV x sec.)	3283032	4388088	11845989	8062539	3293045	1799171	7334174	4236220	11385966	5076470	7325059	1093965	471274	3066445	7843049	6535786	742890
			Height (µV)	286977	300546	479316	303006	179356	367145	614914	248370	678348	583056	756401	101648	43787	464719	880008	640806	98265
			Area (%)	2.78	3.72	10.04	6.83	2.79	1.53	6.22	3.59	9.65	4.30	6.21	0.93	0.40	2.60	6.65	5.54	0.63
			Amount(pmol/0.2ml)	5834.56	7151.18	14365.13	8869.51	7601.96	8502.17	7560.98	3997.97	7952.18	5186.03	7500.77	832.77	597.53	4288.96	8401.25	6117.67	862.12
			% Amount	5.51	6.76	13.57	8.38	7.18	8.03	7.14	3.78	7.51	4.90	7.09	0.79	0.56	4.05	7.94	5.78	0.81

continuation of Appendix 7

Nest	Month	Sample		Asp	Glu	Ser	Gly	His	Thr	Arg	Ala	Pro	Tyr	Val	Met	Cys	Ile	Leu	Phe	Lys
S 058	Apr (A058)	1.8 mg	Ret. time (min.)	6.917	8.167	9.833	11.150	15.550	17.950	18.200	18.683	19.783	23.750	24.767	25.050	26.250	27.067	27.283	27.850	29.083
			Area (µV x sec.)	430692	697289	2603325	2168854	873666	1565700	1700530	1429185	4180235	1542392	2871245	537364	590377	1173443	3121535	2299868	1546875
			Height (µV)	41773	59443	146342	110986	45580	143474	141942	117857	330747	200639	399831	65846	81669	174426	412621	294671	129813
			Area (%)	1.26	2.04	7.63	6.36	2.56	4.59	4.99	4.19	12.26	4.52	8.42	1.58	1.73	3.44	9.15	6.74	4.54
			Amount(pmol/0.2ml)	832.97	1352.33	3744.71	2863.63	1574.10	3396.22	1693.24	1836.32	3655.01	1594.81	3528.43	517.10	4040.02	1474.66	3542.01	2651.53	1345.21
			% Amount	2.10	3.35	9.45	7.23	3.97	8.57	4.27	4.64	9.23	4.03	8.91	1.31	10.20	3.72	8.94	6.69	3.40
	Jul (Au058)	1.7 mg	Ret. time (min.)	6.917	8.133	9.783	11.083	15.467	17.900	18.150	18.650	19.750	23.750	24.750	25.033	26.233	27.050	27.250	27.833	29.050
			Area (µV x sec.)	250546	609722	2900782	2633013	937727	1869079	1771982	1446812	5116164	1232106	3054713	566129	1098132	1301440	3283386	2664508	1552547
			Height (µV)	24068	53030	161323	130548	49447	155160	143472	117724	391869	151200	420410	67340	154648	195580	434594	312866	128022
			Area (%)	0.65	1.59	7.57	6.7	2.45	4.88	4.62	3.78	13.35	3.22	7.97	1.48	2.87	3.40	8.57	6.95	4.05
			Amount(pmol/0.2ml)	522.40	1187.17	4120.30	3362.94	1694.69	3674.45	1711.47	1834.25	4332.33	1217.28	3706.53	527.26	7913.75	1641.88	3726.05	2809.10	1326.27
			% Amount	1.15	2.61	9.06	7.39	3.73	8.08	3.76	4.03	9.52	2.68	8.15	1.16	17.40	3.61	8.19	6.18	2.92
	Aug (Se058)	1.9 mg	Ret. time (min.)	6.967	8.183	9.800	11.150	15.650	17.917	18.283	18.750	19.850	23.800	24.817	25.117	26.350	27.133	27.333	27.917	29.167
			Area (µV x sec.)	881768	1462174	4622153	3534738	1277906	2671085	4000064	1661597	5266591	2377027	3140436	478091	151390	1314379	3463022	2962702	2447197
			Height (µV)	83467	117754	230912	163376	69572	204756	300211	127062	415996	311034	396615	51299	11281	206152	445062	337442	171530
			Area (%)	1.80	2.99	9.46	7.23	2.61	5.46	8.18	3.40	10.77	4.86	6.42	0.98	0.31	2.69	7.08	6.06	5.01
			Amount(pmol/0.2ml)	1643.34	2745.68	5782.43	4319.58	2192.49	4346.98	3434.73	2024.28	4697.57	2563.76	3664.56	412.60	405.04	1773.46	4060.33	3088.74	1737.92
			% Amount	3.36	5.62	11.83	8.83	4.48	8.89	7.02	4.14	9.61	5.24	7.49	0.84	0.83	3.63	8.30	6.32	3.55
S 062	Apr (A062)	2.4 mg	Ret. time (min.)	7.250	8.433	9.917	11.217	15.650	17.833	18.233	18.583	19.667	23.667	24.650	24.917	26.183	26.967	27.200	27.750	28.950
			Area (µV x sec.)	766976	1300379	7172316	6248858	2560939	4958637	4210703	4257279	11996724	3824537	8020525	1107229	763693	3238436	8076030	6285761	472745
			Height (µV)	75895	118057	331626	252006	142613	316851	405305	267656	692393	471799	789931	115367	109899	487011	898253	652001	75089
			Area (%)	0.83	1.41	7.79	6.79	2.78	5.39	4.57	4.62	13.03	4.15	8.71	1.20	0.83	3.52	8.77	6.83	0.51
			Amount(pmol/0.2ml)	1588.93	2824.94	9949.05	7378.51	6056.53	7339.81	4982.74	4307.50	8117.03	4199.89	7831.81	943.24	1385.19	4492.65	8574.69	6223.76	668.91
			% Amount	1.82	3.23	11.39	8.45	6.94	8.40	5.71	4.93	9.29	4.81	8.97	1.08	1.59	5.14	9.82	7.13	0.77
	Jul (Au062)	1.7 mg	Ret. time (min.)	6.917	8.133	9.767	11.083	15.500	17.867	18.183	18.650	19.767	23.750	24.767	25.050	26.267	27.067	27.283	27.850	29.117
			Area (µV x sec.)	593899	1133090	3875204	3170734	1243191	2538062	2764254	1668729	5367482	2442552	3369514	592317	107812	1436433	3609126	2943293	1910586
			Height (µV)	57122	95175	204742	152181	67409	194706	217587	129862	407655	314965	454995	70281	13080	209833	477629	347332	141283
			Area (%)	1.30	2.49	8.51	6.96	2.73	5.57	6.07	3.66	11.78	5.36	7.40	1.30	0.24	3.15	7.92	6.46	4.19
			Amount(pmol/0.2ml)	1102.23	2095.18	5208.85	3915.11	2254.79	4615.99	2594.19	2022.35	4507.27	2467.83	4005.85	547.25	399.29	1754.55	4086.51	3107.60	1466.53
			% Amount	2.38	4.52	11.24	8.44	4.86	9.96	5.60	4.36	9.72	5.32	8.64	1.18	0.86	3.78	8.81	6.70	3.16
	Aug (Se062)	2.0 mg	Ret. time (min.)	7.000	8.183	9.750	11.100	15.700	17.867	18.300	18.733	19.817	23.800	24.817	25.117	26.283	27.133	27.333	27.917	29.267
			Area (µV x sec.)	1239273	2233778	6954769	5234989	1893254	3820916	6077602	2469407	7667611	3248286	4615229	801956	431269	1942638	5166986	4252063	3736994
			Height (µV)	118292	170698	316044	217568	108725	272652	422101	170736	537255	41296	535967	62850	32224	298874	615261	439734	198596
			Area (%)	1.73	3.11	9.70	7.30	2.64	5.33	8.47	3.44	10.69	4.53	6.43	1.12	0.60	2.71	7.20	5.93	5.21
			Amount(pmol/0.2ml)	2276.72	3947.14	7890.92	5755.78	3330.72	5796.67	4823.46	2715.46	6085.78	3398.30	4936.98	499.68	992.50	2543.97	5594.89	4024.74	2071.44
			% Amount	3.41	5.92	11.83	8.63	4.99	8.69	7.23	4.07	9.13	5.10	7.40	0.75	1.49	3.81	8.39	6.04	3.11

continuation of Appendix 7

Nest	Month	Sample		Asp	Glu	Ser	Gly	His	Thr	Arg	Ala	Pro	Tyr	Val	Met	Cys	Ile	Leu	Phe	Lys
m o1	June	1.8 mg	Ret. time (min.)	6.983	8.233	9.867	11.200	15.700	18.000	18.283	18.750	19.850	23.817	24.833	25.133	26.333	27.133	27.350	27.917	29.133
			Area (µV x sec.)	466307	879516	3529958	2950672	1101516	2312582	2167536	1657401	5180428	1749998	3266108	413852	627839	1320993	3508033	2771260	1891415
			Height (µV)	44669	74484	186935	140857	59920	185585	180639	132408	405220	236134	413065	49576	80389	205381	446288	332087	154187
			Area (%)	1.11	2.10	8.44	7.05	2.63	5.53	5.18	3.96	12.39	4.18	7.81	0.99	1.50	3.16	8.39	6.63	4.52
			Amount(pmol/0.2ml)	937.67	1763.74	4693.23	3722.79	1911.91	3937.66	2072.41	2108.89	4574.19	1947.71	3814.77	399.61	2343.51	1767.06	4071.37	3039.74	1524.21
			% Amount	2.10	3.95	10.52	8.34	4.28	8.82	4.62	4.73	10.25	4.36	8.55	0.90	5.25	3.96	9.12	6.81	3.42
m 02	June	1.8 mg	Ret. time (min.)	6.967	8.183	9.817	11.167	15.717	17.933	18.300	18.750	19.850	23.817	24.817	25.133	26.333	27.150	27.350	27.933	29.217
			Area (µV x sec.)	1509712	1935969	5266849	3801440	1430933	3034838	4300181	1986998	5706951	2653197	3638705	475311	175038	1527150	3930388	3180578	2785664
			Height (µV)	139412	147693	253871	171897	80088	223391	327366	147515	438561	339803	438440	53880	14018	236513	491609	367729	179445
			Area (%)	2.75	3.52	9.59	6.92	2.60	5.52	7.83	3.62	10.39	4.83	6.62	0.87	0.32	2.78	7.15	5.79	5.07
			Amount(pmol/0.2ml)	2660.86	3425.08	6351.05	4545.42	2498.23	4744.86	3744.12	2347.97	4955.91	2800.39	4046.46	432.05	481.83	2025.76	4480.01	3365.87	1835.45
			% Amount	4.86	6.26	11.60	8.30	4.56	8.67	6.84	4.29	9.05	5.12	7.39	0.79	0.88	3.70	8.18	6.15	3.35
m 03	June	1.8 mg	Ret. time (min.)	6.967	8.250	9.917	11.250	15.683	18.050	18.283	18.783	19.883	23.833	24.833	25.150	26.317	27.150	27.350	27.933	29.050
			Area (µV x sec.)	164305	402496	2147540	2000082	642062	1301967	1479851	1130285	4065119	323837	2449501	364117	1373887	1016228	2592810	2139143	1343490
			Height (µV)	15500	35405	123212	102626	32118	122679	124142	98611	341622	38274	328115	44725	189253	161858	348015	255034	134761
			Area (%)	0.55	1.34	7.17	6.68	2.14	4.35	4.94	3.77	13.57	1.08	8.18	1.22	4.59	3.39	8.66	7.14	4.49
			Amount(pmol/0.2ml)	407.14	876.91	3115.00	2709.61	1103.69	2594.51	1428.71	1574.01	386.11	320.30	3039.10	363.04	5397.16	1405.39	3185.32	2334.69	1284.84
			% Amount	1.16	2.49	8.86	7.70	3.14	7.38	4.06	4.48	10.94	0.91	8.64	1.03	15.35	4.00	9.06	6.64	3.65
m 04	June	2.0 mg	Ret. time (min.)	6.983	8.217	9.850	11.167	15.600	17.967	18.233	18.733	19.833	23.800	24.800	25.117	26.300	27.117	27.317	27.900	29.100
			Area (µV x sec.)	235149	617119	3356193	2897576	1070781	2189294	2024047	1517749	5237760	1194466	3172449	386332	1029858	1306470	3394364	2777942	1918549
			Height (µV)	22717	54017	180910	140241	55387	177005	170952	125060	405869	166273	402429	48141	140375	205200	435017	324809	156637
			Area (%)	0.57	1.51	8.20	7.08	2.61	5.35	4.94	3.71	12.79	2.92	7.75	0.94	2.51	3.19	8.29	6.78	4.68
			Amount(pmol/0.2ml)	538.40	1299.27	45544.02	3706.47	1780.12	3754.45	1962.04	1992.59	4581.63	1373.10	3717.65	388.79	4026.12	1765.55	3969.75	2973.14	1554.41
			% Amount	1.22	2.95	10.32	8.42	4.04	8.52	4.45	4.52	10.40	3.12	8.44	0.88	9.14	4.01	9.01	6.75	3.53
bn 1	September	1.9 mg	Ret. time (min.)	6.917	8.083	9.700	11.033	15.517	17.783	18.200	18.633	19.750	23.733	24.750	25.050	26.250	27.050	27.267	27.833	29.333
			Area (µV x sec.)	1639657	2393482	5704938	4556691	1395708	3259943	5583574	2638831	5994184	3050578	3672424	695405	203567	1794811	4613511	3675225	4003998
			Height (µV)	149939	176231	272889	199054	77596	236791	400911	178371	446888	383826	464860	74633	14364	268058	582791	404245	195831
			Area (%)	2.58	3.77	8.98	7.17	2.20	5.13	8.79	4.15	9.44	4.80	5.78	1.09	0.32	2.83	7.26	5.79	6.30
			Amount(pmol/0.2ml)	2730.41	3841.48	6917.35	511.52	2572.44	5617.97	4777.64	2774.09	4942.03	2993.67	4091.23	576.83	467.40	2214.83	4967.34	3600.50	2043.47
			% Amount	4.53	6.38	11.48	8.49	4.27	9.33	7.93	4.61	8.20	4.97	6.79	0.96	0.78	3.68	8.25	5.98	3.39
bn 2	September	1.8 mg	Ret. time (min.)	6.917	8.117	9.733	11.050	15.533	17.817	18.200	18.650	19.767	23.750	24.767	25.050	26.167	27.067	27.283	27.850	29.267
			Area (µV x sec.)	1462762	2127469	5273108	4260551	1293355	2878363	5161668	2412211	5781951	3047313	3499102	690032	176828	1703435	4342150	3483127	3216602
			Height (µV)	133981	161415	258847	189252	71925	218969	374938	168532	438076	378657	454684	75321	12429	255907	560692	388407	179722
			Area (%)	2.48	3.61	8.95	7.32	2.20	4.89	8.76	4.10	9.82	5.17	5.94	1.17	0.30	2.89	7.37	5.91	5.46
			Amount(pmol/0.2ml)	2450.48	3522.28	6565.33	4861.32	2359.59	5193.65	4468.30	2621.61	4844.38	2954.20	4003.16	581.51	364.73	2118.77	4782.25	3463.33	1873.09
			% Amount	4.29	6.17	11.51	8.52	4.20	9.10	7.83	4.59	8.49	5.18	7.02	1.02	0.64	3.71	8.38	6.07	3.28

continuation of Appendix 7

Nest	Month	Sample		Asp	Glu	Ser	Gly	His	Thr	Arg	Ala	Pro	Tyr	Val	Met	Cys	Ile	Leu	Phe	Lys
bn 3	September	1.8 mg	Ret. time (min.)	6.933	8.150	9.767	11.083	15.533	17.883	18.200	18.667	19.767	23.767	24.783	25.067	26.283	27.083	27.300	27.867	29.133
			Area (µV x sec.)	395252	882096	3873431	3343874	1018588	2444978	2725143	1911688	5580378	2605056	3135162	586462	80778	1508778	3862321	3140984	1919527
			Height (µV)	37143	75811	203272	156635	55436	190754	222188	14688	425225	331793	421863	68624	8256	227027	506373	352566	142705
			Area (%)	0.85	1.90	8.36	7.22	2.20	5.28	5.88	4.13	12.05	5.63	6 77	1.27	0.17	3.26	8.34	6.78	4.15
			Amount(pmol/0.2ml)	751.76	1677.98	5172.01	4028.79	1881.44	4521.90	2649.00	2280.01	4701.96	2596.33	3719.11	535.99	143.20	1890.47	4327.27	3152.93	1481.56
			% Amount	1.65	3.69	11.36	8.85	4.13	9.94	5.82	5.01	10.33	5.70	8.17	1.18	0.31	4.15	9.51	6.93	3.26
bn 5	September	1.8 mg	Ret. time (min.)	6.950	8.133	9.733	11.067	15.583	17.833	18.217	18.667	19.767	23.750	24.783	25.067	26.333	27.100	27.300	27.867	29.367
			Area (µV x sec.)	984142	1860750	5869652	4522555	1481131	3377661	4658797	2468192	6956242	3173983	4037302	634663	42973	1873490	4887337	3951314	2919352
			Height (µV)	93612	146354	279021	196489	83570	236938	362845	173973	498289	405055	519865	72792	6632	281170	619513	428015	173399
			Area (%)	1.56	2.95	9.30	7.17	2.35	8.35	7.38	3.91	11.03	5.03	6.40	1.01	0.07	2.97	7.75	6.26	4.63
			Amount(pmol/0.2ml)	1742.33	3197.79	7071.09	5046.05	2758.71	5621.45	4324.27	2705.93	5511.63	3155.78	4567.27	564.33	57.02	2318.47	5274.93	3806.36	1806.22
			% Amount	2.93	5.37	11.88	8.48	4.63	9.44	7.26	4.55	9.26	5.30	7.67	0.95	0.10	3.89	8.86	6.39	3.03
bn 6	September	1.9 mg	Ret. time (min.)	6.967	8.167	9.767	11.133	15.683	17.883	18.267	18.683	19.800	23.767	24.767	25.083	26.267	27.117	27.317	27.883	29.283
			Area (µV x sec.)	2306697	2639990	6533921	4621391	1623464	3810109	4631851	3066984	6550.56	3499935	4566585	577241	416381	2053341	5221077	3843327	3981603
			Height (µV)	202148	188917	299306	198872	92407	255487	403494	203521	484601	411977	523908	56700	32723	303375	621751	441189	202483
			Area (%)	3.41	3.90	9.66	6.83	2.40	5.63	6.85	4.53	9.68	5.17	6.75	0.85	0.62	3.04	7.72	5.68	5.89
			Amount(pmol/0.2ml)	3801.90	4360.57	7476.37	5260.30	2856.32	5430.17	4611.47	3234.31	5482.98	3394.02	4826.87	453.32	1006.50	2581.37	5653.41	4048.12	2119.34
			% Amount	5.71	6.55	11.23	7.90	4.29	8.15	6.92	4.86	8.23	5.10	7.25	0.68	1.51	3.88	8.49	6.08	3.18
e 1	August	1.7 mg	Ret. time (min.)	6.983	8.567	9.983	11.300	15.700	18.117	18.267	18.783	19.883	23.800	24.833	25.133	26.317	27.150	27.350	27.933	29.033
			Area (µV x sec.)	194615	199742	1209417	1333785	268160	478218	1054536	989591	3776758	233071	2326427	309253	685979	974426	2109386	1526478	910579
			Height (µV)	14499	17601	75094	72598	12041	63470	91195	90684	325446	26064	311788	37510	92033	153898	285748	201614	107933
			Area (%)	0.92	0.94	5.69	6.28	1.26	2.25	4.96	4.66	17.78	1.10	10.95	1.46	3.23	4.59	9.93	7.19	4.29
			Amount(pmol/0.2ml)	388.93	472.90	1923.24	1913.81	520.02	1330.29	1053.33	1448.57	3660.91	219.88	2890.01	308.65	2670.12	1339.24	2623.90	1845.87	954.25
			% Amount	1.51	1.83	7.45	7.42	2.02	5.16	4.08	5.61	14.19	0.85	11.20	1.20	10.35	5.19	10.17	7.15	3.70
e 2	November	1.8 mg	Ret. time (min.)	6.983	8.267	9.983	11.300	15.683	18.117	18.267	18.783	19.850	23.817	24.833	25.150	26.333	27.150	27.367	27.933	29.050
			Area (µV x sec.)	201598	227967	1264335	1367674	273554	523448	1187705	1089829	4915196	272173	2742696	372205	754845	1203653	2471705	1724559	1164502
			Height (µV)	14381	20186	79150	75227	12559	67382	102956	98772	395425	30531	360471	42861	100240	189641	325713	218118	124766
			Area (%)	0.81	0.91	5.06	5.47	1.10	2.10	4.75	4.36	19.68	1.09	10.98	1.49	3.02	4.82	9.89	6.90	4.66
			Amount(pmol/0.2ml)	368.79	531.55	2023.70	1983.50	535.10	1413.82	1187.33	1576.57	4462.06	256.62	3334.54	348.99	2900.34	1636.26	2984.24	1996.89	1161.68
			% Amount	1.34	1.84	6.99	6.85	1.85	4.88	4.10	5.44	15.41	0.89	11.51	1.21	10.01	5.65	10.30	6.90	4.01
e 3	October	2.0 mg	Ret. time (min.)	6.967	8.200	9.783	11.133	15.683	17.933	18.300	18.733	19.817	23.800	24.800	25.100	26.317	27.133	27.333	27.900	29.217
			Area (µV x sec.)	1082741	1509290	5742676	4171668	988737	3127069	3485329	2362935	6758673	2498966	4109517	477306	359865	2035073	4211606	3441764	2987472
			Height (µV)	100347	123338	272042	183039	53934	227653	297147	171658	490720	332463	490342	52247	30445	304319	508714	395213	185795
			Area (%)	1.87	2.60	9.90	7.20	1.71	5.39	6.01	4.08	11.66	4.31	7.09	0.82	0.62	3.51	7.26	5.94	5.15
			Amount(pmol/0.2ml)	1950.34	2872.38	6801.09	4840.69	1737.89	4835.86	3399.82	2730.05	5553.03	2740.02	4520.37	419.74	942.60	2589.22	4634.23	3617.36	1913.70
			% Amount	3.47	5.11	12.09	8.60	3.09	8.60	6.04	4.85	9.87	4.87	8.03	0.75	1.68	4.60	8.24	6.43	3.40