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REPRODUCTIVE ECOLOGY AND CONSERVATION OF THE LILAC-CROWNED PARROT (*AMAZONA FINSCHI*) IN JALISCO, MEXICO

By

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ABSTRACT

The reproductive ecology and resource requirements of the Lilac-crowned Parrot (*Amazona finschi*) were studied in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve, western Mexico. Food resource availability was determined by monthly phenology transects in deciduous and semi-deciduous forest. Resource utilisation by parrots was evaluated through observations of diet, habitat use, and crop samples of nestlings. Reproductive ecology was determined through studies of breeding behaviour, nest success, reproductive output, and nestling growth rates.

There was significant temporal and spatial variability in food resource abundance, with semi-deciduous forest providing greater food resources for parrots during the dry season, while food resource abundance increased in deciduous forest during the rainy season. A critical period of food resource scarcity occurred in May - June at the end of the dry season. Lilac-crowned Parrots were pre-dispersal seed predators, exhibiting high variability in diet and habitat use, which corresponded with fluctuations in food resource availability.

Nesting behaviour of the Lilac-crowned Parrot was distinct from most psittacines in the high synchrony of nest initiation, low nest site fidelity, infrequent feeding visits, and short nest attendance. High nest predation resulted in a low 40% nest success, with a reproductive output of 1.0 fledglings per egg-laying female. Third-hatched nestlings exhibited slower growth rates than older siblings, though this did not result in mortality. Finally, there was significant variation between years in the size and growth rates of nestlings, which corresponded with annual fluctuations in food resource abundance.

Many of the distinct aspects of Lilac-crowned Parrot reproductive ecology may be related to food resource availability and predation risks. The results demonstrated the potential influence of environmental factors on parrot reproduction, with fragmentation of semi-deciduous forest impacting parrot populations through food limitation during the dry season, and high rates of nest predation.

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INTRODUCTION

1.1. CONSERVATION STATUS OF PARROTS IN MEXICO

The parrot family (Psittacidae) contains more endangered species than any other major bird family, and significantly more threatened species than expected for the family size (Collar & Andrew 1988; Bennett & Owens 1997). More than one third of the 142 species of parrot in the Neotropics (tropical America) are threatened or at risk of extinction (Collar & Juniper 1992). Of the 21 species of Psittacidae in Mexico, 7 are considered endangered while a further 8 species are regarded as threatened (NOM-059-ECOL-1994). Among these is the Lilac-crowned Parrot (*Amazona finschi*) which is endemic to the Pacific Coast of Mexico from Sonora to Oaxaca (Forshaw 1989).

The principal threats to wild parrot populations are capture for the pet trade and habitat destruction (Roet et al. 1981; Collar & Juniper 1992; Mulliken et al. 1992; Thomsen & Mulliken 1992). Psittacines are the second largest bird group in international trade, even though almost all psittacine species are included in either Appendix I or II of CITES which limits such trade (Mulliken et al. 1992). Central and South America is also the second largest export region for wild birds in trade, with the majority of birds from this region being psittacines (Mulliken et al. 1992). In 1982 - 1988 a minimum of 1.8 million Neotropical psittacines were exported by mainland Neotropical countries, 43% of a total 4.2 million psittacines traded world-wide (Thomsen & Brautigam 1991; Thomsen & Mulliken 1992).

In Mexico, pressure for commercial trade has been most severe along the Pacific Coast, with 86.2% of reported trade during 1982 - 1983 occurring in this region (Iñigo-Elias & Ramos 1991). In 1983, the main capture areas for parrots in Mexico were Sinaloa, Nayarit, Jalisco, and Oaxaca (Iñigo-Elias & Ramos 1991). During this period, 17,260 Lilac-crowned Parrots were captured, making it the third most traded species in Mexico (Iñigo-Elias & Ramos 1991). International trade of Lilac-crowned Parrots diminished after a government ban in 1982, however this did not control capture for domestic trade (Iñigo-Elias & Ramos 1991).

In addition to pressures from international trade, deforestation in Mexico and conversion of land for food production is proceeding at a rapid rate (Dirzo & Garcia 1992; Maass 1995). Tropical dry deciduous forest in particular is considered one of the most threatened forest types, and a priority for conservation (Beissinger et al. 1996). Janzen (1988) estimates that less than 2% of the original extent of tropical dry forest now remains in a relatively intact state, with only 0.09% (480 km^2) having official conservation status. In Mexico, tropical dry forests cover extensive areas of the Pacific lowlands from south Sonora to Chiapas (Rzedowski 1994). Masera et al. (1992, 1996) estimate that tropical deciduous forest in Mexico is being deforested at a rate of 1.9% per year (306,000 hectares/year), which is almost equal to that for tropical humid rainforest (2.0% per year). Along the coast of Jalisco in particular, deforestation of tropical forests has proceeded at a rate of 1.48% per year since 1973 (Miranda 1998).

The Lilac-crowned Parrot has therefore experienced severe pressure from both wildlife trade and habitat destruction throughout its range. Hence, there is a need for conservation strategies based on biological knowledge if viable populations of this threatened endemic species are to be maintained in the region.

1.2. BACKGROUND STUDIES ON AMAZON PARROTS

Despite their popularity and long association with human societies, very little is known of the ecology of parrot populations in the wild (Snyder et al. 1992). Initial studies consisted mainly of surveys on the status and distribution of parrots (Ridgely 1981). Ecological studies were primarily conducted on *Amazona* species of the Caribbean islands (Snyder et al. 1987; Gnam & Rockwell 1991; Lindsey et al. 1991, 1994; Wilson et al. 1995), as these were considered most threatened due to limited distribution, habitat availability, and the pressures of wildlife trade. Hence, the majority of studies of have been conducted on island species, and little is known of how this compares with the ecology of *Amazona* parrots on the continent of Central and South America (Enkerlin-Hoeflich 1995). Moreover, no studies have been conducted on the Lilac-crowned Parrot, though Enkerlin-Hoeflich (1995) has conducted research on the breeding ecology of the closely related Red-crowned Parrot (*Amazona viridigenalis*) in north-eastern Mexico.

1.3. DEALING WITH A VARIABLE ENVIRONMENT

Though apparently homogeneous and stable, tropical environments are in fact spatially and temporally variable (Karr 1976; Karr & Freemark 1985). Most tropical forests exhibit seasonal variation in plant energy production with a decline in plant food resources during part of the year (Daubenmire 1972; Frankie et al. 1974; Foster 1982a; Leigh & Windsor 1982; Lieberman 1982; Rathcke & Lacey 1985; Terborgh 1986a; Fleming et al. 1987; Primack 1987; Bullock & Solis-Magallanes 1990; Janson & Emmons 1990; Guevara et al. 1992; Lugo & Frangi 1993; Murali & Sukumar 1994; Peres 1994; White 1994). Furthermore, heterogeneity in the availability of plant resources between different areas and habitats creates environmental patchiness (Foster 1980) which results in a dynamic process of habitat selection in tropical bird communities (Karr & Freemark 1985). This variability and patchiness is however seasonally predictable (Colwell 1974; Karr & Freemark 1985), and animals should exhibit life histories adaptive to this.

Strategies employed by the animal community to deal with environmental variability in food resources may include dietary switching, seasonal breeding, changes in range use, or migration (Wiens 1976, 1985; Leighton & Leighton 1983; Terborgh 1986b; Fleming 1992; van Schaik et al. 1993). In general, where there is high temporal or spatial variability in resource abundance, animals should track resources closely and exhibit a more seasonal and less sedentary life (Wiens 1976, 1985; Fleming 1992).

Energetically costly activities such as reproduction usually coincide with periods of relative food abundance (Perrins 1970; Fogden 1972; Martin 1987; Fleming 1992). Though birds may be genetically constrained to breed at specific times of the year, variability in the food resource may influence egg production, nest initiation, clutch size, and energetic limitations on parents and young (Perrins 1970; Martin 1987; Godfray et al. 1991). Animal populations may also exhibit daily or seasonal foraging movements consisting of habitat shifts, altitudinal or latitudinal migrations, or nomadic wanderings, which result in temporal variations in animal abundance correlated with fluctuations in plant resources (Wiens 1976, 1985; Fleming 1992; van Schaik et al. 1993). The distribution and defendability of resources will also influence social organisation with territorial defence of concentrated, reliable resources, and nomadic flocks arising where there are widely spaced, patchy or unpredictable resources (Wiens 1976, 1985; Fleming 1992). However, the response of animal communities to environmental patchiness is poorly understood for most species and tropical habitats (Wiens 1976).

1.4. BIRD COMMUNITIES AND RESOURCE VARIABILITY

Studies have demonstrated seasonal variations in the abundance and composition of tropical bird communities (Fogden 1972; Karr 1976; Karr et al. 1982). However, little is known of how these population fluctuations are linked to food resources (Karr & Freemark 1985). Bird species in tropical forests appear to distinguish between vertical foraging levels, with the result that some species forage predominantly in the understorey of the forest, while other species forage in the canopy (Pearson 1971).

Spatial and temporal variation in understorey frugivorous bird populations have been correlated with fluctuations in food resource abundance between habitats and elevations indicating that bird populations track food resources (Levey 1988; Blake & Loiselle 1991; Loiselle & Blake 1991; Poulin et al. 1993). However, most studies on the relation of tropical bird populations to resource availability have been conducted on understorey bird communities (Fogden 1972; Karr 1976; Levey 1988; Blake & Loiselle 1991; Loiselle & Blake 1991; Poulin et al. 1992, 1993), though canopy bird species comprise 40 - 50% of all tropical forest bird species (Karr 1990; Robinson & Terborgh 1990). Canopy trees have greater seasonality and exhibit different fruiting and flowering peaks to trees in the understorey (Frankie et al. 1974; Opler et al. 1980). Hence, birds of the canopy may experience greater environmental patchiness in the availability of food resources, and are predicted to be more seasonal than understorey bird species (Pearson 1971; Karr 1976).

Few studies have investigated the relation of canopy bird populations to food resources, however canopy populations have been found to exhibit temporal variations in abundance (Greenberg 1981; Loiselle 1988), and canopy bird flocks have territories four times larger than those for understorey flocks (Munn 1985; Terborgh et al. 1990).

1.5. VARIABILITY IN PSITTACINE POPULATIONS

Parrots dominate canopy bird communities, and constitute the highest biomass of canopy granivores in tropical forests (Loiselle 1988; Terborgh et al. 1990). Little information exists on the relation of parrot populations to food resources, though evidence of temporal variability in parrot diet, movements, and social organisation has been obtained.

Cockatoos in Australia form seasonal nomadic flocks, and make latitudinal migrations to feeding areas, particularly when food resources may be limited (Saunders 1980; Rowley & Chapman 1991; Smith & Moore 1992). The Major Mitchell Cockatoo (*Cacatua leadbeateri*) forms nomadic flocks which range over an area of 300 km^2 to exploit patchy food resources along the western Australian wheatbelt (Rowley & Chapman 1991). Movements of hundreds of kilometres were recorded for re-introduced Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) in Arizona (Snyder et al. 1994). Seasonal variations in diet have also been noted for some parrot species (Galetti 1993; Wermundsen 1997). Finally, temporal variations in the abundance of parrot populations encountered in surveys may be related to seasonal variations in food resource availability (Loiselle 1988; Renton 1994; Enkerlin-Hoeflich 1995).

Snyder et al. (1987) suggested that the Puerto Rican Parrot (*Amazona vittata*) may exhibit seasonal variations in diet and make altitudinal migrations to track food resources. Lugo and Frangi (1993) demonstrated temporal and spatial variation in the availability of food resources for the Puerto Rican Parrot, though no studies on this species have investigated the impact of this environmental variability on the wild parrot population. In general, few studies of psittacines have incorporated information on the phenology of food plants, and no studies have analysed the relation between parrot populations and food resources, or how parrots deal with environmental variability.

Though parrots are principally seed predators, the behaviour of granivores in response to food availability is similar to that of frugivores (Poulin et al. 1994a). Indeed, granivores may be more mobile and variable than frugivores due to the high synchrony in seed production employed by plants to avoid predation (Janzen 1969, 1971; Augspurger 1981; van Schaik et al. 1993). Parrots are principally wide ranging species whose numbers tend to fluctuate greatly (Terborgh et al. 1990). Hence, it may be expected that seed predators such as parrots will track food resources more closely in order to exploit temporal and spatial abundances in plant seed production.

1.6. CONSERVATION IMPORTANCE

Low fecundity is one of the main factors making bird species vulnerable to decline (Bennett & Owens 1997). Hence, data on fecundity and the reproductive output of parrots are of particular importance to determine the ability of wild populations to withstand pressures from trade (Thomsen & Brautigam 1991), or evaluate the harvesting potential of species (Beissinger & Bucher 1992a,b). Information on growth rates also enables evaluation of the condition of nestlings and their chances of survival, and may be used as an index of habitat quality and the viability of wild populations (Saunders 1986). Knowledge of the factors which limit reproduction may enable assessment of the capacity for increase of parrot populations, and the potential impact of environmental factors on threatened populations.

Understanding the relationship of parrot populations to food resources is central to conservation as this determines the key resources, habitats, and areas required to maintain healthy parrot populations throughout the year. Food resource availability may be critical to the viability of wild parrot populations, particularly during the breeding season when food supply may affect breeding success (Saunders 1986). For example, food resource limitation may have been responsible for the poor growth of White-tailed Black Cockatoo chicks in agricultural areas of Australia (Saunders 1986), eventually resulting in extirpation of the population which was unable to locate dispersed fragments of native forest (Saunders 1990).

Moreover, as seed predators, parrots may have an important impact on forest ecosystems, particularly in fragmented or disturbed habitats (Galetti 1993). With current rates of deforestation, the habitat available for parrots is increasingly reduced to forest remnants within a mosaic of agricultural land. It is therefore, important to conserve sufficient areas and habitats for parrots, and to predict the impact of fragmentation on parrot populations (Saunders 1986, 1990, 1991; Galetti 1993).

Patch dynamics have practical significance when related to the management of populations or habitats. Species may use different habitats during stressful periods, therefore the entire habitat range of a species needs to be known for effective conservation (Karr & Freemark 1985). Understanding population responses to environmental patchiness may also help predict the impact of habitat fragmentation on different species of animals (Wiens 1985). Hence, basic knowledge is required on how patch dynamics are expressed in nature, and how populations and organisms respond to them (Wiens 1976, 1985).

1.7. AIMS AND OBJECTIVES

The study aims to investigate the relationship between parrot populations and food resources, and to analyse how parrots deal with environmental variability. The relation of parrot populations to food resources will be examined in Chapter 3, particularly with regard to determining whether parrot populations track temporal and spatial variations in food resource availability. The reproductive ecology of the Lilac-crowned Parrot will be addressed in Chapters 4 to 6, and compared with that of other parrot species. Chapter 4 describes the breeding behaviour of the Lilac-crowned Parrot, as compared with other island and mainland Amazon species. Chapter 5 determines the fecundity and reproductive output of the Lilac-crowned Parrot population, and discusses the potential limiting factors on parrot reproduction. Chapter 6 describes nestling growth rates for a Neotropical parrot, and evaluates the influence of hatching order and annual fluctuations in environmental conditions on nestling size and growth. The implications of the study for the conservation of parrot populations will be considered in Chapter 7, particularly with respect to the potential impacts of habitat fragmentation on wild populations, and implications for the design of protected areas.

Hence, the study examines the relation between temporal and spatial variations in food resource availability, and parrot diet, habitat use, and reproduction, in order to determine whether parrots track food resources, and evaluate the impact of environmental variability on reproduction. The principal aims of the research are:

1. Test whether there is temporal and spatial variability in food resource availability for parrots, both between habitats and seasons, creating environmental patchiness.

2. Test for temporal variations in parrot diets and food niche breadths between seasons and years, and whether this is related to resource availability.

3. Determine whether there is temporal and spatial variability in habitat use by parrots, and whether this is related to spatial variations in resource availability.

4. Describe the breeding behaviour of the Lilac-crowned Parrot, and compare this with that observed for mainland and island Amazon species.

5. Evaluate the fecundity and reproductive output of the Lilac-crowned Parrot population, and the factors limiting reproduction.

6. Determine nestling growth rates, and test for the influence of hatching order and annual fluctuations in environmental conditions on nestling growth.

CHAPTER 2

STUDY SITE, SPECIES, AND GENERAL METHODS

2.1 STUDY SITE

2.1.1. LOCATION

The study was conducted at the 13,142 hectare Chamela-Cuixmala Biosphere Reserve ($19^0$22'N $104^0$56'W to $19^0$35'N $105^0$03'W), in the state of Jalisco on the Pacific Coast of Mexico (Appendix 1). The reserve is situated between Puerto Vallarta, 180 km to the north, and Manzanillo, 125 km to the south. The southern border of the reserve is bounded by the Rio Cuitzmala, with the northern border falling south-east of Salinas Chamela. Federal Highway 200 Barra de Navidad-Puerto Vallarta runs along the western edge of the reserve, less than 2 km from the Pacific Ocean, while the eastern edge is bounded by the main tributary of the Arroyo Caiman. The Cuixmala Ecological Foundation has a field station within the reserve at km 45 of Federal Highway 200 ($19^0$25'N $104^0$58'W). The Chamela Biological Station of the National Autonomous University of Mexico (UNAM) is located at the north-western edge of the reserve at km 59 of Federal Highway 200 ($19^0$33'N $105^0$05'W).

2.1.2. HISTORICAL BACKGROUND AND HUMAN IMPACTS

The National Autonomous University of Mexico (UNAM) first established the Chamela Biological Station in 1971, and has been conducting biological research in the area for the past 26 years. In the early 1970s, construction was completed of Federal Highway 200 along the Pacific coast between Puerto Vallarta and Manzanillo, and of a dam in the Tomatlan region.

Such development resulted in extensive clearing of forested areas which has increased rapidly over recent years, with deforestation along the coast of Jalisco occurring at a rate of 2.2% per year between 1986 - 1992 (Miranda 1998). In addition, although semi-deciduous forest comprises less than 10% of the land area along the coast of Jalisco, this forest type has been deforested at twice the rate of deciduous forest, due to the fact that semi-deciduous forest occurs in flat, humid areas near water-courses (Miranda 1998).

The advent of the highway and beach resort tourism along the coast also had an impact on wild parrot populations in the area of the reserve. Local informants report that during the late 1960s to 1970s there was intensive trapping of wild adult parrots, as well as poaching of nestlings, for sale to tourists along the resort beaches (H. Rangel pers. comm.). The Military Macaw (*Ara militaris*), which previously was frequently encountered in the region (H. Rangel pers. comm.), was last observed in the Chamela-Cuixmala area in 1983 (A. Miranda pers. comm.). Populations of military macaws persist in more remote areas of the region, but are highly vulnerable to poaching of nestlings (pers. obs.). The Yellow-headed Parrot (*Amazona oratrix*) has also dramatically declined in numbers with only a few last individuals remaining in the reserve (pers. obs.).

In October 1986, the Cuixmala and Teopa beaches were established as sanctuaries for the protection of marine turtles, and in 1988 the Cuixmala Ecological Foundation began collaboration with UNAM to create a reserve. The Chamela-Cuixmala Biosphere Reserve was established by presidential decree on 30 December 1993.

2.1.3. CLIMATE

Climate data for the study site collected at the Chamela Biological Station from 1977 to 1988 are provided by Bullock (1986, 1988). Additional climate data for 1990 to 1997 were recorded at the Cuixmala Ecological Foundation's station (19°25'N 104°58'W), located 12 km south of the Chamela Biological Station. Annual rainfall data from 1990 to 1997 are presented in Table 1, while eight year monthly averages for temperature and rainfall at the Cuixmala station are presented in Table 2.

Table 1: Rainfall totals (mm) for the Cuixmala Ecological Foundation Station at the Chamela-Cuixmala Biosphere Reserve from 1990 to 1997

Month	1990	1991	1992	1993	1994	1995	1996	1997
January	0	0	534	70	0	0	0	12.5
February	0	0	15	0	0	0	0	0
March	0	0	0	0	0	0	0	21
April	0	0	0	0	0	0	0	13.5
May	1	0	38	0	0	0	0	0
June	361.5	129	52.5	267.5	87.5	67	175.5	25
July	63.5	40.5	127.5	237	125	113	152	193.5
August	168.5	120	70	285	37.5	258.5	377	31.5
September	113	172.5	175	305.5	65	332.5	12	112.5
October	105	32.5	17.5	87.5	215	0	308	216.5
November	0	7.5	0	110	0	2	27.5	61
December	0	17.5	95	0	0	7	0	14
Annual Total	812.5	519.5	1124.5	1362.5	530	780	1052	701
Total days >1mm rain	54	45	61	51	44	50	53	40
<u>Rainfall Year (June-May)</u>								
Total	811.5	1106.5	607.5	1292.5	530	780	1099	654
June-Nov	811.5	502	442.5	1292.5	530	773	1052	640
Dec-May	0	604.5	165	0	0	7	47	14

Table 2: Monthly climactic summary for the Cuixmala Ecological Foundation Station at the Chamela-Cuixmala Biosphere Reserve, from 1990 to 1997. Eight year means presented with standard deviations.

Month	Mean minimum temperature (°C)	Mean maximum temperature (°C)	Mean total rainfall (mm)	Mean days with >1mm rain
Jan.	15.3 ± 2.71	32.4 ± 3.85	77.1 ± 186.2	2.0 ± 3.78
Feb.	15.1 ± 2.65	32.4 ± 3.64	1.9 ± 5.3	0.38 ± 1.06
March	14.8 ± 2.98	31.9 ± 3.68	2.6 ± 7.4	0.25 ± 0.71
April	16.2 ± 2.49	31.6 ± 3.60	1.7 ± 4.8	0.5 ± 1.41
May	19.3 ± 2.57	32.1 ± 3.19	4.9 ± 13.4	0.38 ± 0.52
June	22.5 ± 2.20	33.5 ± 3.06	145.7 ± 116.7	7.13 ± 3.27
July	23.5 ± 1.07	34.2 ± 2.86	131.5 ± 64.0	8.5 ± 2.0
Aug.	23.2 ± 1.23	34.0 ± 3.19	188.1 ± 123.6	11.7 ± 1.38
Sept.	23.3 ± 1.12	34.0 ± 3.62	167.9 ± 118.3	10.57 ± 3.21
Oct.	22.5 ± 1.62	33.8 ± 2.97	109.4 ± 113.6	7.0 ± 4.0
Nov.	20.6 ± 2.04	33.5 ± 3.63	21.0 ± 40.5	1.86 ± 1.77
Dec.	18.1 ± 2.64	32.6 ± 3.51	17.1 ± 34.98	0.86 ± 1.57

The study site has a dry tropical climate exhibiting a marked seasonality in precipitation, and a prolonged annual drought (Table 1). Average annual rainfall at the Cuixmala station from 1990 to 1997 was 883 ± 313.4 mm (range 519.5 - 1362.5 mm, $n = 7$), with a mean of 51 ± 5.76 days per year (range 44 - 61 days, $n = 7$) of at least 1 mm of rain. This is similar to the average annual rainfall of 706.6 ± 143.4 mm, with 53 ± 6 days per year of rain from 1978 to 1988 recorded at the Chamela Biological Station (Bullock 1988).

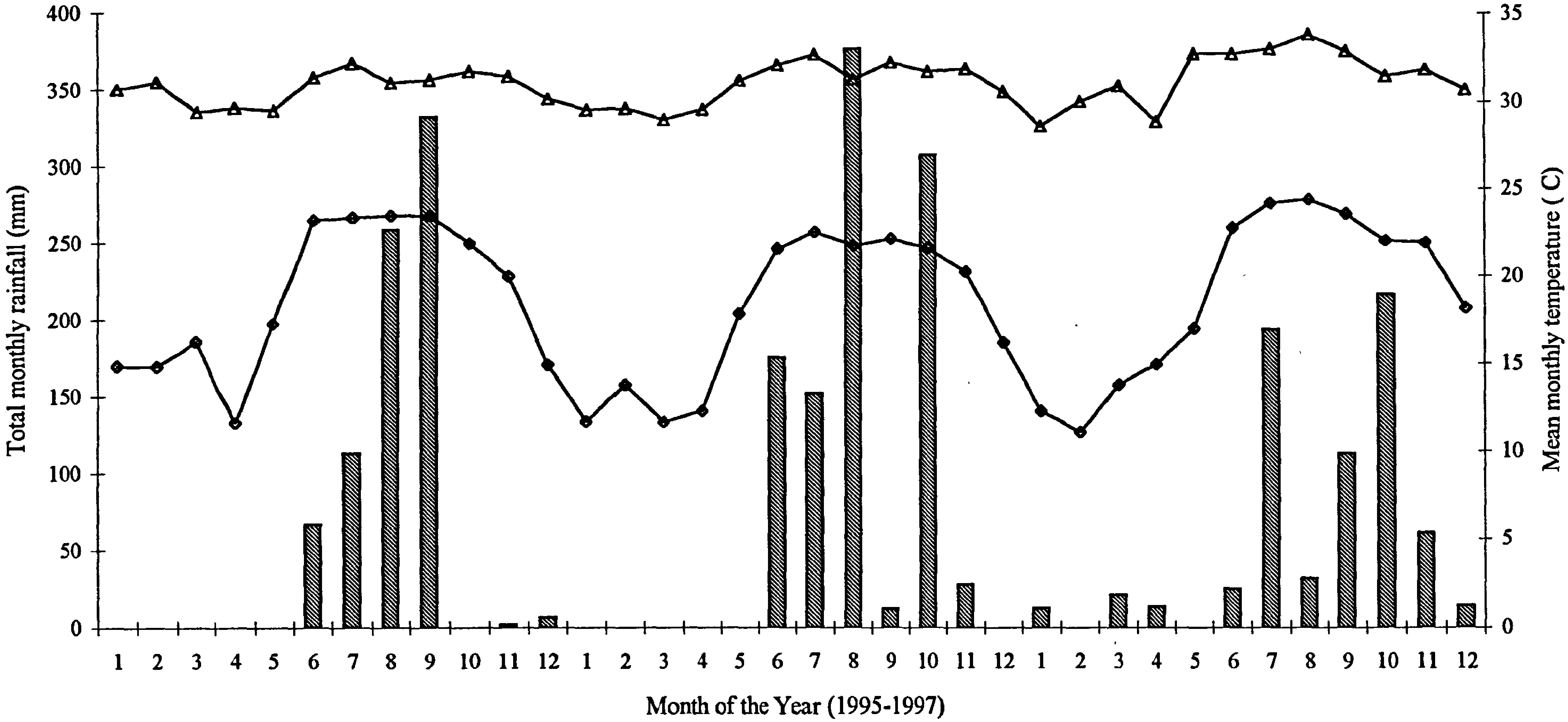
Bullock (1986) defined the rainy season as commencing from the first 10 mm of rainfall in May or June through to the last day with at least 10 mm of rainfall in October or November. For 1990 to 1997 this gives a mean duration of the rainy season from 16 June ± 7.9 days (range 1 - 23 June, $n = 7$) through to 15 October ± 15.3 days (range 21 September - 4 November, $n = 7$), with 85% of the total annual rainfall occurring in June to October. Monthly rainfall averages for 1990 to 1997 exceeded 50 mm and 5 days of rain in June to October, with August and September being the months of maximum average rainfall (Table 2), corresponding with the monthly averages recorded from 1977 to 1988 at the Chamela Biological Station (Bullock 1988).

During most years some rainfall also occurs between December to February, however the sum of rainfall in these three months only exceeded 50 mm in two of the eight years from 1990 to 1997, and only 4 of the past 19 years (Table 1; Bullock 1988). Rainfall during this period is generally associated with occasional tropical cyclones which hit the area, and may heavily bias estimates of mean monthly rainfall. The exceptional rainfall of January and February 1992 resulted from four storms which hit the area during the 1991 - 1992 El Niño weather phenomena in the Pacific Ocean, while the rainfall in January 1993 resulted from one storm. In general, there is a prolonged drought over the four months from mid-February to late May. Most notably, rainfall in March has only occurred twice in the past 20 years, while 1997 was the only year since 1977 in which rainfall was recorded for the month of April. This gives monthly rainfall averages of 1.21 ± 4.63 mm for March, and 0.64 ± 2.95 mm for April since 1977 (Bullock 1986, 1988; Table 1).

Tropical cyclones and hurricanes make landfall more frequently in some areas of the Mexican Pacific coast than others (Bullock 1986). The Chamela-Cuixmala Biosphere Reserve may be considered an area of low hurricane frequency, however the adjacent 125 km stretch of coast from Rio Cuitzmala to Rio Armeria is an area of high hurricane frequency (Bullock 1986). On 23 - 27 October 1959 an hurricane hit the coast approximately 82 km from the study site, and on 31 August 1971 Hurricane Lily hit along the stretch of coast between San Patricio and Tomatlan either side of the study site (Bullock 1986). Hence, there is a possibility of infrequent hurricanes along the coast, which may affect tropical forest structure and composition. The periodic weather phenomena of elevated sea surface temperatures in the Pacific Ocean known as 'El Niño', and the associated phenomena 'La Niña', can also impact the area, either through prolonged droughts or severe winter storms, as with the 1991 - 1992 El Niño.

The annual mean temperature from 1990 to 1997 was 26.3^{0}C, similar to the yearly mean of 24.9^{0}C from 1977 to 1984 (Bullock 1986). Average minimum temperatures were low during January to March, but were above 22^{0}C from June to October (Table 2). The lowest minimum temperature recorded from 1990 to 1997 was 9^{0}C, while the highest maximum temperature was 42^{0}C. Mean maximum temperatures varied by only 2.6^0 between months (range 31.6^{0}C - 34.2^{0}C), however, there was a greater fluctuation of 8.7^0 (range 14.8^{0}C - 23.5^{0}C) in mean minimum temperatures (Table 2). Bullock (1986) demonstrated a significant variation in mean minimum temperatures between months which marked distinct breaks between the seasons. Figure 1 illustrates the pattern of monthly rainfall and mean monthly temperatures during the study years of 1995 to 1997.

Figure 1: Total monthly rainfall and mean minimum and maximum temperatures at the Cuixmala Ecological Station, 1995-1997.



2.1.4. TOPOGRAPHY AND VEGETATION

The reserve has a hilly topography varying in elevation from 20 m to 520 m above sea level. Slope gradients below 6^0 are infrequent, while gradients above 21^0 are common (Bullock 1986). Many small drainages form between the hills and ridges, and are known locally as 'arroyos'. In general, these drainages only have running water during a few months of the year in the rainy season. During the dry season, ground water is only available in a few water-holes in the dry arroyos, and is absent from the hills. The only permanent river within the reserve is the Rio Cuitzmala on the southern boundary.

The dominant vegetation type on the slopes is tropical dry deciduous forest, classified as 'bosque tropical caducifolio' by Rzedowski (1994). Tropical deciduous forest usually has a canopy height of between 8 - 12 m with a dense forest undergrowth, while many tree species have short, ramified trunks not exceeding 50 cm in diameter (Rzedowski 1994). However, the main characteristic of this forest type is that the majority of trees drop their leaves for 5 - 8 months of the year (Rzedowski 1994). Species composition of the forest is diverse (Lott et al. 1987), and varies depending on aspect, soil, exposure, and local factors (Lott 1993). Common tree species in tropical deciduous forest are *Amphipterygium adstringens*, *Bursera instabilis*, *Caesalpinia* spp., *Ceiba aesculifolia*, *Cordia* spp., *Crescentia alata*, *Croton pseudoniveus*, *Ficus cotinifolia*, *Jatropha* spp., *Lonchocarpus* spp., *Lysiloma microphyllum*, *Plumiera rubra*, *Spondias purpurea*, and *Trichilia trifolia* (Lott 1993).

By comparison, small areas of semi-deciduous forest occur in the larger arroyos and more humid valleys. Termed 'bosque tropical subcaducifolio' by Rzedowski (1994) the main characteristic of this forest type is that a large number of the tree species retain their leaves throughout the year, or drop leaves for only 1 - 3 months of the year. Structural features of this forest type are a canopy height of between 15 - 30 m, with tree species having thick, straight trunks of between 30 - 80 cm diameter and up to 1 - 3 m diameter (Rzedowski 1994). Species diversity in semi-deciduous forest is also high, though species composition is distinct to that in deciduous forest (Lott et al.

1987). Tree species characteristic of semi-deciduous forest are *Astronium graveolens, Brosimum alicastrum, Bursera arborea, Couepia polyandra, Cynometra oaxacana, Enterolobium* spp., *Ficus insipida, Hura polyandra, Sciadodendron excelsum, Sideroxylon capiri, Tabebuia donnell-smithii, Tabebuia rosea, Thouinidium decandrum,* and *Vitex hemsleyi* (Lott 1993).

Another distinctive forest-type in the reserve is the monodominant forest of *Celaenodendron mexicanum,* which occurs as discontinuous patches within the tropical deciduous forest mosaic. *Celaenodendron* forests are found only along the Pacific coast from Mazatlan ($23^0$14'N) to Manzanillo (19^0N), and occur at low elevations within 10 km of the coast (Martijena & Bullock 1994). In contrast with the high diversity of other forest types, this forest is dominated by a single species of canopy tree at most size classes of trunk diameter (Martijena & Bullock 1994).

The lower portion of the reserve close to the ocean also comprises coastal dune vegetation, and wetland communities. Aquatic vegetation dominated by *Typha domingensis* occurs in freshwater lagoons at the mouth of the Rio Cuitzmala. Near to the coast, the lagoons grade into mangrove swamps of *Laguncularia racemosa,* and *Rhizophora mangle.* Riparian areas in the lower floodplain of the Rio Cuitzmala experience seasonally destructive flooding, and comprise species such as *Astianthus viminalis, Hippomane mancinella,* and *Salix gooddingii* (Lott 1993).

2.2. STUDY SPECIES

2.2.1. SPECIES DESCRIPTION AND DISTRIBUTION

The Lilac-crowned Parrot (*Amazona finschi*) has predominantly green plumage, with violet blue primary feathers on the wing, and a red speculum at the base of the first five secondary wing feathers. This gives the appearance of a red and blue band on the upper wing when the parrots are in flight. The species is characterised by a red fore-head, green cheeks, and mauve or lilac hind-crown and neck (Forshaw 1989). The

Lilac-crowned Parrot is very similar in appearance to the closely related Red-crowned Parrot (*Amazona viridigenalis*), which is endemic to north-eastern Mexico (Forshaw 1989). The Lilac-crowned Parrot is endemic to the Pacific Coast of Mexico, and is restricted in distribution from south-eastern Sonora to Oaxaca (Forshaw 1989). The species tends to occur in forested areas from sea-level to 1,720 m, and does not appear to occur above 2,000 m elevation (E. Santana pers. com.).

2.2.2. SPECIES BACKGROUND

No studies have been conducted on the ecology and reproductive biology of the Lilac-crowned Parrot in the wild. Previous information from the mid 1940s to the late 1970s consists principally of notes on abundance and distribution, in which large flocks of hundreds of individuals were frequently recorded outside of the breeding season (Forshaw 1989). Anecdotal reports on captive breeding of the Lilac-crowned Parrot give an incubation period of 28 days for the eggs, with the young chick leaving the nest after 60 days (Mann & Mann 1978).

Up to the late 1970s, the species was considered fairly common and widespread throughout its range, with abundant habitat still available (Ridgely 1981). However, Ridgely (1981) noted that capture of wild Lilac-crowned Parrots was increasing dramatically as parrot dealers turned their attention to this species. During 1982-1983 along the Pacific Coast, 17,260 Lilac-crowned parrots were captured for trade, making this the third most captured species in Mexico (Iñigo-Elias & Ramos 1991). The exportation of Mexican wildlife was banned by the Mexican government in 1982, which limited international trade but did not control domestic trade (Iñigo-Elias & Ramos 1991). The Lilac-crowned Parrot is now regarded in Mexico as a threatened endemic species (NOM-059-ECOL-1994), however, poaching of wild nestlings for local trade is still common and widespread (pers. obs.).

2.3. GENERAL METHODS FOR NEST STUDIES

2.3.1 NEST SITE LOCATION

The breeding biology and reproductive success of the Lilac-crowned Parrot was determined by studies of nests at the Chamela-Cuixmala Biosphere Reserve. Nest searches were conducted in January to February 1996 and 1997 during the nest prospecting and early incubation phases of the parrot nesting cycle. No additional nests were located later in the nesting cycle due to the secretive behaviour of breeding pairs which made detection of nest sites difficult. Preliminary observations in February to March 1995 had determined the peak activity period for parrots to be in the early morning and late afternoon. Therefore, nest searches were conducted during the first four hours following sunrise and the last four hours prior to sunset. A cavity was considered a potential nest site if one or both of the adult parrots were observed entering the cavity. The cavity was considered an active nest site if one of the adult parrots remained within the cavity for longer than 20 mins. Nest site fidelity was determined from the incidence of re-use of nest cavities between successive years

The map location of each nest site, and where possible the tree where food transfer from the male to the female occurred, were obtained using a geographic positioning system (GPS) giving X and Y co-ordinates in the UTM format. The distance between active nests, and from the nest to the food transfer tree, was calculated using the equation:

$$\text{Distance (m)} = \sqrt{(X_1 - X_2)^2 + (Y_1 - Y_2)^2}$$

where: X_1, X_2 = X co-ordinates of two different points

Y_1, Y_2 = Y co-ordinates of two different points

2.3.2. ACCESS TO NEST CAVITIES

Access to nest cavities was achieved using single-rope ascending techniques (SRT) with a 25 m caving rope, climbing harness, and ascenders as outlined by Perry (1978), Perry & Williams (1981), and Wheelock (1988). In addition, a tree bole-climbing technique was employed using webbing slings and an etrier as described by Donahue & Wood (1995). Both SRT and bole-climbing techniques are now considered standard low-tech methods for canopy research (Dial & Tobin 1994, Moffet & Lowman 1995; Lowman & Wittman 1996). However appropriate training and awareness of safety are essential before applying such techniques in field research (Whitacre 1981).

2.3.3. HANDLING OF NESTLINGS

The determination of reproductive output, nestling growth rates, and nestling diet, required regular inspection of parrot nests, and handling of nestlings. At each nest inspection, standardised measurements were taken of the nestlings, and a sample of the crop contents was collected to evaluate nestling diet. All measurements were conducted at the nest entrance to minimise handling time and potential stress for the nestlings. Disposable gloves and a face mask were also used when handling nestlings to avoid potential disease transmission between nestlings and researcher. The procedures used for data collection and the handling of nestlings conformed to the Ornithological Council guidelines for the use of wild birds in research (Guant et al. 1997).

CHAPTER 3

RESOURCE AVAILABILITY AND UTILISATION

3.1. ABSTRACT

The pattern of food resource abundance and utilisation by Lilac-crowned Parrots was evaluated in the tropical dry deciduous and semi-deciduous forests of the Chamela-Cuixmala Biosphere Reserve, western Mexico. Monthly fruiting phenology transects were conducted in different forest types to determine temporal and spatial variability in resource abundance. Resource utilisation by parrots was evaluated through observations of diet, habitat use, and crop samples of nestlings. There was significant temporal and spatial variability in food resource abundance, with semi-deciduous forest providing greater food resources for parrots during the dry season, while food resource abundance increased in deciduous forest during the rainy season. The critical period of food resource scarcity occurred during May - June at the end of the long dry season drought. Lilac-crowned Parrots were predominantly pre-dispersal seed predators, and exhibited high flexibility in diet, incorporating dietary switching, as well as niche breadth contraction and expansion, which corresponded with temporal variations in food resource availability. There was low overlap in parrot diets between seasons and years, with parrots exhibiting a narrow food niche breadth during the late dry season when resource availability declined. Parrots also demonstrated spatial variation in habitat use, corresponding to fluctuations in the availability of food resources in different habitats. Finally, Lilac-crowned Parrots made long-distance seasonal altitudinal migrations during the period of greatest food resource scarcity at the end of the dry season. This flexibility in diet, spatial scales, and mobility, enables parrots to closely track and exploit seed resources, which exhibit high temporal and spatial variability in abundance.

3.2 INTRODUCTION

3.2.1. FRUITING PHENOLOGY AND RESOURCE AVAILABILITY

Studies on the periodicity of leaf production, flowering and fruiting in tropical forests were stimulated after Janzen (1967) high-lighted the synchrony in reproductive activity of trees in tropical deciduous forest, with most species flowering and fruiting during the dry season. Further studies in tropical deciduous forests have demonstrated marked seasonality in plant productivity, with leaf flush occurring during the brief rainy season, while flowering and fruiting activity are concentrated during the dry season (Daubenmire 1972; Frankie et al. 1974; Lieberman 1982; Bullock & Solis-Magallanes 1990; Guevara et al. 1992; Murali & Sukumar 1994). Tropical deciduous forests may be expected to exhibit periodicity in plant production, due to the marked seasonality in rainfall which is restricted to only a few months of the year, and the extended dry season occurring in such forests (Bullock 1986, 1988).

Comparative phenology studies in wetter lowland forests also demonstrate seasonal variation in plant energy production, though this is less marked than in dry deciduous forests, with slight peaks in fruit production during the rainy season, and a decline in plant food resources during the dry season (Frankie et al. 1974; Terborgh 1986a; Janson & Emmons 1990; Peres 1994; White 1994). Tropical forest on Barro Colorado Island exhibits a double peak in flowering and fruiting activity (Smythe 1970a; Foster 1982a), which may correspond with its status as intermediate between dry and wet forests (Hartshorn 1983).

In general, fleshy fruits tend to be produced during the rainy season, while dehiscent or wind-dispersed fruits tend to ripen during the dry season (Daubenmire 1972; Lieberman 1982; Guevara et al. 1992). The predominance of dehiscent or wind-dispersed plant species in tropical deciduous forest may account for the marked seasonality of fruiting during the dry season of such forests (Janzen 1967; Daubenmire 1972). Furthermore, plant species which do not rely on animal vectors for dispersal may evolve high synchrony in fruit production as a strategy to avoid predation by satiating potential seed predators (Janzen 1969, 1971; Augspurger 1981).

Such fluctuations in the availability of plant resources, even in forests with less marked seasonality in rainfall, has consequences for the animal community. Variation in soil types, habitats, and micro-climates in tropical forests result in heterogeneity in the availability of plant resources between different areas, creating environmental patchiness (Foster 1980). This variability is however seasonally predictable (Colwell 1974; Karr & Freemark 1985), and animals should exhibit life histories adaptive to this.

3.2.2. VARIABILITY IN DIET AND RESOURCE UTILISATION

Animal communities may employ a variety of strategies to deal with environmental variability in food resources, including dietary switching, concentrating on a few key resources, seasonal breeding, habitat shifts or migration, and social organisation (Wiens 1976, 1985; Leighton & Leighton 1983; Terborgh 1986a, b; Fleming 1992; van Schaik et al. 1993; Peres 1994). Early studies demonstrated that tropical bird communities exhibit marked seasonal variations in abundance and composition (Fogden 1972; Karr 1976; Karr et al. 1982; Karr & Freemark 1985). This temporal variation is greater in frugivore and nectarivore bird communities, as opposed to insectivore communities which are essentially stable (Martin & Karr 1986; Poulin et al. 1994a).

Temporal and spatial variation in understorey frugivorous bird communities is associated with corresponding variations in food resource abundance, indicating that bird communities may track food resources within habitats, across altitudinal elevations, and between successional stages of forest habitat (Levey 1988; Blake & Loiselle 1991; Loiselle & Blake 1991, 1992, 1994; Poulin et al. 1993). More direct evidence of the ability of frugivores to track variations in food resource abundance was provided by Rey (1995), demonstrating that the most abundant frugivores in

Mediterranean olive orchards were able to track the rapid changes in food resource abundance created by harvesting rotas.

Most studies on the relationship of bird communities to resource variability have been conducted on frugivore communities. However, the behaviour of granivores in response to food availability is similar to that of frugivores (Poulin et al. 1994a). In fact, granivores may need to be more mobile and variable than frugivores in order to exploit highly variable and synchronised seed crops (Janzen 1969, 1971; Smythe 1970a; Augspurger 1981; van Schaik et al. 1993). High variability in diet shifts, diversity, and finch abundance has been demonstrated for granivorous ground finches on the Galapagos, and related to the abundance and distribution of seed resources (Smith et al. 1978; Grant & Grant 1980; Schluter 1982a, b; Boag & Grant 1984; Price 1987). In general, finch diets became less varied and more specialised as resource abundance declined, with bird species frequently switching to consume alternate food items at different times of the year (Smith et al. 1978; Schluter 1982a, b). This diet switching may arise due to the marked temporal variations in resource availability which occur in complex environments, with some resources only being available at certain times of the year (Smith et al. 1978; Schluter 1981, 1982a).

Tropical bird species are frequently opportunistic in diet, and may take advantage of additional food types across feeding guilds (Poulin et al. 1994b). However, though birds may consume a variety of food items, the bulk of the diet is usually comprised by only a small proportion of these (Lack 1954; Ward 1965; Newton 1967; Banbura et al. 1994; Bancroft & Bowman 1994; Kleintjes & Dahlsten 1994). Bird diets may vary in diversity and the specific items consumed in response to seasonal variations in the abundance and availability of food resources (Smith et al. 1978; Calver & Wooller 1981; Schluter 1982a, b; Boag & Grant 1984; Price 1987). Analysis of nestling diets has demonstrated temporal variability in the items comprising the major proportion of the diet, both within a year (Ward 1965; Barba & Gil-Delgado 1990; Banbura et al. 1994; Bancroft & Bowman 1994), and between years (Banbura et al. 1994; Bancroft & Bowman 1994). These studies suggest that the predominance of certain items in nestling diets may be related to availability. However, the relationship between consumption and resource availability is likely to be complex (van Horne & Bader 1990), and some food items may be preferred even when they are scarce due to their protein or mineral contents (Sakai & Carpenter 1990).

Canopy bird species comprise 40 - 50% of all tropical forest bird species (Karr 1990; Robinson & Terborgh 1990), and may experience high variability in food resources due to the greater seasonality of canopy trees compared to the understorey (Frankie et al. 1974; Opler et al. 1980). However, few studies have investigated the relation of canopy bird populations to food resources, though canopy populations exhibit temporal variations in abundance (Greenberg 1981; Loiselle 1988), and canopy flocks have territories four times larger than understorey flocks (Munn 1985; Terborgh et al. 1990). Furthermore, fluctuations in the abundance of Hornbills were correlated with fruit abundance, suggesting that these canopy frugivores may track the availability of fruit resources (Kinnaird et al. 1996; Whitney & Smith 1998).

Large-bodied frugivores and parrots dominate canopy bird communities (Loiselle 1988; Terborgh et al. 1990). Most parrot species are primarily granivorous in nature, with seeds forming a major component of the diet (Saunders 1980; Beeton 1985; Rowley 1990; Rowley & Chapman 1991; Galetti 1993; Gilardi 1996; Enkerlin-Hoeflich & Hogan 1997), though some parrot species may be frugivorous (Snyder et al. 1987; Wermundsen 1997), or consume a large proportion of invertebrates (O'Donnell & Dilks 1994). However, little is known of the relation of parrots to food resources, though there is evidence of high temporal variability in parrot diet, movements, and social organisation.

Seasonal variations in diet, with switching of the main items consumed, have been noted for many Australian parrots (Saunders 1980; Beeton 1985; Rowley 1990; Rowley & Chapman 1991; O'Donnell & Dilks 1994), and some Neotropical parrot species (Snyder et al. 1987; Galetti 1993; Wermundsen 1997). Temporal variations in the abundance of parrot populations encountered in surveys may be related to seasonal variations in food resource availability (Loiselle 1988; Renton 1994; Enkerlin-Hoeflich 1995). Australian parrots also exhibit large scale seasonal movements, frequently forming nomadic flocks outside of the breeding season, and making latitudinal migrations of over 100 km between feeding areas (Saunders 1980; Rowley & Chapman 1991; Smith & Moore 1992).

However, few studies of psittacines have incorporated information on the phenology of food plants, and no studies have examined the relationship between parrot populations and food resources, even though most parrot species rely on food types (i.e., seeds and fruits) which may demonstrate high temporal and spatial variability in abundance. It may be predicted that seed predators such as parrots will track food resources closely in order to exploit temporal and spatial abundances in plant seed production.

Understanding the relationship of parrot populations to food resources enables determination of the key resources, habitats, and areas required to maintain healthy parrot populations throughout the year. In particular, food resource availability may be critical to the viability of wild parrot populations during the breeding season, when food supply may affect breeding success (Saunders 1986). With current rates of deforestation, the habitat available for parrots is increasingly reduced to forest remnants within a mosaic of agricultural land. It is therefore, important to conserve sufficient areas and habitats for parrots, and to predict the impact of fragmentation on parrot populations (Saunders 1986, 1990, 1991; Galetti 1993).

An ability to closely track resource availability may enable some species to survive in heavily cultivated landscapes (Rey 1995). This may be the case for some Australian parrots which have adapted to exploit agricultural crops along the Australian wheatbelt (Saunders 1980; Beeton 1985; Rowley 1990; Rowley & Chapman 1991), while populations of other cockatoo species declined as a result of increasing cultivation (Saunders 1986, 1990, 1991). Hence, basic knowledge is required on how patch dynamics are expressed in nature, and how populations and organisms respond to them (Wiens 1976, 1985).

3.3 METHODS

The study was conducted at the Chamela-Cuixmala Biosphere Reserve ($19^0$22'N $104^0$56'W to $19^0$35'N $105^0$03'W), in Jalisco on the Pacific Coast of Mexico. Resource availability in different forest types throughout the year was determined by monthly phenology transects, while Lilac-crowned Parrot resource utilisation was determined through observations of feeding birds, and crop samples of nestlings.

3.3.1. FRUITING PHENOLOGY TRANSECTS

Various methods may be used to evaluate food resource abundance including fruit traps, fruit trails and phenology transects. Fruit traps have many limitations in determining resource availability for the animal community, and results from fruit traps do not correlate with results from fruit trails and phenology transects (Chapman et al. 1994). It was decided to employ phenology transects in the present study as this method enables evaluation of habitat variation in resource availability (Chapman et al. 1994).

Habitat selection

Phenology transects were placed in three habitat types of deciduous forest, semi-deciduous forest, and along watercourses (known locally as 'arroyos'). Areas of semi-deciduous forest between the Arroyo Chamela and the Rio Cuitzmala were identified from aerial photographs of the region taken during the dry season (INEGI 1973). As semi-deciduous forest retains leaf cover during the dry season, this forest type could be easily distinguished as darker shaded areas in the photographs.

Deciduous forest is the dominant vegetation type at the study site, however, the area which could be surveyed was limited to some extent by the feasibility of access along existing road or trail systems. In addition, deciduous forest is not homogenous, with many species exhibiting a clumped distribution (Hubbell 1979; Thorington et al. 1982). Hence phenology transects were dispersed as widely as possible within the study area, and were constructed off from main road or trail systems to avoid recording edge species. Transects were also varied with respect to aspect, and included placement on a south-east slope ($n = 3$), south-west slope ($n = 2$), north-east slope ($n = 3$), north-west slope ($n = 2$), along a ridge top ($n = 3$), and in deciduous forest at the base of a slope ($n = 2$). The aim was to spread transects within the study site to obtain an overall impression of resource availability in deciduous forest.

Watercourses within the study site comprised predominantly vegetation characteristic of deciduous forest, but with some mixture of semi-deciduous species due to a slightly higher soil humidity than on the slopes. Hence, watercourses were included as a third habitat type in the phenology study. Transects were established along four main watercourses in the study site: Arroyo Caiman, Arroyo Carayes, Arroyo Cajones, and Arroyo Limbo. Placement of transects along these watercourses was determined by dividing the main watercourses and their tributaries on the map into 500 m numbered sections, which were then randomly selected. Each 200 m transect was established within the 15 selected 500 m sections, locating the selected point in the field using a geographical positioning system (GPS). As watercourses may be 2 - 5 m wide, fruiting species were recorded within 3 m of either edge of the watercourse.

Phenology transects

A total of 45 phenology transects of 200 m x 6 m were established, with 15 transects in each of the three habitat types. Transects were monitored by the same observer during the second and third weeks of each month from January 1996 through to July 1997 (with the exception of December 1996). All fruit or seed bearing trees greater than 10 cm diameter at breast height (DBH) were recorded when detected within a 3 m band on either side of the transect line. The size category of 10 cm DBH was chosen for the lower limit of tree size as the intention of the study was to evaluate canopy variation in food resource abundance, and this was the lower tree size limit established in previous phenology studies (Bullock & Solis-Magallenes 1990; Chapman et al. 1994). Where a tree occurred on the boundary of the 3 m transect width, the tree was included if the mid-point of the trunk was rooted within the transect area (Gentry 1982).

For each fruiting tree encountered, the distance along the transect was recorded, as well as the distance of the tree from the transect line. Tree species were identified in the field, and by comparison with samples in the University of Mexico herbarium at the Chamela Biological Station. The DBH of each fruiting tree was measured, while fruit abundance was visually assessed using 10x40 binoculars, and an estimate of fruit abundance made by counting. Visual estimation of the number of fruit on the tree involved a greater potential bias, as counting was more difficult for taller tree species of dense foliage, or species which produced large numbers of small fruit. Hence, the DBH of fruit or seed bearing trees was preferred as an estimate of abundance as this variable is the most accurate predictor of fruit crop biomass and number, and is highly correlated with rank values from visual estimation (Chapman et al. 1992, 1994). Where the trunk was branched below breast height (@1.3 m), the DBH of each trunk branch was measured and summed to give a total DBH for that tree. This was more frequent in deciduous forest, and tree species were included in the transects if the sum of the branched trunks was greater than 10 cm diameter. Finally, the colour and stage of ripeness of fruit or seed crops were also recorded.

Determination of the resource

Wiens (1976) states that ecological studies need to evaluate the environment as perceived by the study animal, and hence the resource under investigation should be organism-defined. Therefore, when evaluating food resource abundance for Lilac-crowned Parrots, fruit or seed crops of tree species in the transects were included in the analysis at the stage of ripeness when they are consumed by parrots. Furthermore, certain plant species, such as many *Lonchocarpus* species, may be excluded as potential food resources for parrots due to a high level of toxicity in the seeds (Janzen 1969; Janzen et al. 1990). Other species, such as *Crescentia alata*, *Guazuma ulmifolia*, and *Hura polyandra*, may not be available as a food resource to Lilac-crowned Parrots due to the size and durability of the shell which many herbivores are unable to open (Janzen 1982; Janzen & Martin 1982). Finally, species such as *Bursera arborea*, *Bursera instabilis*, *Heliocarpus pallidus*, *Jacaratia mexicana*, *Jacquinia pungens*, and *Tabebuia* species, do not appear to be recognised as a food resource by Lilac-crowned Parrots, for despite being common at the study site, Lilac-crowned Parrots were never observed to feed on the fruits or seeds of these species.

Hence for the purpose of analysis, general fruiting phenology was evaluated including all plant species recorded in the phenology transects, while food resource abundance was evaluated by incorporating only actual or potential Lilac-crowned Parrot food plant species. Where there was no clear reason for excluding a particular species as a food item for Lilac-crowned Parrots, the plant species was included in the analysis as a potential food resource.

Data analysis

The total number of fruiting trees, and their DBH was summed over all transects in each of the three habitat types in order to obtain habitat-wide estimates of resource abundance in each month. For the purpose of the phenology study, June was included as a dry season month as in both 1996 and 1997 the first rains did not commence until the end of June, after phenology transects for that month had been completed.

Preliminary analysis determined that the data did not deviate significantly from the normal distribution required for parametric analysis (Zar 1996). Hence, seasonal variation in overall fruiting phenology and food resource abundance was analysed by two-way ANOVA on the number of trees and sum of DBH of fruiting trees in each habitat type during the dry and rainy season. The general linear model was used to account for missing values for the month of December. Between year differences in food resource abundance were also tested by two-way ANOVA on the number of trees and sum of DBH of fruiting trees for each habitat type during the dry season of 1996 and 1997. Finally, between year differences in the number of food species available during the dry season were tested by one-way ANOVA.

3.3.2. PARROT DIET OBSERVATIONS

The diet of Lilac-crowned Parrots throughout the year was determined by observations of feeding activity. During each month of the year, trails were regularly walked in deciduous, and semi-deciduous forest, and along watercourses during the first four hours of the morning and the last three hours of the afternoon when parrots conduct the majority of foraging activity. When feeding parrots were encountered the date, time, location, food species and habitat type were all noted, as well as the number of parrots observed feeding on each food resources, and the plant part eaten i.e., fruit pulp, seed, or flower. A feeding bout was recorded as one observation of one or more parrots feeding on one food source. If the parrots changed to another food source during the period of observation, this was recorded as a second feeding bout (Galetti 1993).

Diet observations were analysed using the number of individuals observed feeding on a particular resource, and the number of feeding bouts. Levins' and Hurlbert's standardised niche breadths were calculated for parrot diets during different periods of the year. Diet overlap between the dry and rainy season was evaluated using a variety of similarity and niche overlap measures. Levins' standardised niche breadth indice was also calculated from observations of Lilac-crowned Parrot diets during four periods of the year corresponding to the early dry season (January - March), the late dry season (April - June), early rainy season (July - September), and the late rainy season or rainy-dry transition (October - December). These niche breadth indices were then correlated with the number of food species available during each three month period as determined by the phenology transects. Finally, chi-square contingency analysis was conducted to test for differences in the number of feeding bouts recorded in each of the three habitat types during the four periods of the year.

3.3.3. NESTLING DIETS

Collection of crop samples

At each nest inspection, samples of the crop contents were taken from nestlings following the procedure developed by Enkerlin-Hoeflich et al. (in press). Crop samples were taken from 12 nestlings in 5 nests during 13 April - 14 May in 1996, and from 9 nestlings in 4 nests during 30 March - 21 May in 1997. All crop samples were taken using the plastic cylinder of an open-ended 3 ml syringe which was inserted down the parrot gullet to the crop. The crop was then gently massaged to manoeuvre the food contents into the cylinder of the syringe, thereby extracting a sample of the crop contents. The sample was then transferred from the syringe to a zip-lock plastic food storage bag, which was labelled with the date, nest, and chick number. Crop samples were not taken until the nestlings were more than 20 days of age as recommended by E. Enkerlin-Hoeflich (pers. comm.). In addition, samples were not taken if there was little food in the crop, as determined by visual inspection of crop expansion.

Preparation of samples

Prior to weighing, samples were placed on absorbent paper for 15 mins to drain any excess water. For each crop sample, the date, nest, and chick number were recorded. The number of different food items in each sample was noted, and the total sample weight taken with a portable electronic balance of 0.01 g precision. Individual food items were then separated out and differentiated by type, size, shape, and colour. Food items were then identified to species by comparison with samples collected from the field. Where a food item could not be identified to species it was assigned a number.

For seed items, the number of seeds of each species were counted, and weighed on a portable electronic balance (200 g capacity, 0.01 g precision). The biomass of each seed food item in the crop sample was then determined as a proportion of the total sample weight. Fruit pulp could not be reliably weighed therefore, fruit items in the diet were noted on a presence-absence basis only.

Data analysis

Dietary variety was determined as the number of different food items in each crop sample, while composition of the diet was evaluated both by the frequency of occurrence and proportional biomass of each food item in the crop samples. One-way ANOVAs were conducted to test for differences between siblings and between nests in the number of different food items, and the frequency of occurrence of each food item in the crop samples. Annual variation in dietary variety was also tested by one-way ANOVA on the number of food items in crop samples between 1996 and 1997. Niche breadth indices and similarity measures described below were also applied to evaluate overlap in diets between 1996 and 1997.

3.3.4. FOOD NICHE BREADTH AND SIMILARITY ANALYSES

Niche breadth

Food niche breadth and diet overlap were estimated both for nestling diets between 1996 and 1997, and for observations of adult diets between different seasons of the year. Niche breadth was evaluated using the Levins' and Hurlbert's niche breadth indices as detailed below:

Levins' niche breadth indice B was standardised on a scale of 0 - 1 (Levins 1968; Colwell & Futuyma 1971):

$$B = 1 / [\, \mathrm{n} \sum p_i^2]$$

Where B = Levins' standardised niche breadth indice, p_i = the proportion of individuals using resource state i, and n = the number of resource states.

Hurlbert's niche breadth (Hurlbert 1978) was also calculated for parrot diets over the dry season and the rainy season, incorporating a measure of the proportional abundance of resources in each season, and standardised on a scale of 0 - 1:

$$B' = \frac{[1 / \sum (p_i^2 / a_i)] - a_{\min}}{1 - a_{\min}}$$

Where: B' = Hurlbert's standardised niche breadth, p_i = proportion of individuals using resource i, a_i = proportional availability of resource i, and $a_{\min}$ = proportion of least abundant resource.

For both niche breadth indices, a value close to 0 indicates dietary specialisation, while a value close to 1 indicates a broad niche width (Colwell & Futuyma 1971; Hurlbert 1978).

Similarity measures

Similarity or overlap in nestling diets between years, and in adult diets between seasons, was evaluated using a variety of similarity measures. Shared species in the diet between the two years and seasons was evaluated using the coefficient of Jaccard:

$$S = \frac{a}{a + b + c}$$

Where S = Jaccard's similarity coefficient, a = the number of species in both sample A and B, b = the number of species occurring only in sample B, c = the number of species occurring only in sample A.

The percent similarity in diet between years and seasons was also determined using the Renkonen index:

$$P = \sum \text{minimum } (p_{1i}, p_{2i})$$

Where P = percent similarity between samples 1 and 2, p_{1i} = percent of species i in sample 1, and p_{2i} = percent of species i in sample 2.

Finally, the Morisita index of similarity was calculated for quantitative data on occurrence of food items in the diet between years and seasons:

$$C = \frac{2 \sum p_{ij} p_{ik}}{\sum^{n} p_{ij} \left[(n_{ij} - 1) / (N_j - 1) \right] + \sum^{n} p_{ik} \left[(n_{ik} - 1) / (N_k - 1) \right]}$$

Where C = Morisita index of similarity, p_{ij} p_{ik} = proportion of resource i in sample j and sample k, n_{ij} n_{ik} = frequency of resource i in samples j and k, and N_j N_k = total number of individuals in sample j and sample k.

3.4. RESULTS

3.4.1. FRUITING PHENOLOGY AND RESOURCE AVAILABILITY

Seasonal variation in food resources

A total of 56 species of tree were recorded in the phenology transects, 36 of which were incorporated in the analysis as actual or potential food resources for Lilac-crowned Parrots (Table 3). A further 20 species were excluded from the analysis as parrot food resources (Table 4), but were included in the analysis of general fruiting phenology. Overall, monthly phenology transects demonstrated a sharp decline in resource abundance by number of trees, number of species, and the sum of DBH of fruiting trees during the late dry season in May and June, gradually rising again in July with the start of the rainy season. This was true both when considering only potential parrot food species (Figs 4 & 5), and including all species recorded in the transects (Figs 2 & 3). Interestingly there was a peak in resource abundance during the dry season months of March and April (Figs 2 - 5), mainly due to the fruiting of *Astronium graveolens*, *Caesalpinia eriostachys*, *Comocladia engleriana*, and *Spondius purpurea*.

Habitat variability in food resources

The pattern of fruiting phenology by habitat type is illustrated both for all species recorded in transects (Fig 6 & 7), and for potential Lilac-crowned Parrot food resources only (Figs 8 & 9). In general, food resource abundance for Lilac-crowned Parrots was greater in semi-deciduous forest during the early dry season months of January - February due mainly to fruiting of *Brosimum alicastrum* (Fig 10). The peak in deciduous forest, and along watercourses, during March and April was due to fruiting of *Comocladia engleriana*, *Spondius purpurea*, *Caesalpinia eriostachys*, and *Ficus cotinifolia* (Fig 10). The sharp April peak in semi-deciduous forest, and to a lesser extent along watercourses, arose from mass fruiting of *Astronium graveolens* (Fig 10). All habitat types began to decline in resource abundance during the late dry season in May - June, however, semi-deciduous forest maintained some food resource abundance during this period due to fruiting of *Astronium graveolens*, *Guarea glabra*, and *Ficus* species (Fig 10).

There was a slight peak in resource abundance along watercourses during July following ripening of *Sciadodendron excelsum* fruit (Fig 11), and the onset of fruiting of deciduous forest species such as *Celaenodendron mexicanum*, *Crataeva tapia*, *Jatropha* species, and *Caesalpinia* species, which commenced fruiting slightly earlier along watercourses than on the slopes, possibly due to a greater soil humidity. The overall increase in resource abundance in deciduous forest, as well as along watercourses, during the latter part of the rainy season was due to fruiting of many deciduous forest species including: *Acacia* species, *Caesalpinia* species, *Celaenodendron mexicanum*, *Crataeva tapia*, *Esenbeckia nesiotica*, *Jatropha* species, *Lysiloma microphyllum*, *Pithecellobium* species, and *Plumeria rubra* (Fig 11).

This general pattern was similar when considering overall fruiting phenology including all species recorded in transects (Figs 6 & 7), as opposed to Lilac-crowned Parrot food resources only (Figs 8 & 9). However, the difference between habitats was less marked for fruiting phenology during the early to mid dry season (Figs 6 & 7) due principally to an abundance of *Heliocarpus pallidus*, and other tree species in deciduous forest, which retained ripe seeds over a long period of time. However, Lilac-crowned Parrots were never observed to feed on *Heliocarpus* seeds, possibly due to the extremely small size of seeds (@3mm diameter), and parrots tended to consume immature seeds rather than mature seeds.

Seasons and habitats did not differ significantly in food resource abundance over the course of a year. However, habitats did differ in their response to seasons. Semi-deciduous forest had greater resource abundance for Lilac-crowned Parrots during the dry season, which declined during the rainy season (Figs 8 & 9). Conversely, deciduous forest had lowest resource abundance during the dry season, which increased during the rainy season to gradually overtake semi-deciduous forest (Figs 8 & 9). This interaction between seasons and habitats in food resource abundance was significant both for number of food trees (Table 7), and sum of DBH of food trees (Table 8). There was a similar interaction between habitats and seasons with regard to general fruiting phenology (Tables 5 & 6), however, this was only significant with respect to the sum of DBH of fruiting trees (Table 6)

Table 3: Species included as parrot food items in analysis of phenology transects.

Family	Species	Period recorded	Phase recorded
Anacardiaceae	*Astronium graveolens*	April - June	unripe + ripe seed
Anacardiaceae	*Comocladia engleriana*	March - May	unripe + ripe seed
Anacardiaceae	*Spondius purpurea*	March - May	unripe seed
Apocynaceae	*Plumeria rubra*	Sept - March	unripe seed
Araliaceae	*Sciadodendron excelsum*	July - Aug	ripe fruit
Bombacaceae	*Ceiba aesculifolia*	Feb - April	ripe seed
Burseraceae	Unidentified *Bursera* spp.	Nov	ripe seed
Capparaceae	*Crataeva tapia*	Sept - April	unripe seed
Euphorbiaceae	*Celaenodendron mexicanum*	July - Feb	unripe + ripe seed
Euphorbiaceae	*Cnidoscolus spinosus*	July - Aug	unripe seed
Euphorbiaceae	*Jatropha chamelensis*	July - Aug	unripe seed
Euphorbiaceae	*Jatropha malacophylla*	July	unripe seed
Euphorbiaceae	*Jatropha standleyi*	Aug - Sept	unripe seed
Leguminosae	Unidentified *Acacia* spp.	Nov - Dec	unripe seed
Leguminosae	*Albizia* spp.	Sept - Oct	unripe seed
Leguminosae	*Bauhinia ungulata*	Jan - Feb	unripe seed
Leguminosae	*Caesalpinia eriostachys*	Jan - March	unripe seed
Leguminosae	*Caesalpinia platyloba*	July - Oct	unripe seed
Leguminosae	*Ceasalpinia pulcherrima*	Nov - Dec	unripe seed
Leguminosae	*Caesalpinia sclerocarpa*	Sept - Nov	unripe seed
Leguminosae	*Erythrina lanata*	April - May	unripe + ripe seed
Leguminosae	*Lysiloma microphyllum*	Oct - March	unripe seed
Leguminosae	*Pithecellobium mangense*	Nov - Jan	unripe seed
Leguminosae	*Pithecellobium lanceolatum*	Sept - Oct	unripe seed
Leguminosae	Unidentified legume spp. 1	June - July	unripe seed
Leguminosae	Unidentified legume spp. 2	April/July	unripe seed
Meliaceae	*Guarea glabra*	April - June	ripe seed
Moraceae	*Brosimum alicastrum*	Jan - March	unripe + ripe seed

Moraceae	*Ficus cotinifolia*	throughout	ripe fruit
Moraceae	*Ficus insipida*	throughout	ripe fruit
Myrtaceae	*Psidium sartorianum*	March - May	ripe seed
Nyctaginaceae	*Guapira macrocarpa*	May/July	ripe fruit
Polygonaceae	*Coccoloba barbadensis*	Sept - Nov	unripe seed
Polygonaceae	*Coccoloba liebmannii*	Nov - March	unripe seed
Rutaceae	*Esenbeckia nesiotica*	Aug - Oct	unripe seed
Sapotaceae	*Sideroxylon capiri*	March - June	unripe seed

Table 4: Species recorded in phenology transects but excluded as food items.

Family	Species	Unripe fruit	Ripe fruit
Apocynaceae	*Thevetia ovata*	Sept - Oct	Oct - Nov
Bignoniaceae	*Crescentia alata*	July - Nov	Dec - April
Bignoniaceae	*Tabebuia rosea*	April - May	Dehiscent
Burseraceae	*Bursera arborea*	June - Nov	Nov - April
Burseraceae	*Bursera excelsa*	July - Oct	Oct - Feb
Burseraceae	*Bursera heteresthes*	July - Aug	Sept - Oct
Burseraceae	*Bursera instabilis*	June - Oct	Nov - Feb
Caricaceae	*Jacaratia mexicana*	April - June	May - June
Cochlospermaceae	*Cochlospermum vitifolium*	April - June	Kapok
Euphorbiaceae	*Hura polyandra*	Feb - April	April - May
Julianaceae	*Amphipterygium adstringens*	July - Aug	Sept - Jan
Leguminosae	*Lonchocarpus eriocarinalis*	Aug - Oct	Nov - Jan
Leguminosae	*Lonchocarpus lanceolatus*	Oct - Nov	Nov - Jan
Leguminosae	*Lonchocarpus* spp.	Sept - Oct	Nov
Leguminosae	*Pterocarpus orbiculatus*	April - May	June
Simaroubaceae	*Recchia mexicana*	Jan - March	March - May
Sterculiaceae	*Guazuma ulmifolia*	Feb - March	April
Theophrastaceae	*Jacquinia pungens*	Jan - June	Jan - June
Tiliaceae	*Heliocarpus pallidus*	Nov - Dec	Jan - May
Zygophyllaceae	*Guaiacum coulteri*	April - June	

Figure 2: Total number of trees and species in monthly phenology transects (1996).

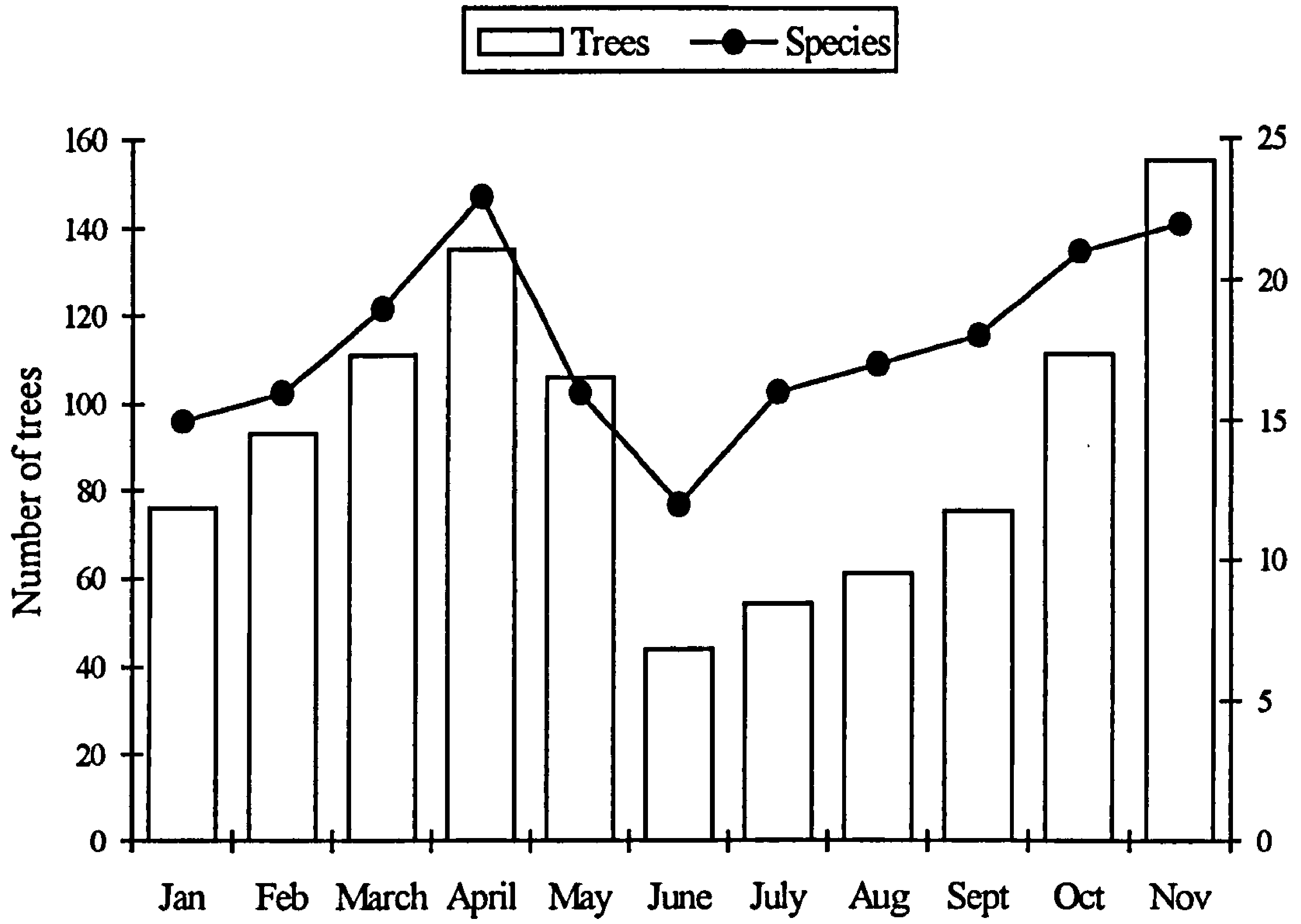


Figure 3: Number and sum of diameter at breast height (DBH) of all fruiting trees in monthly phenology transects (1996).

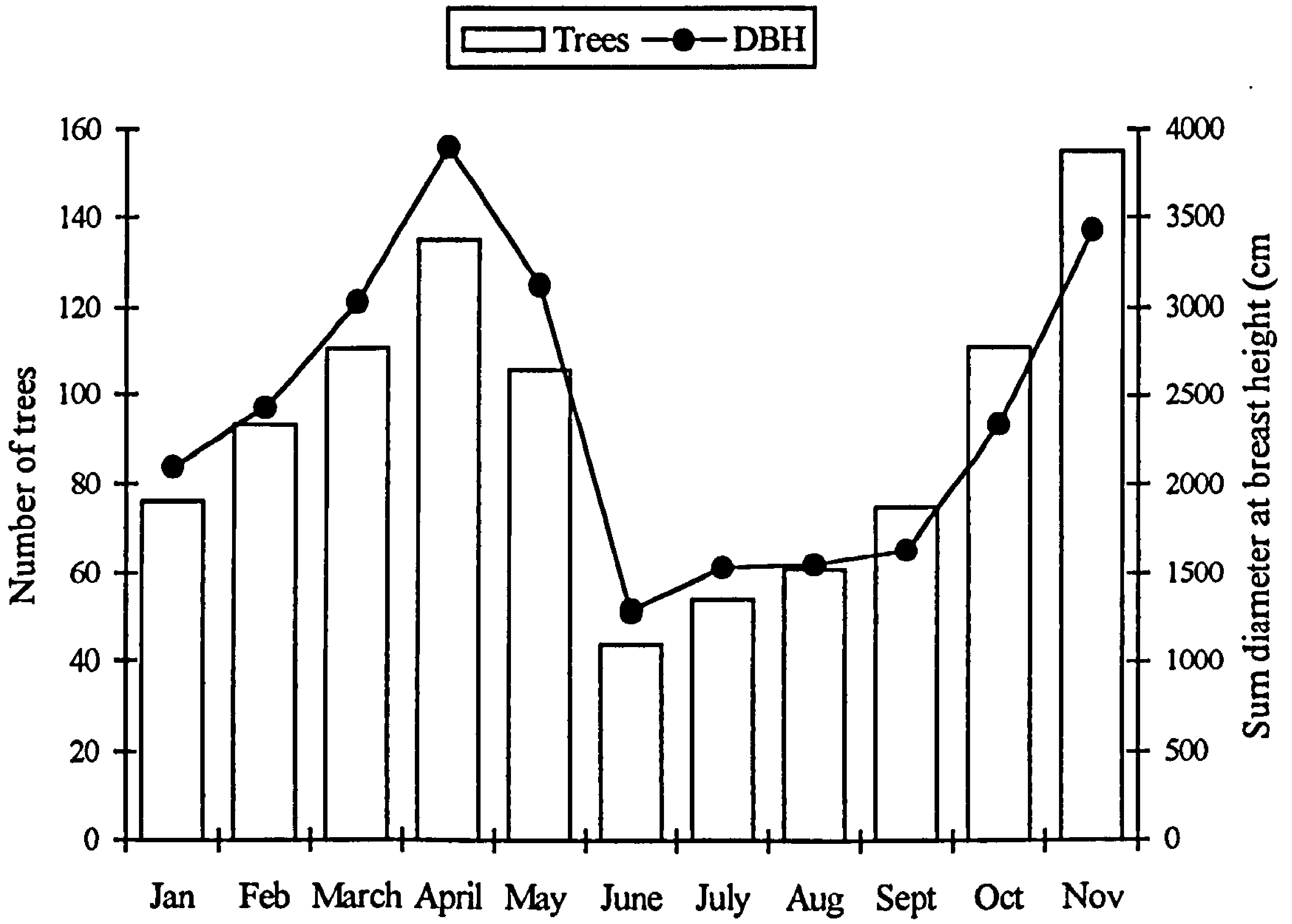


Figure 4: Number of Lilac-crowned Parrot food trees and species available over all monthly phenology transects (1996).

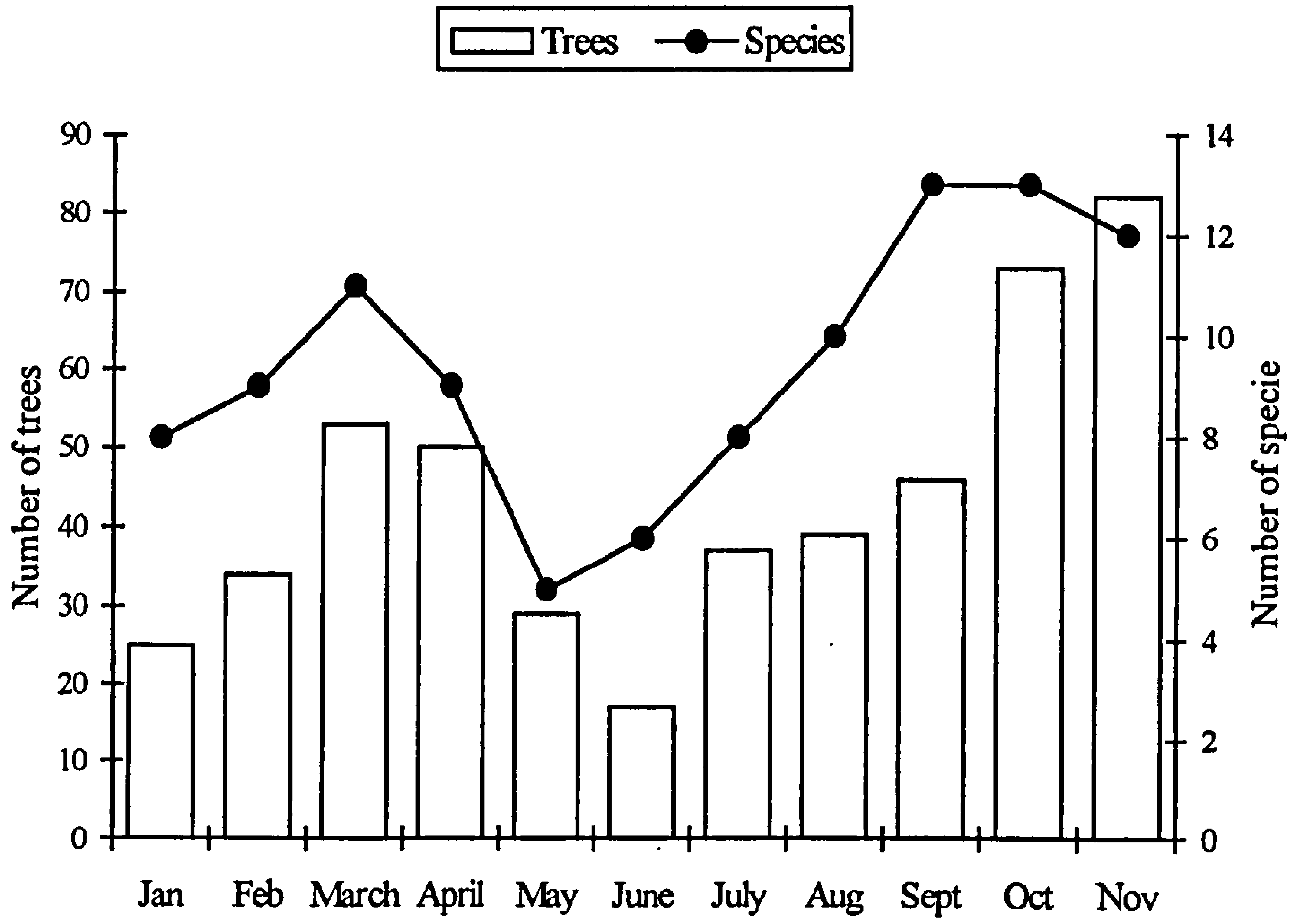


Figure 5: Number and sum of diameter at breast height (DBH) of Lilac-crowned Parrot food trees over all monthly phenology transects (1996).

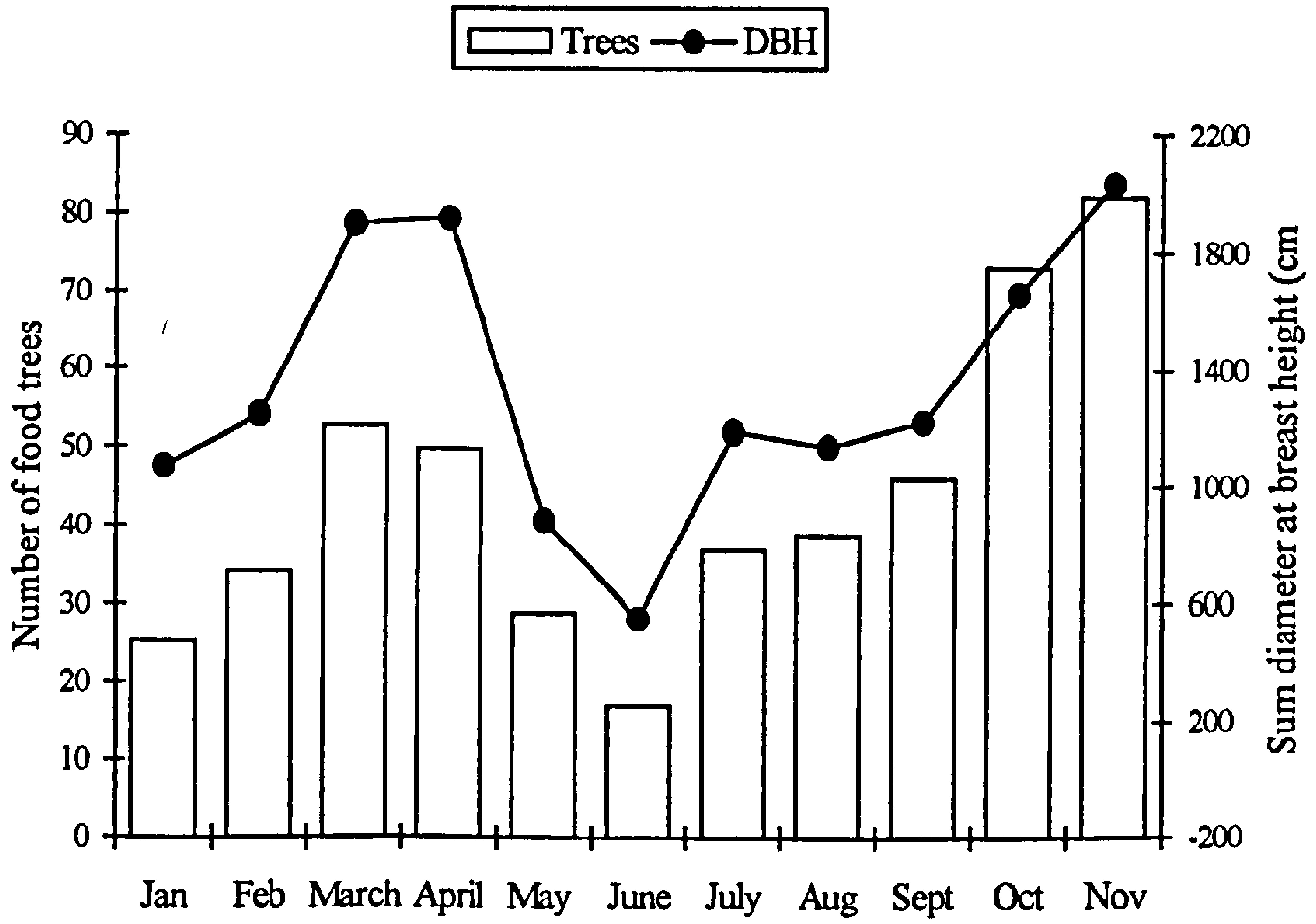


Figure 6: Mean number of fruiting trees of all species per transect by habitat (1996).

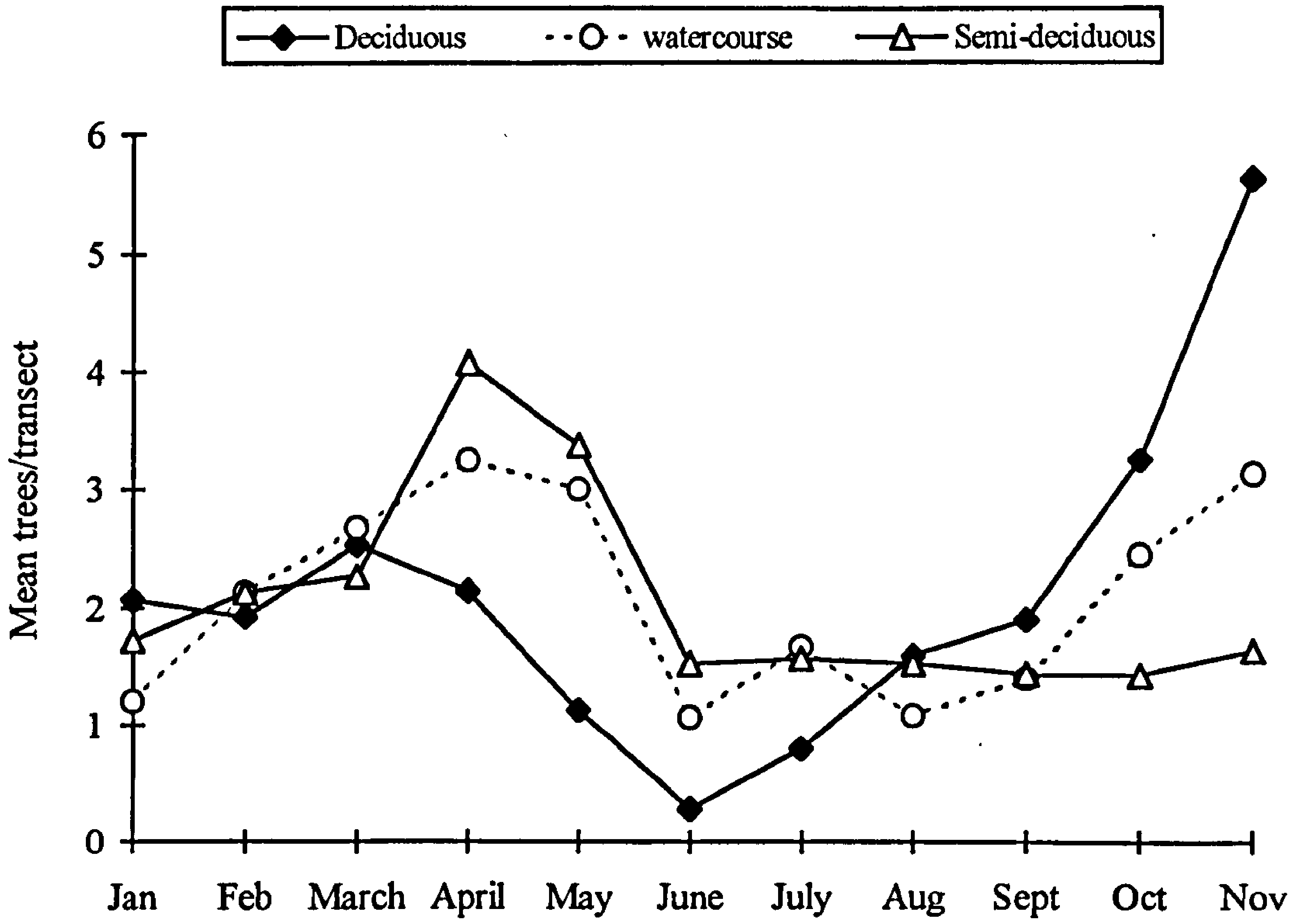


Figure 7: Sum of diameter at breast height (DBH) of fruiting trees of all species in monthly phenology transects by habitat type (1996).

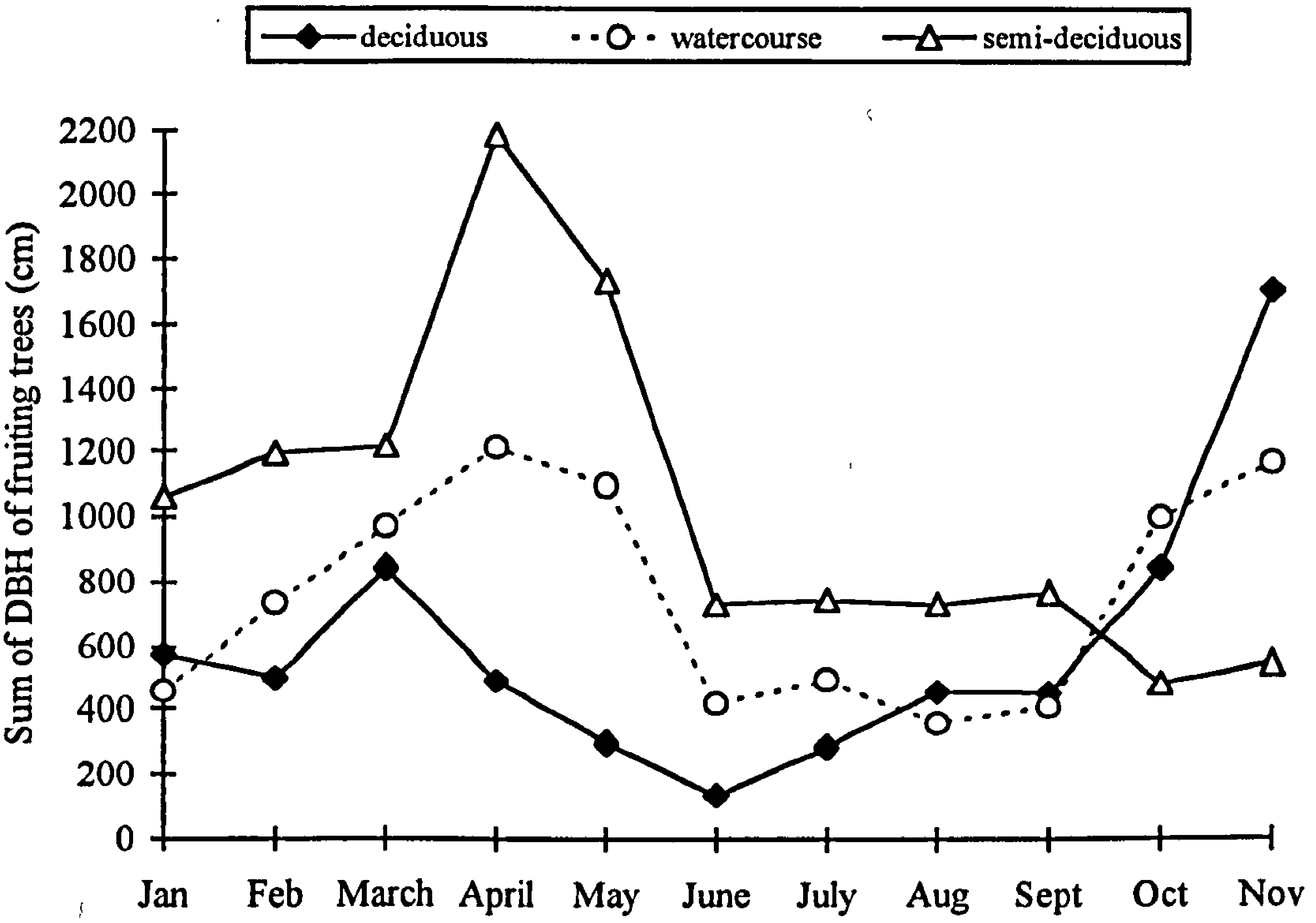


Figure 8: Mean number of food trees per phenology transect by habitat type (1996).

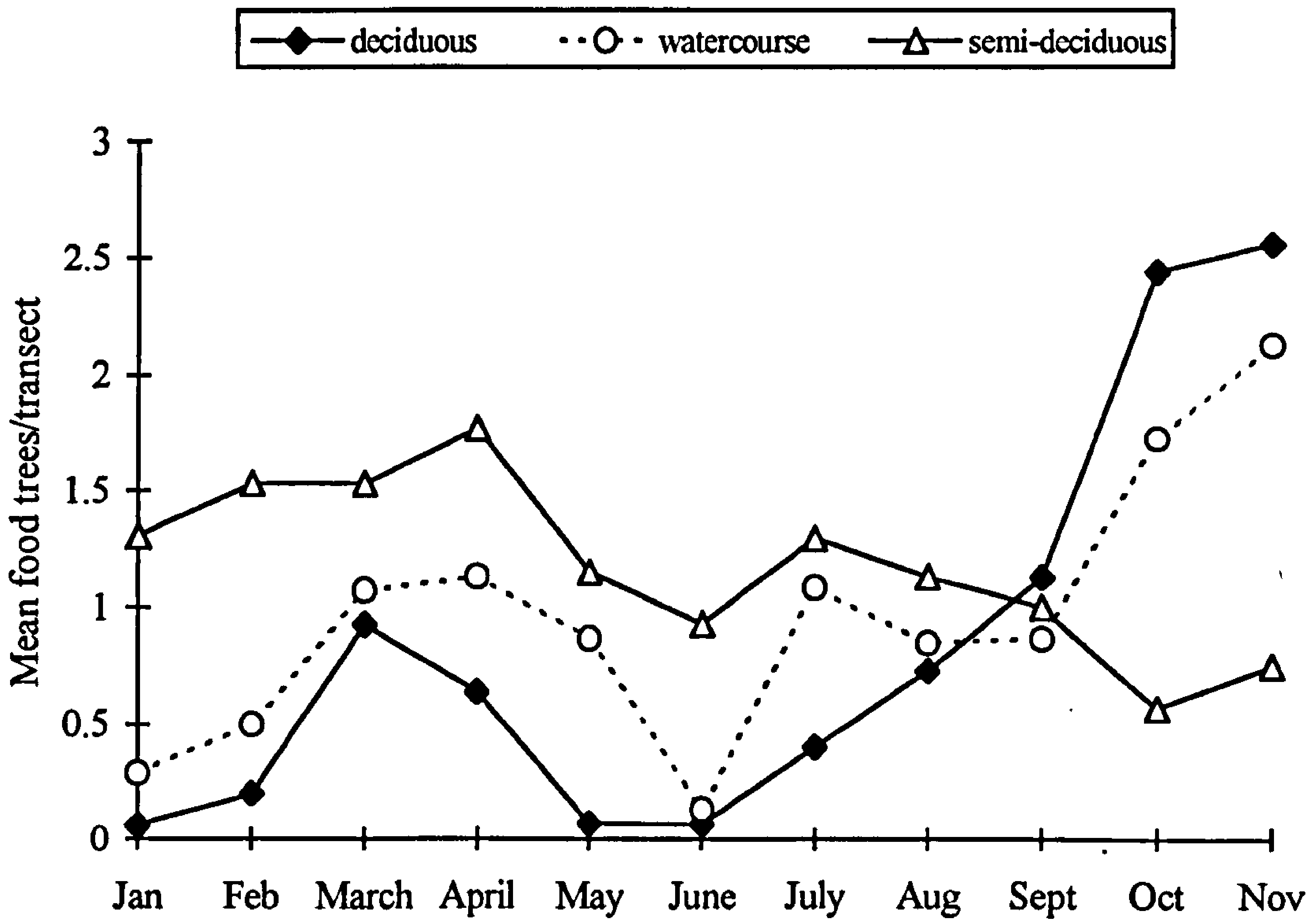


Figure 9: Sum of diameter at breast height (DBH) of Lilac-crowned Parrot food trees in monthly phenology transects by habitat type (1996).

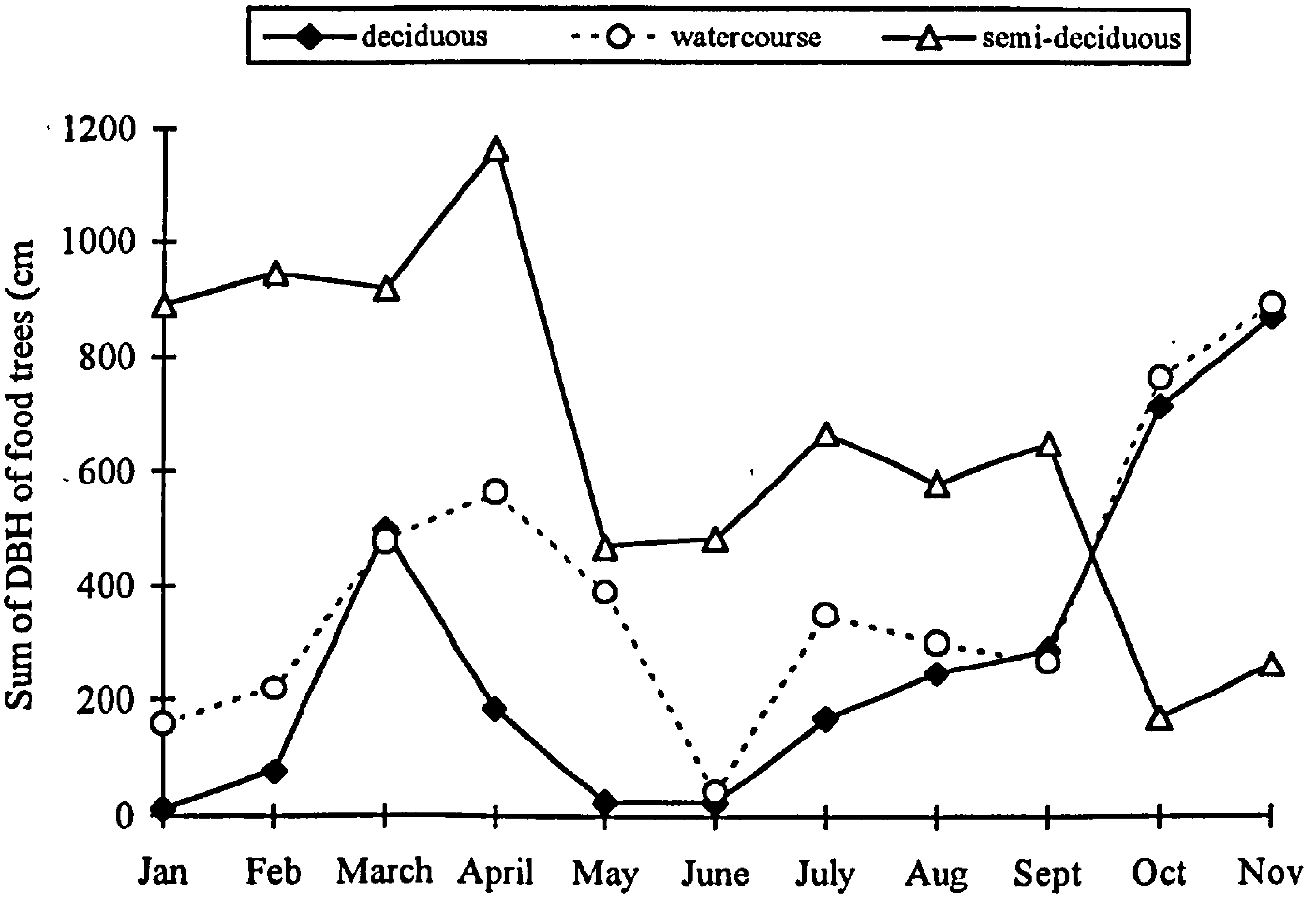
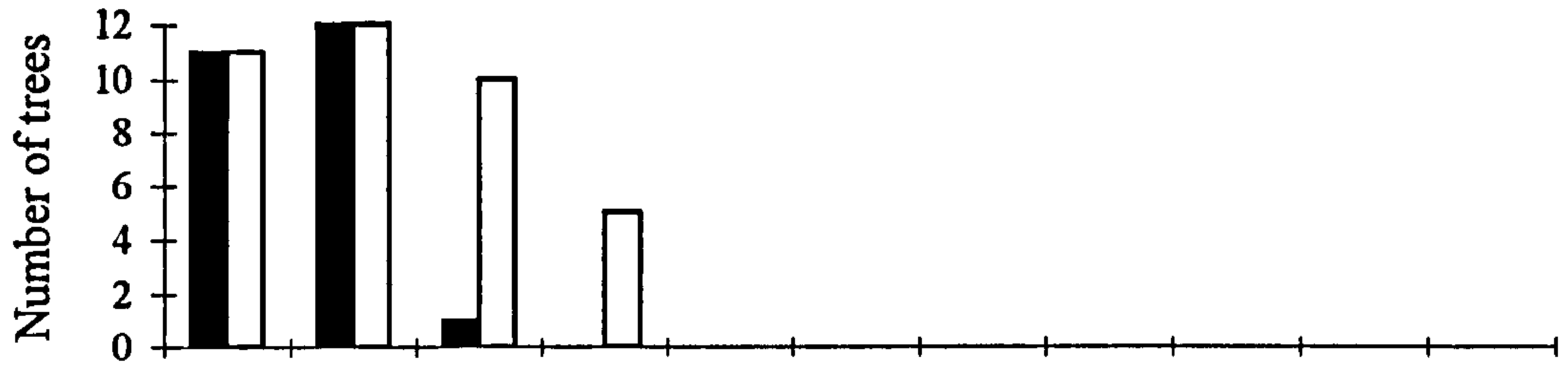
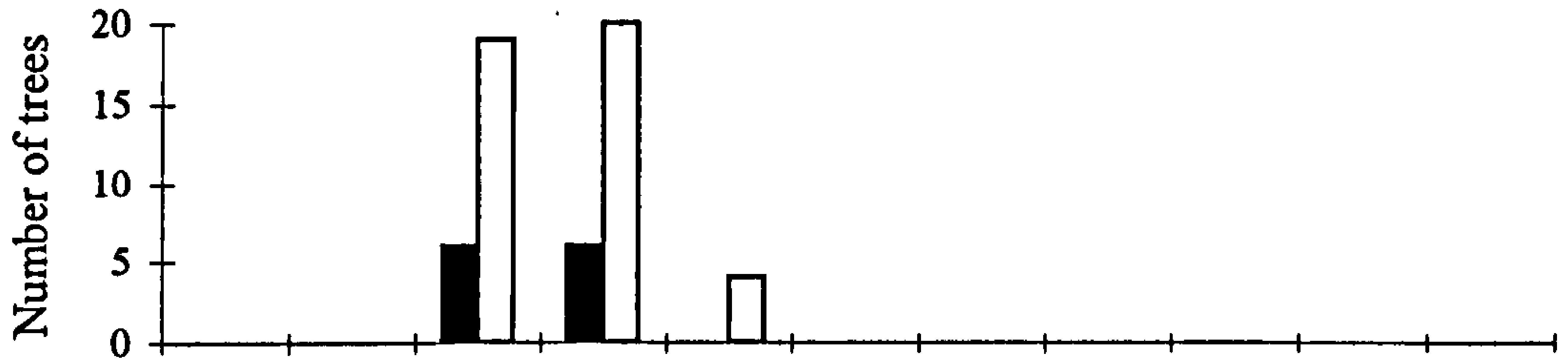


Figure 10: Availability of key food plant species during the dry season of 1996 (dark bars) and 1997 (light bars). Phenology transects were not continued after July 1997.

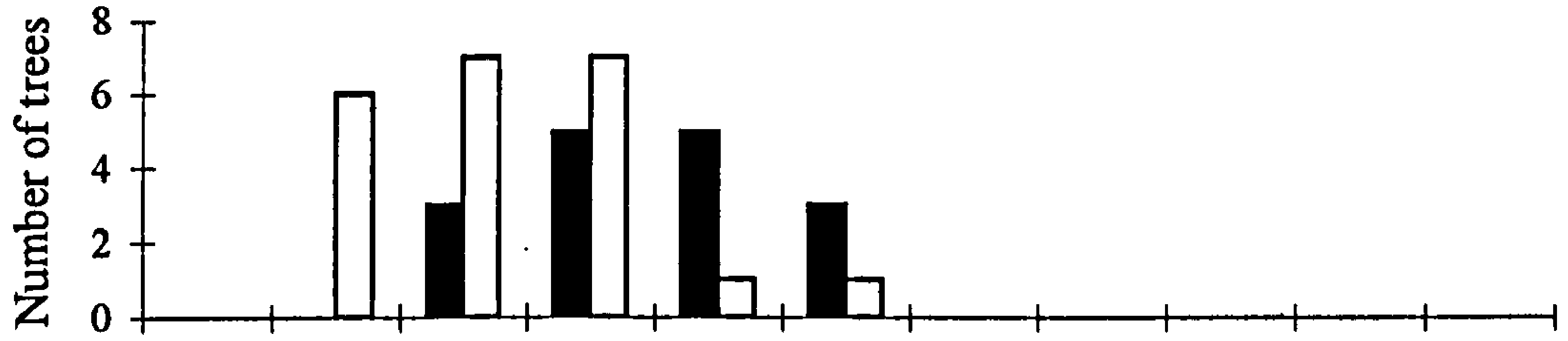
(a) *Brosimum alicastrum*



(b) *Comocladia engleriana*



(c) *Guarea glabra*



(d) *Astronium graveolens*

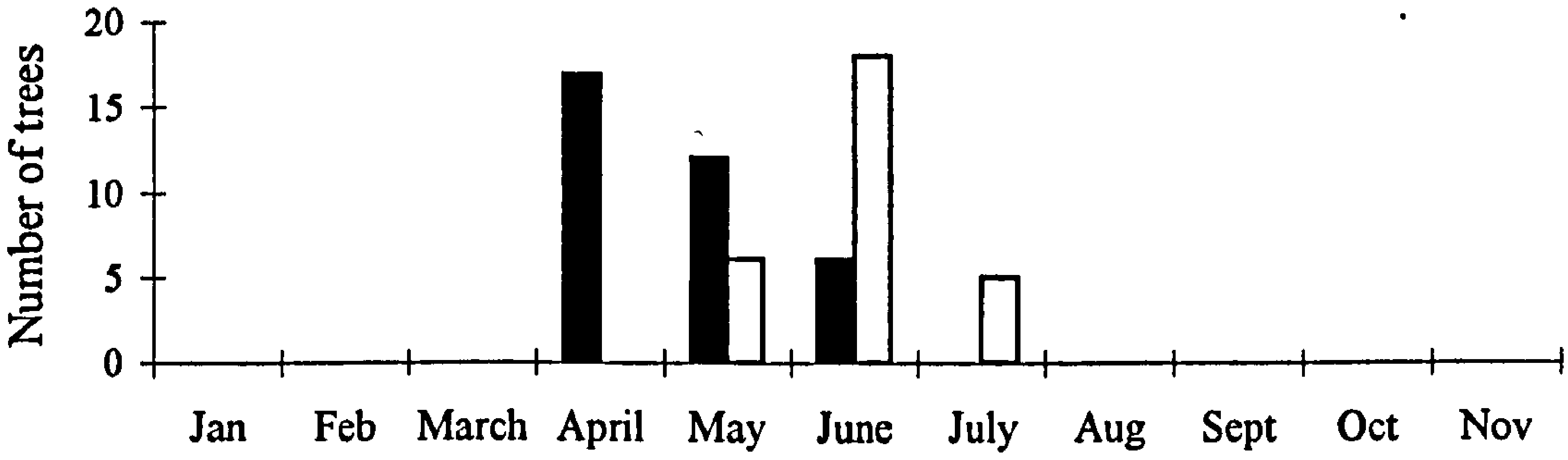
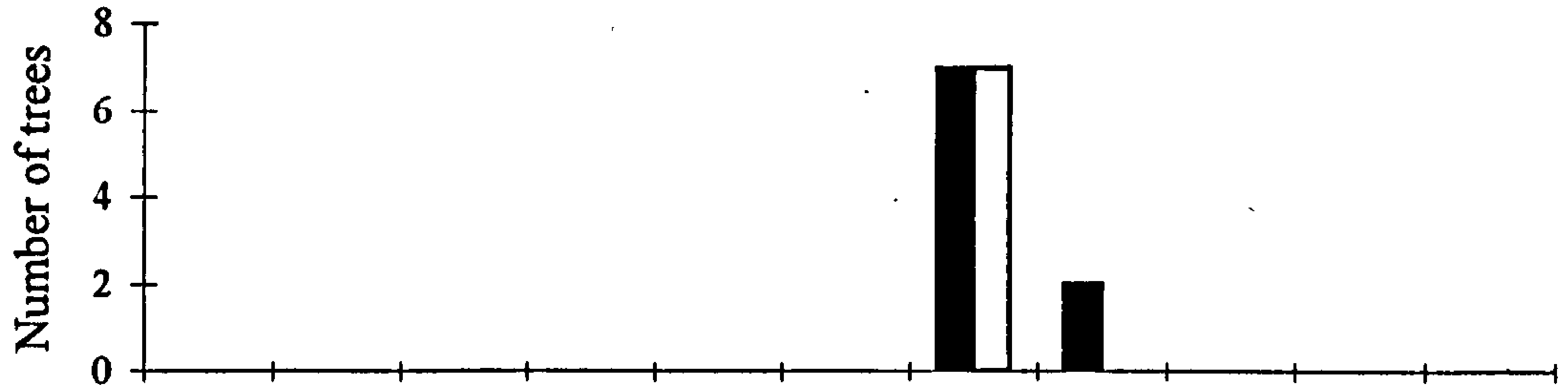
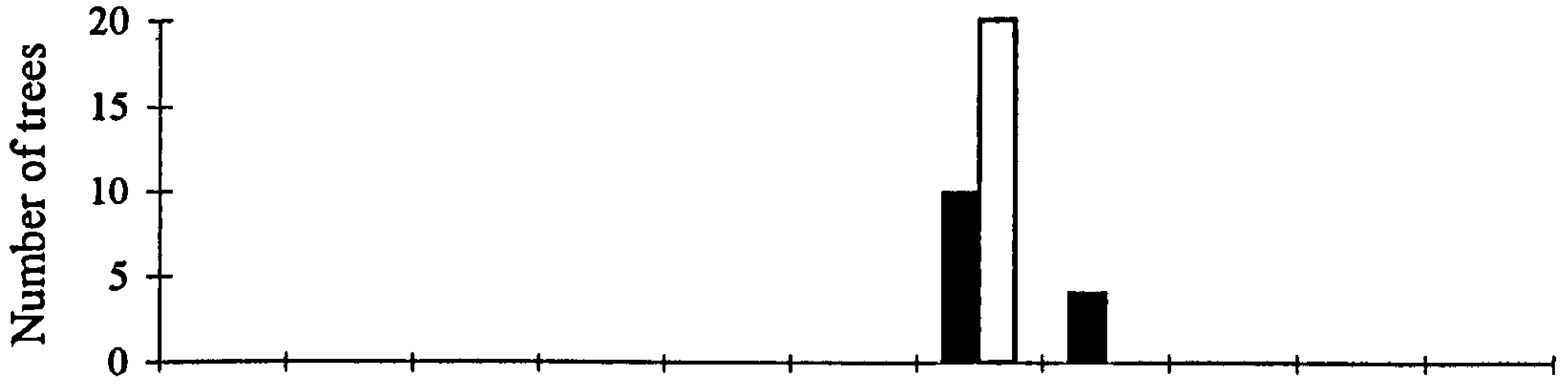


Figure 11: Availability of key food plant species during the rainy season of 1996 (dark bars) and 1997 (light bars). Phenology transects were not continued after July 1997.

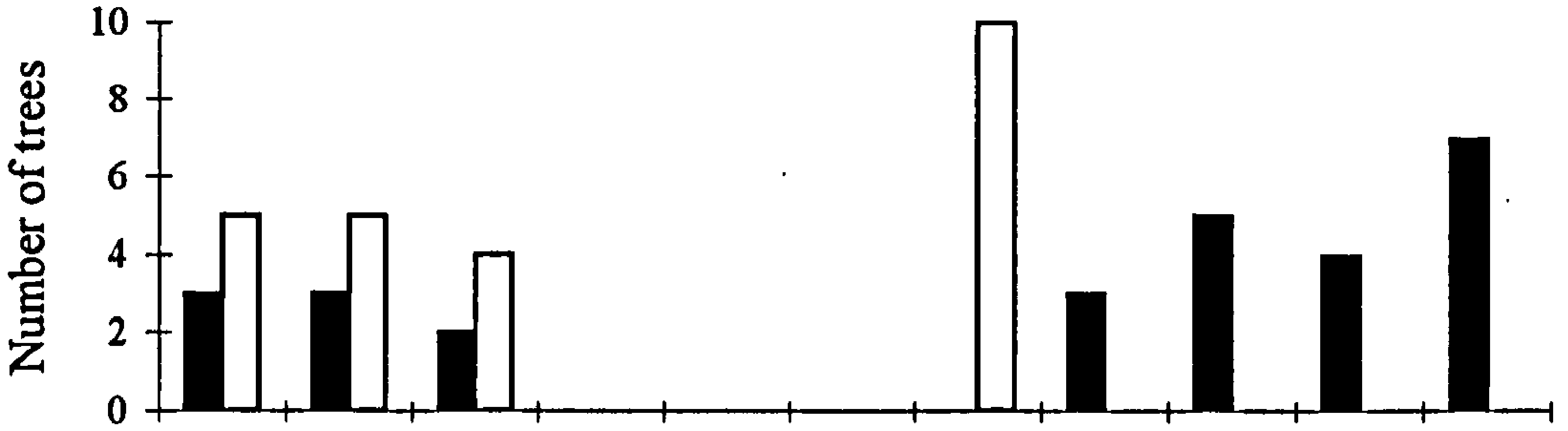
(a) *Sciadodendron excelsum*



(b) *Jatropha malacophyllum*



(c) *Celaenodendron mexicanum*



(d) *Ficus* species

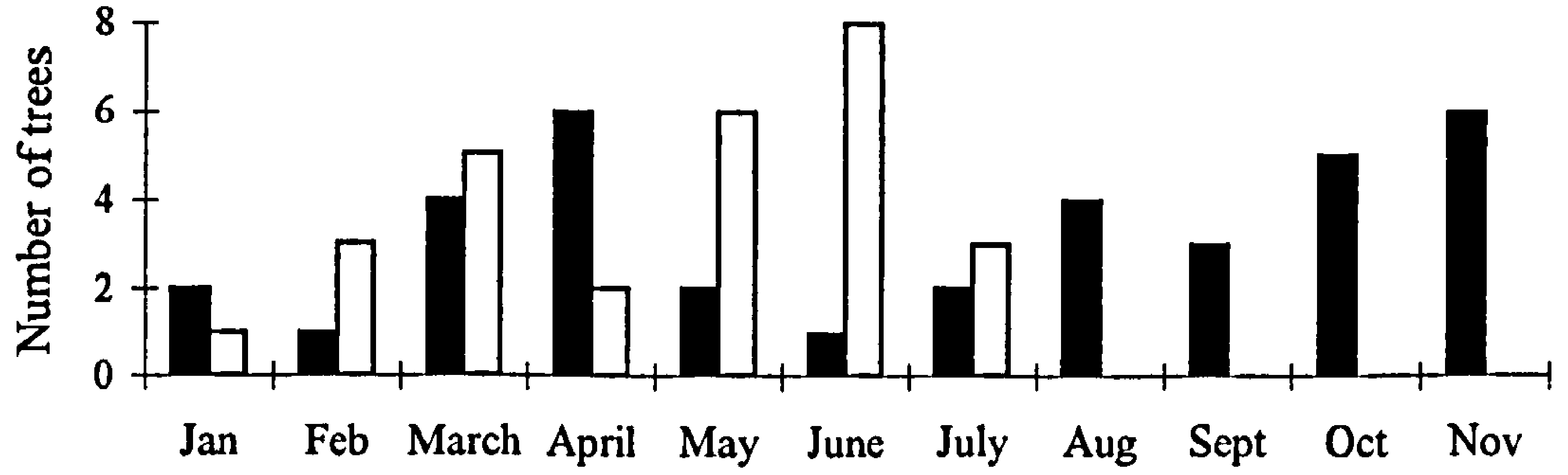


Table 5: Two-way ANOVA using the general linear model on number of trees of all species from phenology transects in three habitat types during the dry season and rainy season (1996).

Source	df	Seq SS	Adj SS	Adj MS	*F* value	Significance level
Season	1	8.0	8.0	8.0	0.03	$P = 0.862$
Habitat	2	89.0	158.1	79.0	0.30	$P = 0.741$
Season*Habitat	2	1345.0	1345.0	672.5	2.58	$P = 0.094$
Error	27	7035.9	7035.9	260.6		
Total	32	8477.9				

Table 6: Two-way ANOVA using the general linear model on the sum of diameter at breast height (DBH) of all species from phenology transects in three habitat types during the dry season and rainy season of 1996.

Source	df	Seq SS	Adj SS	Adj MS	*F* value	Significance level
Season	1	272061	272061	272061	1.78	$P = 0.193$
Habitat	2	1080430	868402	434201	2.84	$P = 0.076$
Season*Habitat	2	1295986	1295986	647993	4.24	$P = 0.025$
Error	27	4125763	4125763	152806		
Total	32	6774241				

Table 7: Two-way ANOVA using the general linear model on number of food trees from phenology transects in three habitat types during the dry season and rainy season of 1996.

Source	df	Seq SS	Adj SS	Adj MS	*F* value	Significance level
Season	1	390.79	390.79	390.79	5.48	*P* = 0.027
Habitat	2	80.79	40.34	20.17	0.28	*P* = 0.756
Season*Habitat	2	829.19	829.19	414.59	5.81	*P* = 0.008
Error	27	1926.20	1926.2	71.34		
Total	32	3226.97				

Table 8: Two-way ANOVA using the general linear model on the sum of diameter at breast height (DBH) of food trees from phenology transects in three habitat types during the dry season and rainy season of 1996.

Source	df	Seq SS	Adj SS	Adj MS	*F* value	Significance level
Season	1	30884	30884	30884	0.49	*P* = 0.491
Habitat	2	787335	654156	327078	5.17	*P* = 0.013
Season*Habitat	2	697164	697164	348582	5.51	*P* = 0.010
Error	27	1708012	1708012	63260		
Total	32	3223396				

Between year variation

More fruiting trees and species were recorded during the dry season of 1997 compared to the dry season of 1996 (Fig 12, Table 9). Analysis by two-way ANOVA demonstrated a significant difference between the years both for number of trees (Table 10), and sum of DBH of fruiting trees (Table 11). Habitats also differed significantly within the dry season both for number of trees (Table 10), and sum of DBH of fruiting trees (Table 11), with semi-deciduous forest demonstrating greater food resource abundance during the dry season than deciduous forest (Figs 8 & 9). Finally, significantly more species of food trees were available during the dry season of 1997 compared to 1996 (one-way ANOVA: $F_{1,10} = 7.34$, $P = 0.022$; Table 9). Hence, there was a greater abundance of food resources during the dry season of 1997 compared to 1996, with all habitat types demonstrating a similar increase in abundance.

Figure 12: Total number of food trees and sum of diameter at breast height (DBH) during the dry season in 1996 and 1997.

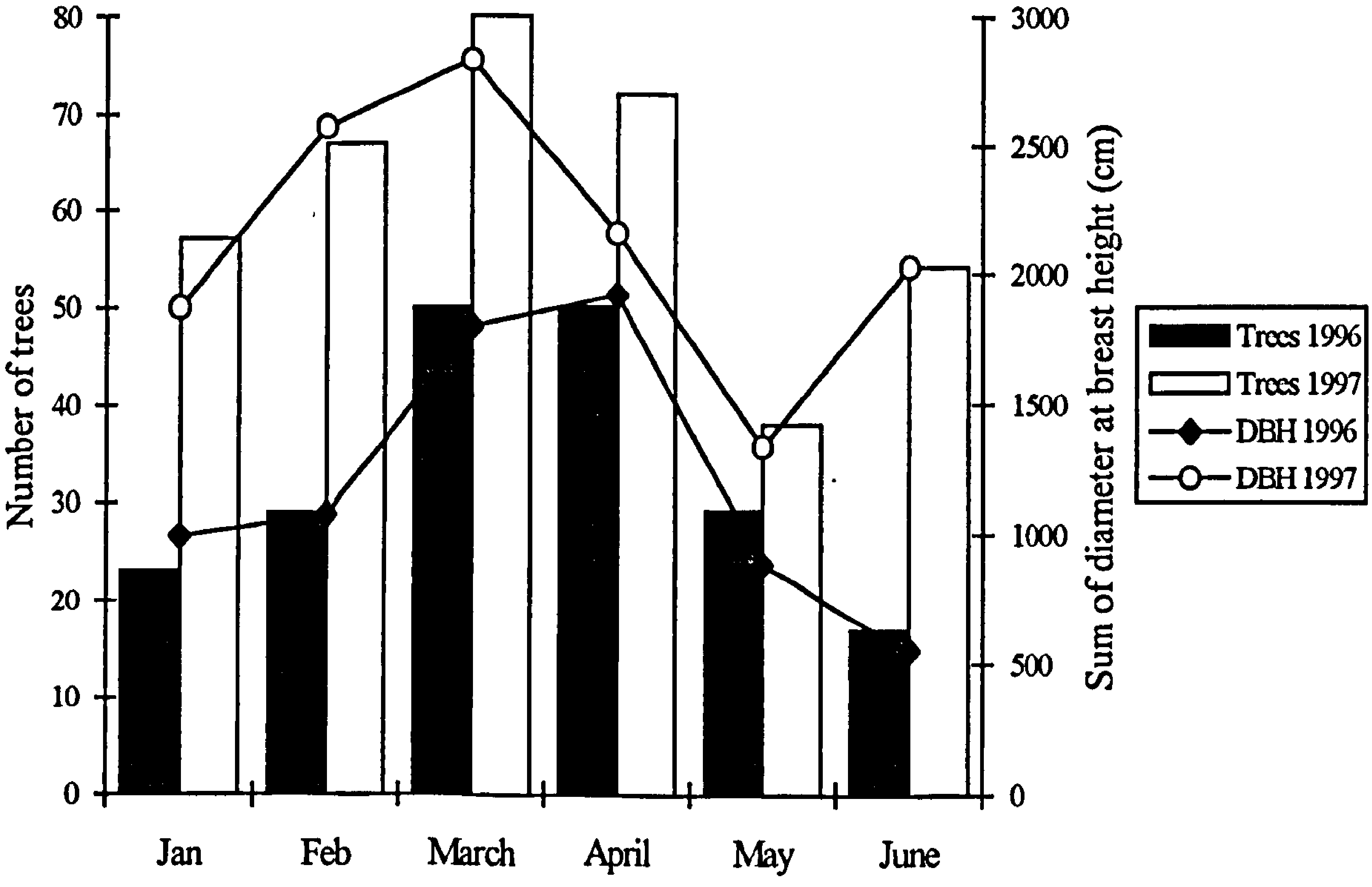


Table 9: Number of potential food species available over all phenology transects during the dry season months of January to June in 1996 and 1997. Mean number of species per month are presented with standard deviations.

Month	1996	1997
January	7	11
February	8	11
March	10	11
April	9	12
May	5	10
June	6	7
Species/month	7.5 ± 1.87	10.33 ± 1.75

Table 10: Two-way ANOVA on the number of food trees from phenology transects in three habitat types during the dry season of 1996 and 1997.

Source	df	SS	MS	*F* value	Significance level
Year	1	802.78	802.78	15.74	$P < 0.0001$
Habitat	2	773.39	386.69	7.58	$P = 0.002$
Year*Habitat	2	39.06	19.53	0.38	$P = 0.685$
Error	30	1530.00	51.00		
Total	35	3145.22			

Table 11: Two-way ANOVA on the sum of diameter at breast height of food trees from phenology transects in three habitat types during the dry season of 1996 and 1997.

Source	df	SS	MS	*F* value	Significance level
Year	1	862505	862505	13.14	$P = 0.001$
Habitat	2	3292468	1646234	25.09	$P < 0.0001$
Year*Habitat	2	50399	25199	0.38	$P = 0.684$
Error	30	1968529	65618		
Total	35	6173902			

3.4.2. SEASONALITY IN PARROT DIETS

Lilac-crowned Parrots were observed to consume 30 food items throughout the year, with an additional 3 food species identified from crop samples of nestling parrots (Table 12). The overall composition of parrot diets throughout the year was predominantly unripe seeds (Fig 13), making Lilac-crowned Parrots primarily pre-dispersal seed predators.

Parrot diet also varied considerably between the dry season and the rainy season (Figs 14 & 15), with little overlap or similarity in food items between the seasons (Table 17). The main food items during the dry season were seeds of *Astronium graveolens* (38.1% of observations), *Brosimum alicastrum* (18.8%), *Celaenodendron mexicanum* (10.3%), *Guarea glabra* (8.5%), and *Comocladia engleriana* (7.6%). However, during the rainy season, the diet comprised mainly seeds of *Celaenodendron mexicanum* and fruits of *Sciadodendron excelsum* (16.7% of observations each), along with seeds of *Jatropha standleyi* (14.4%), *Jatropha malacophyllum* (14%), *Caesalpinia pulcherrima* (13%), and *Esenbeckia nesiotica* (9.7%).

Figure 13: Composition of food types observed in the diet of Lilac-crowned Parrots throughout the year.

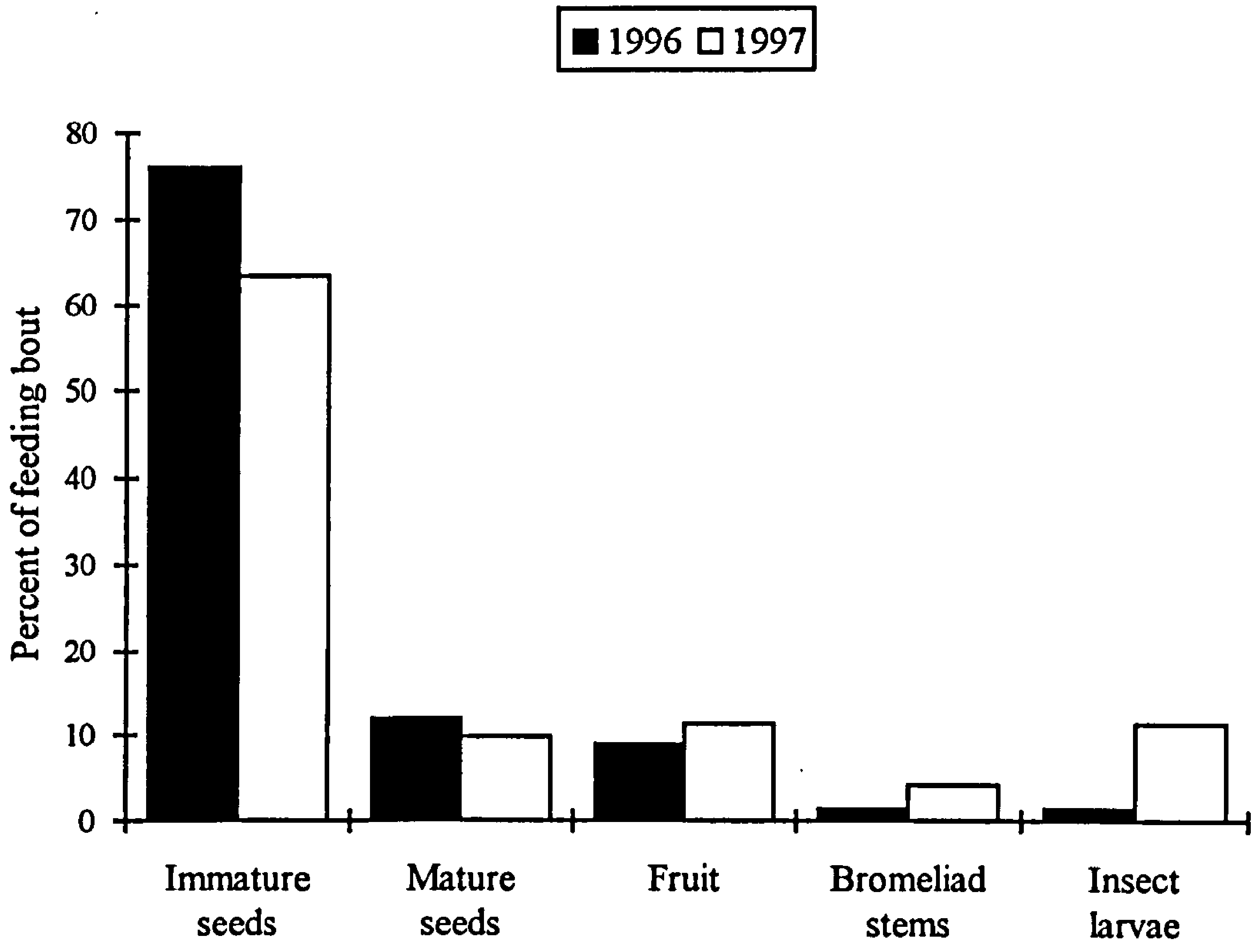


Table 12: Summary of diet observations for the Lilac-crowned Parrot at the Chamela-Cuixmala Biosphere Reserve between 1996 - 1997.

Species	Habitat[1]	Part eaten	No. of Parrots	Feeding bouts	Months
ANACARDIACEAE					
Astronium graveolens	S, W	unrp seed	207	24	May-June
Comocladia engleriana	D	unrp seed	41	3	March-April
*Spondius purpurea**	D	unrp seed	NA	NA	April-May
APOCYNACEAE					
Plumeria rubra	D	unrp seed	12	6	Feb, Sept, Oct
ARALIACEAE					
Sciadodendron excelsum	W	ripe fruit	72	7	July
BOMBACACEAE					
Ceiba aesculifolia	W	rp seed	2	1	March
BROMELIACEAE					
Bromelia spp.	D, S, W	phylum	8	4	July-Sept
BURSERACEAE					
Bursera spp.	D	ripe seed	30	1	Nov
CAPPARACEAE					
Crataeva tapia	W, S	unrp seed	2	1	April
EUPHORBIACEAE					
Celaenodendron mexicanum	W, S	unrp seed	122	16	Feb, March, July
Jatropha malacophylla	D	unrp seed	60	1	July
Jatropha standleyi	D	unrp seed	62	4	July
Sebastiana spp.*		seed	NA	NA	April-May
HOMOPTERA					
Leaf gall larvae of *A. graveolens*	S,W	insect larvae	18	9	April-July
LEGUMINOSAE					
Acacia farnesiana	W	unrp seed	2	1	March
Bauhinia ungulata	D	unrp seed	37	8	Feb-March
Caesalpinia eriostachys	D, W	unrp seed	1	1	Feb
Caesalpinia pulcherrima	D	unrp seed	56	12	Nov
Erythrina lanata	D	unrp seed	2	1	May
Lysiloma microphyllum	D	unrp seed	8	1	March

Pithecellobium dulce	S	sd + pulp	2	1	April
Pithecellobium lanceolatum	D	unrp seed	8	2	Sept-Oct
Unid. Vine 1	D	unrp seed	8	1	Oct
Unident legume spp. 1	W	unrp seed	2	1	July
Unidentified legume spp. 2	W	unrp seed	3	1	March
MELIACEAE					
Guarea glabra	S	ripe seed	46	2	May-June
MORACEAE					
Brosimum alicastrum	S	sd + pulp	102	14	Jan-April
Ficus cotinifolia	D, W	fruit	6	3	Jan-March
Ficus insipida	S	fruit	10	1	May
NYCTAGINACEAE					
*Guapira macrocarpa**	D	ripe fruit	NA	NA	April-May
RUTACEAE					
Esenbeckia nesiotica	D	unrp seed	41	7	Sept, Oct
Unident spp. 3	D	unrp seed	8	1	Jan
SAPOTACEAE					
Sideroxylon capiri	W	unrp seed	10	1	June

* Additional items in diet identified from crop samples

[1] D = deciduous forest, S = semi-deciduous forest, W = watercourse

Figure 14: Percent of observations of Lilac-crowned Parrots feeding on different food items during the dry season (1995 -1997).

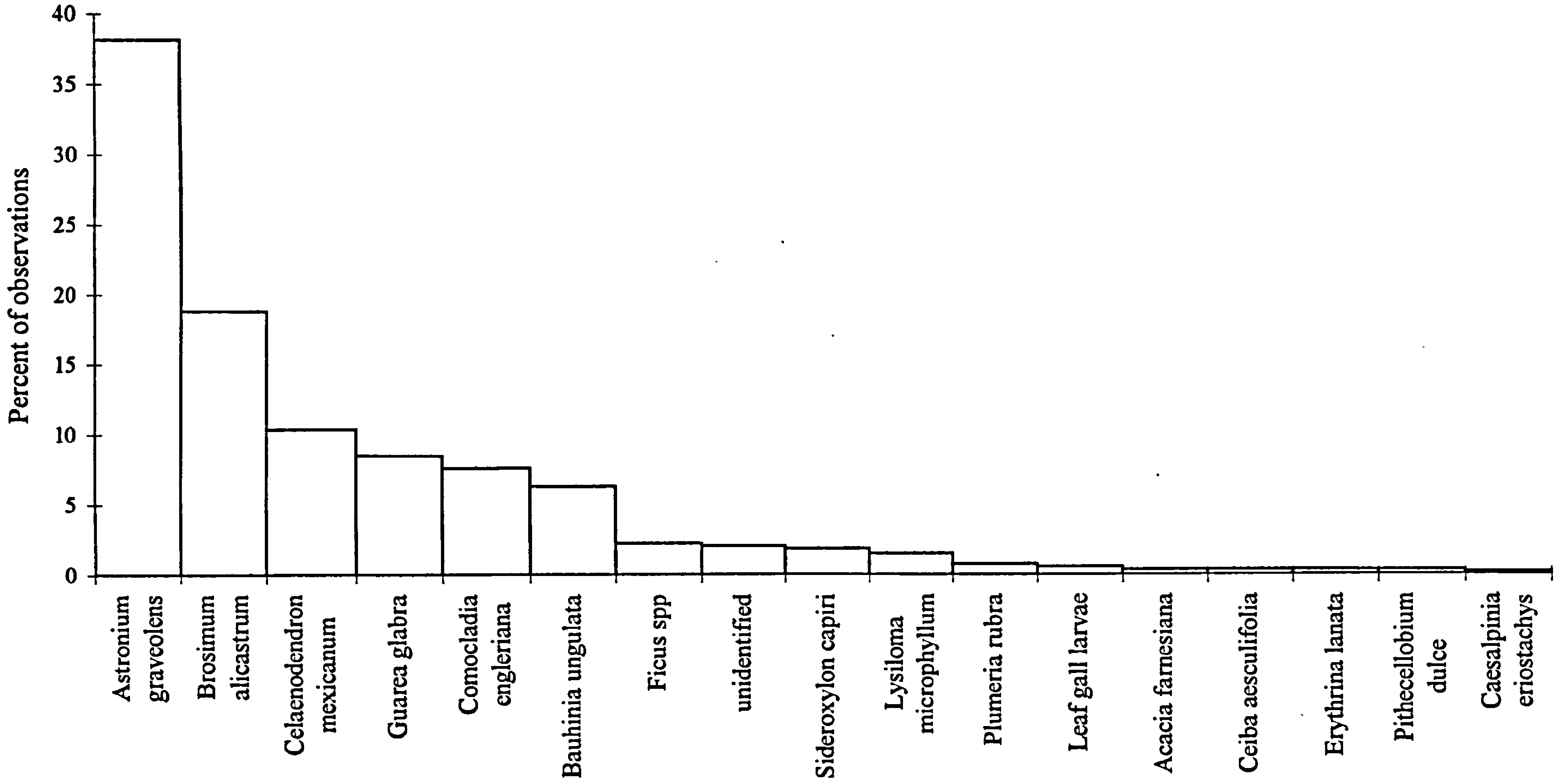
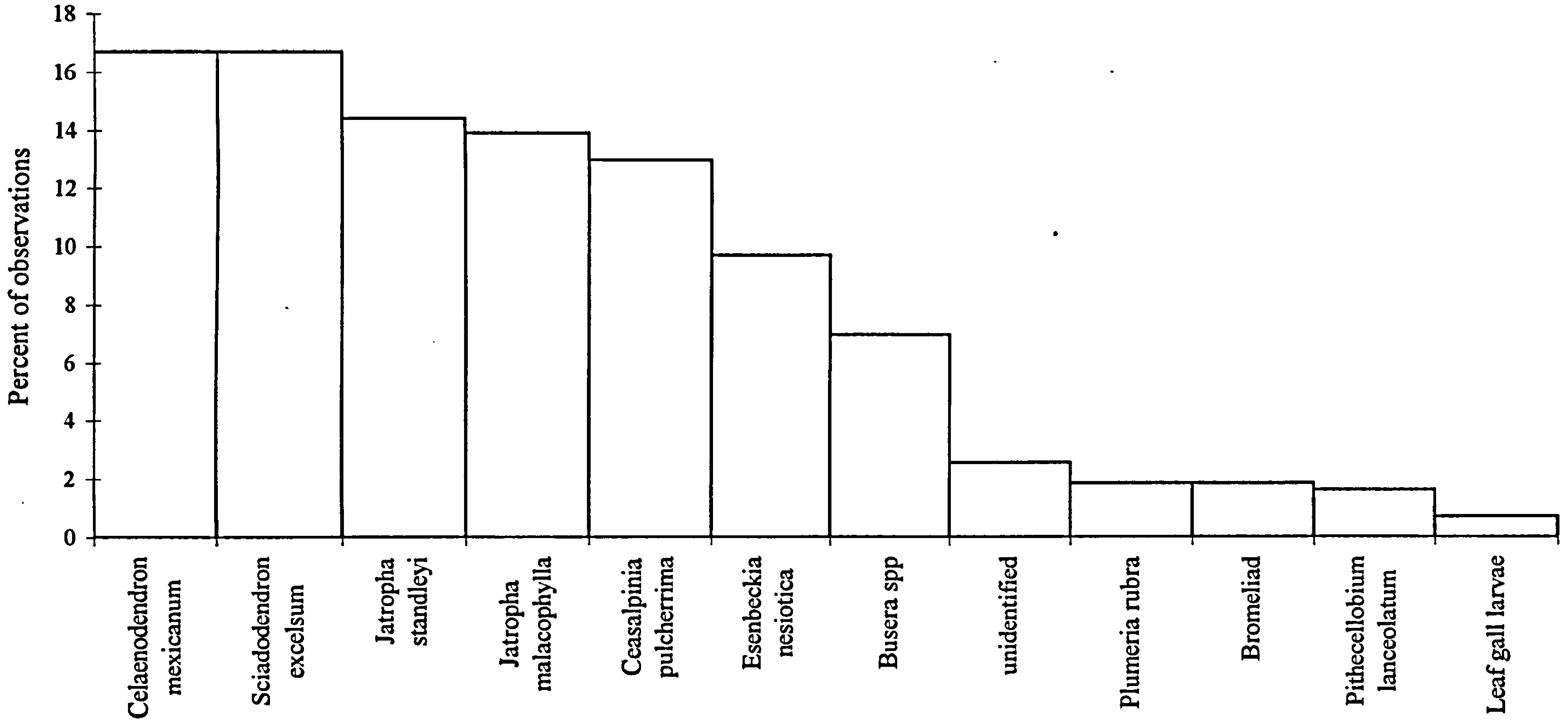


Figure 15: Percent of observations of Lilac-crowned Parrots feeding on different food items during the rainy season (1995 - 1997).



3.4.3. ANNUAL VARIATION IN NESTLING DIET

Dietary composition

A total of 14 food plant species were consumed by nestlings in 1996 (Table 15), compared with 29 food plant species in 1997 (Table 16), with a total of 32 different species recorded in nestling diets over the two years. As for observations of parrot diets throughout the year, composition of nestling diet was predominantly immature seeds, with some fruit, and plant material (Fig 16). The principal seed items in nestling diets during 1996 were *Astronium graveolens*, *Comocladia engleriana*, *Guarea glabra*, and *Crataeva tapia*, while in 1997 the principal seed items in the diet were *Comocladia engleriana*, *Sebastiana* spp., *Carica papaya*, *Guarea glabra*, and two unidentified seed species (Figs 17 - 20). The main fruit items consumed by parrots were *Ficus* species and *Guapira macrocarpa*. In 1997, parrots also consumed the fruit pulp of *Carica papaya*, and *Pithecellobium dulce*, which are two cultivated species.

Small arthropods occurred very infrequently in the diet, and it is likely that these were ingested incidentally with some fruit or seed food items. Small pieces of wood also occurred in almost all crop samples, and indications are that these were intentionally ingested by parrots. The wood items resembled pieces of small twigs rather than wood from the inside walls of the nest cavity. In addition, nesting pairs were occasionally observed biting off small pieces from the end twigs of branches prior to entering the nest cavity to feed the young. The role of wood pieces in the diet is unclear, however, they may help to remove the remains of old food items from the crop, as skins of digested fruits were frequently found wrapped around pieces of wood in the crop samples. The consumption of pieces of wood may also provide additional chemical or nutrient value in the diet, however, this needs to be determined by chemical analysis.

Figure 16: Composition of food types in the diet of Lilac-crowned Parrot nestlings as determined from crop samples.

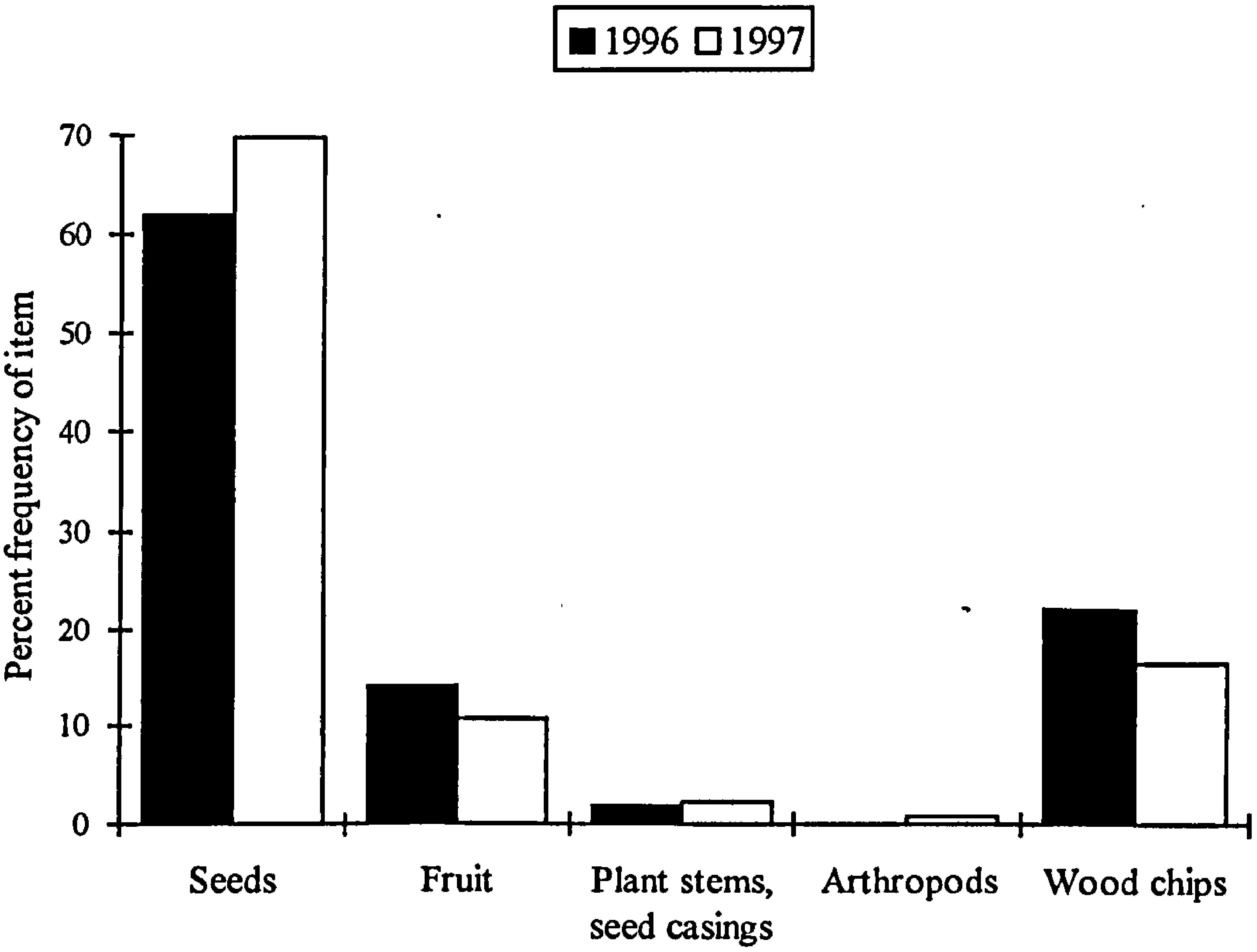


Figure 17: Frequency of food items in the diet of 12 Lilac-crowned Parrot nestlings during 13 April - 14 May 1996.

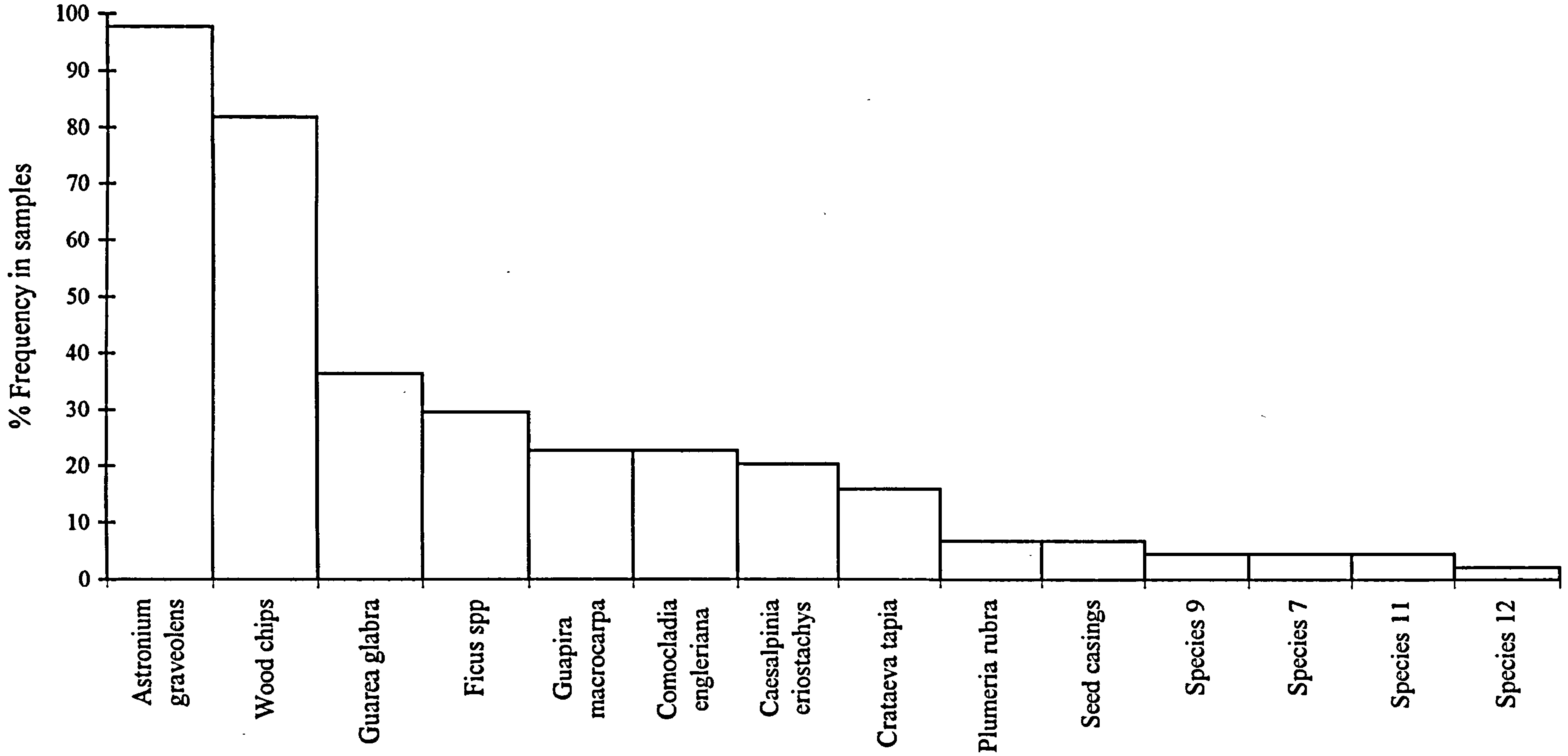


Figure 18: Frequency of food items in the diet of 9 Lilac-crowned Parrot nestlings during 30 March - 21 May 1997.

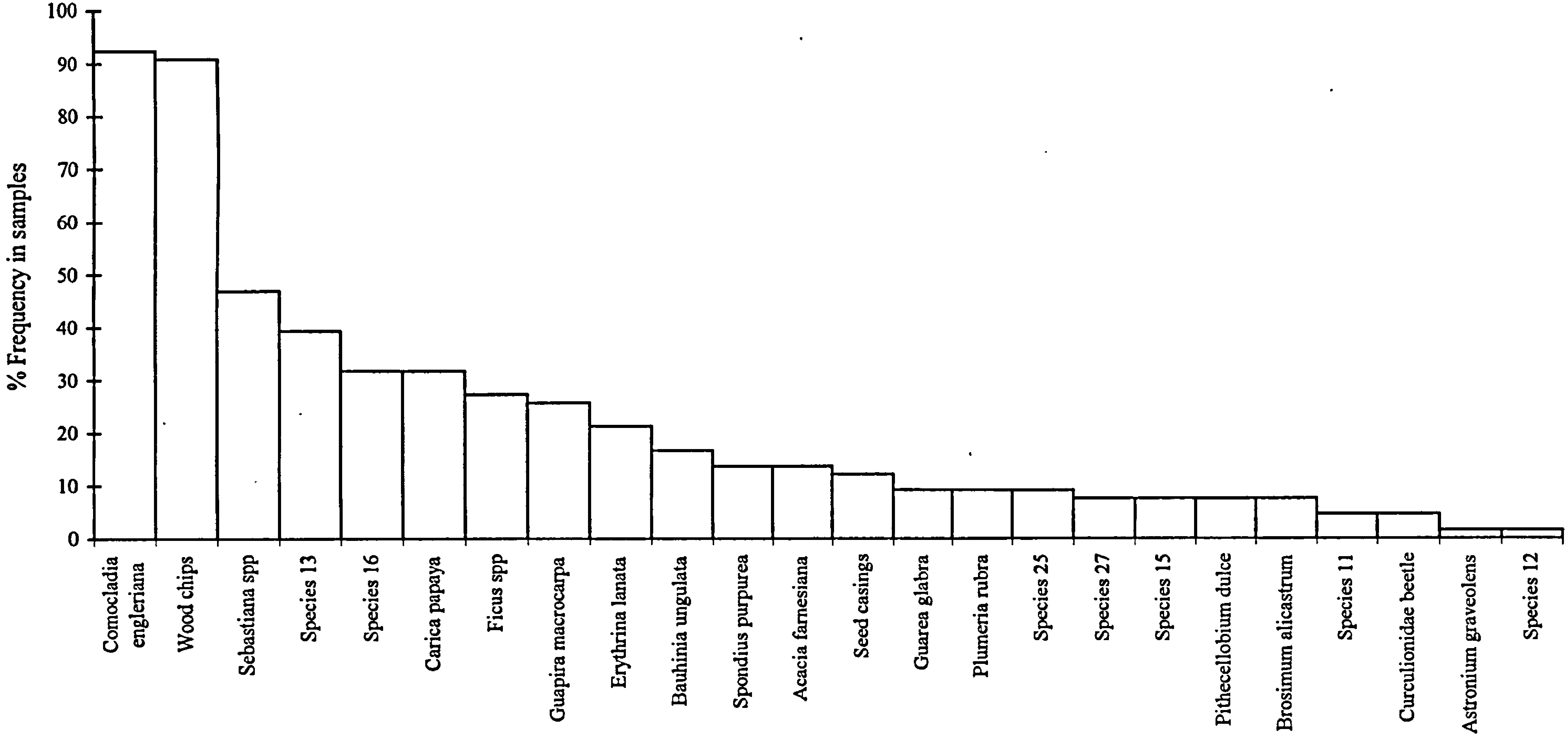


Figure 19: Biomass by proportional weight of food items per crop sample of 12 Lilac-crowned Parrot nestlings during 13 April - 14 May 1996.

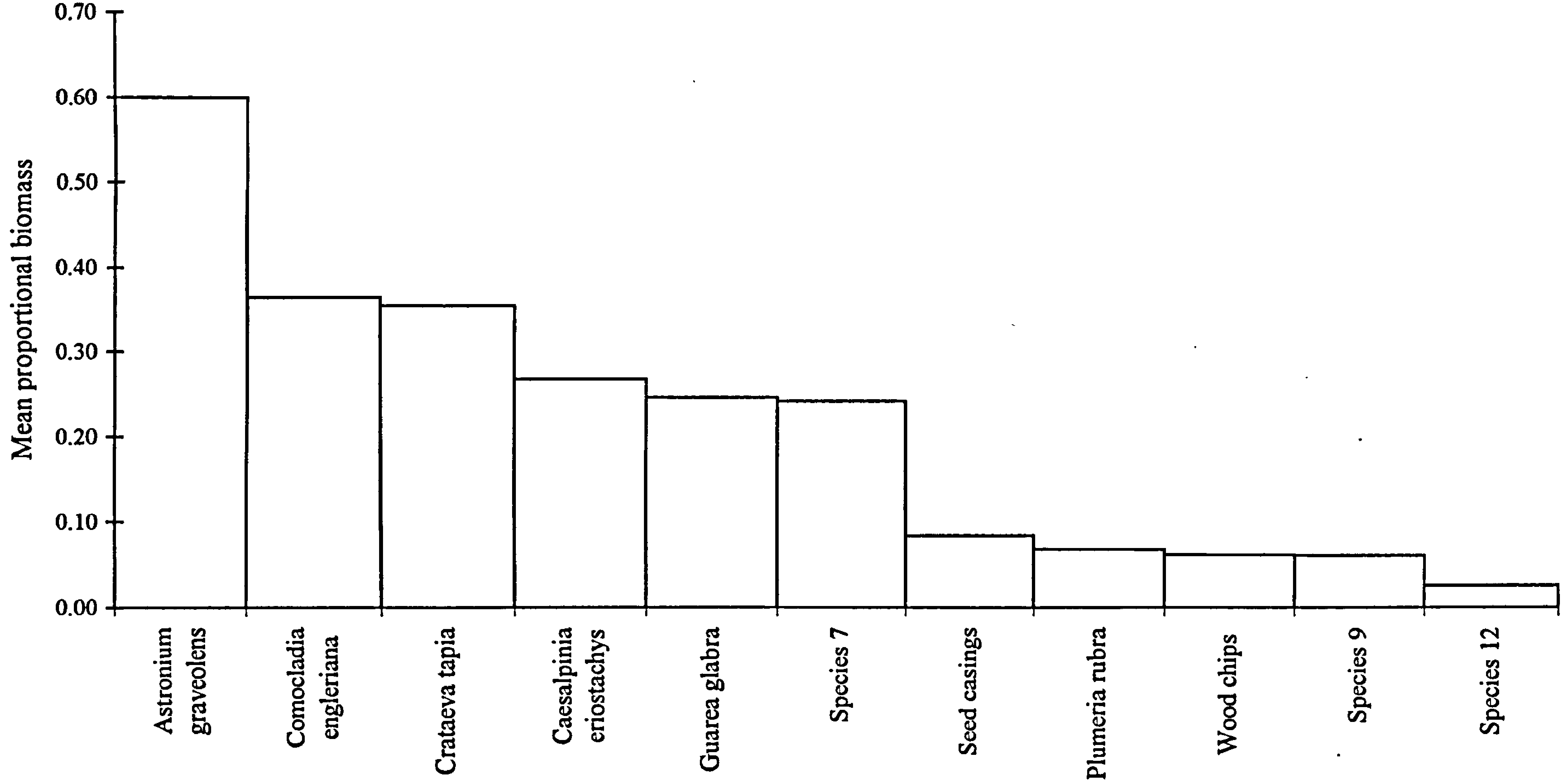
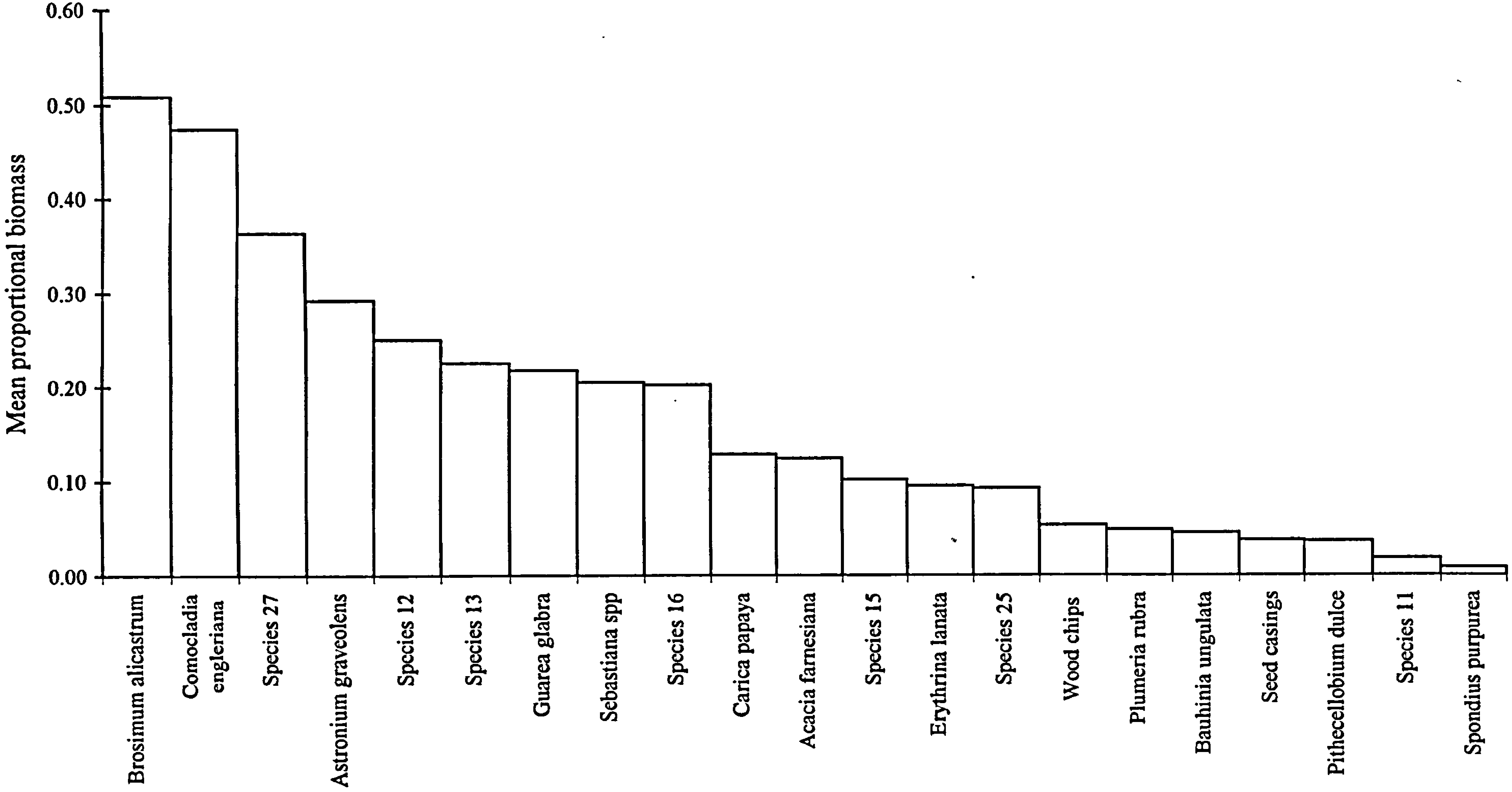


Figure 20: Biomass by proportional weight of food items per crop sample of 9 Lilac-crowned Parrot nestlings during 30 March - 21 May 1997.



Dietary variety

No significant differences were found between crop samples of sibling nestlings for each sample instance. Therefore, crop samples of siblings taken at the same time were pooled to provide a sample for each nest day, representing items fed to nestlings by parent birds per feeding instance at each nest. Analysis by one-way ANOVA also found no significant difference in dietary variety between nests in the same year, indicating that parent birds did not vary individually in diet. However, variety of items in nestling diets differed significantly between years (Table 14), with nestling diets being more varied in 1997 compared to 1996 (Table 13).

Table 13: Mean number of different items in crop samples of Lilac-crowned Parrot nestlings in 1996 and 1997.

Year	Number of samples	Mean number of items	Variance
1996	24	3.89	1.766
1997	35	5.97	2.852

Table 14: One way ANOVA on the number of different items in crop samples of Lilac-crowned Parrot nestlings between 1996 and 1997.

Source of Variation	df	SS	MS	*F* value	Significance level
Year	1	62.57	62.57	25.92	$P < 0.0001$
Error	57	137.6	2.414		
Total	58	200.17			

3.4.4. NICHE BREADTH AND SIMILARITY

Nestling diets between years

There was a low degree of similarity and overlap in nestling diets between the two years (Table 17). However, Levins' standardised niche breadth for nestling diets varied little between the years, with B = 0.406 in 1996, and B = 0.386 in 1997. Hence, although Lilac-crowned Parrots consumed different food items in the two years, there was still the tendency to concentrate on a few specific resources. The number of frequently used resources at a 5% cut-off level was the same in both years, with 7 most frequently used resources by occurrence, and 4 most frequently used resources by biomass in the diet (Tables 15 & 16). However, the actual food items were different with seeds of *Astronium graveolens* being the most frequently used resource in 1996 (Table 15), while seeds of *Comocladia engleriana* were predominant in the diet in 1997 (Table 16). This is due to the fact that *Astronium graveolens* fruited later in June in 1997, and was not available during the nestling period of March to April (Fig 10).

Seasonal diets

As noted in Table 18, Levins' niche breadth was narrower in the dry season being below 0.3 compared to the rainy season, and declined most sharply in the late dry season (April - June). Figure 21 illustrates that changes in the food niche breadth of Lilac-crowned Parrots during each period of the year, were strongly correlated with the number of potential food species fruiting over each three month period, as determined by phenology transects (Pearson's r = 0.963, df = 2, $P < 0.05$). This suggests that food niche breadth of Lilac-crowned Parrots tracks resource abundance, with niche breadth being narrowest when least resources are available. Hurlbert's niche breadth which weights resource use by an estimate of abundance, gave a broader niche value for the dry season in comparison with the rainy season (Table 18). As fewer resources are available in the dry season, parrots may be exploiting those resources which are most abundant. A greater variety of resources are available during the rainy season, hence although parrot diet may broaden in comparison to the dry season, this may be partly due to a greater range of resource availability, with parrots in effect maintaining selectivity in the food resources utilised.

Table 15: Composition of nestling diets in 1996 by percent of overall occurrence and biomass (unidentified food items labelled by species number).

Food item	Percent by relative frequency	Percent by relative biomass
Astronium graveolens	27.6	57.1
wood pieces	23	4.8
Guarea glabra	9.6	10
Ficus species	7.7	NA
Comocladia engleriana	6.4	13.2
Guapira macrocarpa	6.4	NA
Caesalpinia eriostachys	5.8	4.1
Crataeva tapia	4.5	7.1
plant material	1.9	0.93
Species 11	1.9	0
Plumeria rubra	1.9	1.1
Species 7	1.3	1.1
Species 9	1.3	0.53
Species 12	0.64	0.13

Table 16: Composition of nestling diets in 1997 by percent of overall occurrence and biomass (unidentified food items labelled by species number).

Food item	Percent by frequency	Percent by biomass
Comocladia engleriana	16.9	46.0
wood pieces	16.7	4.2
Sebastiana species	8.6	10.5
Species 13	7.5	10
Species 16	5.8	6.2
Carica papaya	5.8	4.4
Ficus species	5	NA
Guapira macrocarpa	4.7	NA
Erythrina lanata	3.9	3.3
Bauhinia ungulata	3.1	0.73
Acacia farnesiana	2.5	1.6
Spondius purpurea	2.5	0.16
plant material	2.2	0.39
Species 25	1.9	0.65
Guarea glabra	1.7	4.0
Plumeria rubra	1.7	0.71
Brosimum alicastrum	1.4	2.9
Pithecellobium dulce	1.4	0.78
Species 15	1.4	0.52
Species 27	1.1	1.4
Curculionidae snout beetle	0.83	NA
Species 11	0.83	0.11
Species 21	0.56	0.13
Species 23	0.56	0.26
Astronium graveolens	0.28	0.46
Caesalpinia eriostachys	0.28	0.13
Species 12	0.28	0.065
Species 24	0.28	0.26
Species 26	0.28	0.065

Table 17: Similarity measures for comparison of nestling diets between years, and observations on adult diet between the dry and rainy season.

Similarity measure	Between years (inc. veg & wood)	Between years (excl. veg & wood)[1]	Between seasons
Percent similarity	40.8%	29.5%	13.6%
Coefficient of Jaccard	0.313	0.267	0.16
Morisita Index	0.544	0.283	0.109

[1] Similarity measures were recalculated excluding plant material and wood pieces occurring in crop samples, as these may not represent actual food items.

Table 18: Niche breadth analysis for Lilac-crowned Parrot diets throughout the year.

Period of year	Levins' standardised niche breadth (*B*)	Hurlbert's niche breadth *B'*	
		By trees	By DBH
Early dry season (Jan - March)	0.302	NA	NA
Late dry season (April - June)	0.100	NA	NA
Peak rainy season (July - Sept)	0.427	NA	NA
Transition rain to dry (Oct - Dec)	0.354	NA	NA
Dry season (Jan - June)	0.221	0.618	0.322
Rainy season (July - Dec)	0.552	0.207	0.136
Overall (Jan - Dec)	0.345	NA	NA

Resource utilisation and availability

Analysis of niche breadth, similarity measures, and composition of the diet all indicate that Lilac-crowned Parrots may adjust food resource use in response to temporal variations in resource abundance. Chi-square contingency analysis also demonstrated a significant difference in the frequency of feeding bouts in different forest types between four periods of year ($\chi^2 = 74.4$, df = 5, $P < 0.0001$). Lilac-crowned Parrots concentrated foraging activity in semi-deciduous forest at the end of the dry season, but switched to deciduous forest following the onset of the rainy season (Fig 22). This corresponds to the pattern of food resource availability in each forest type at different times of the year, with most resources available in semi-deciduous forest at the end of the dry season, while resource abundance increases in deciduous forest following the onset of the rainy season (Figs 8 & 9).

Figure 21: Levins' niche breadth for parrot diets compared with number of food species in phenology transects during four periods of the year. Pearson's $r = 0.963$, df = 2, $P < 0.05$.

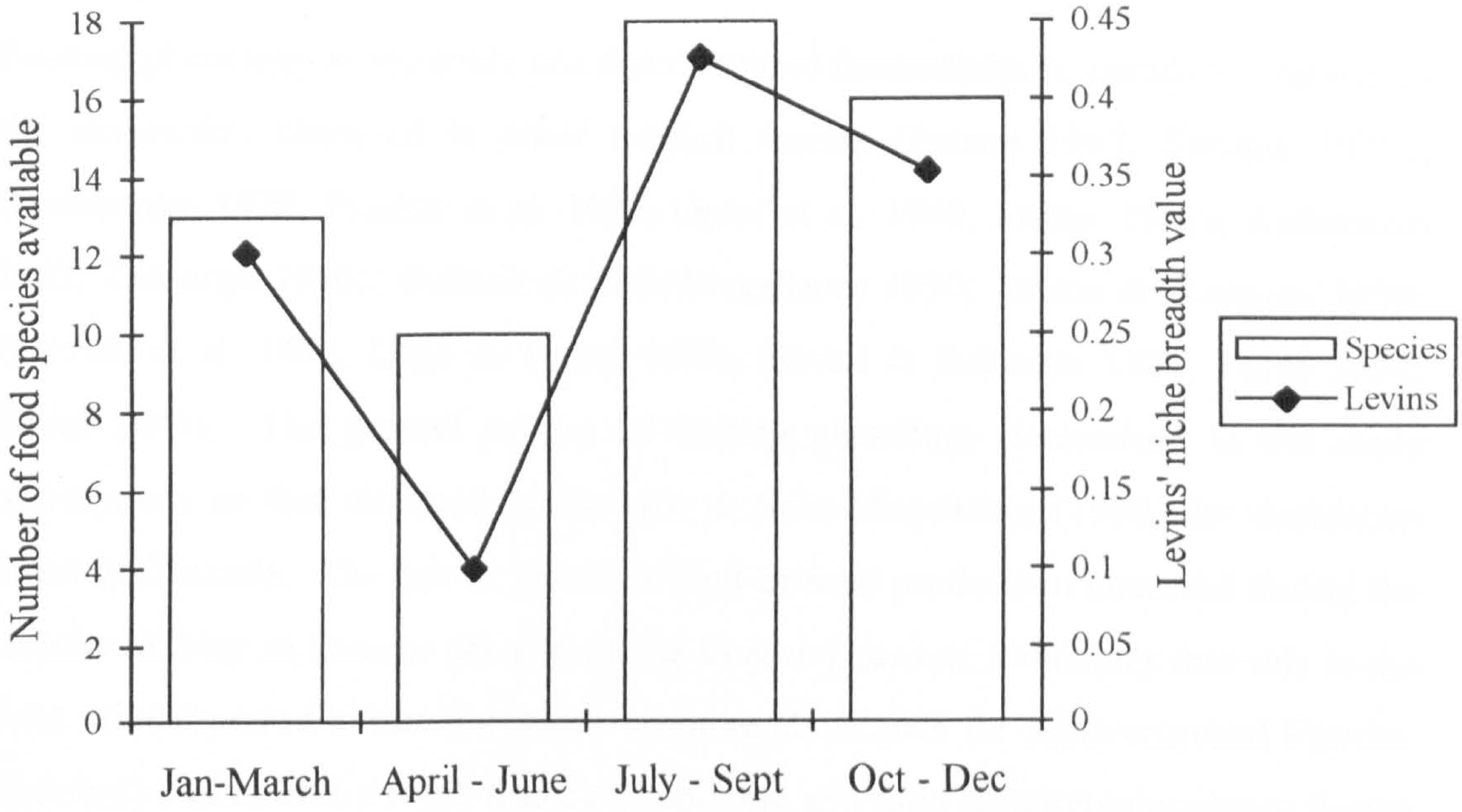
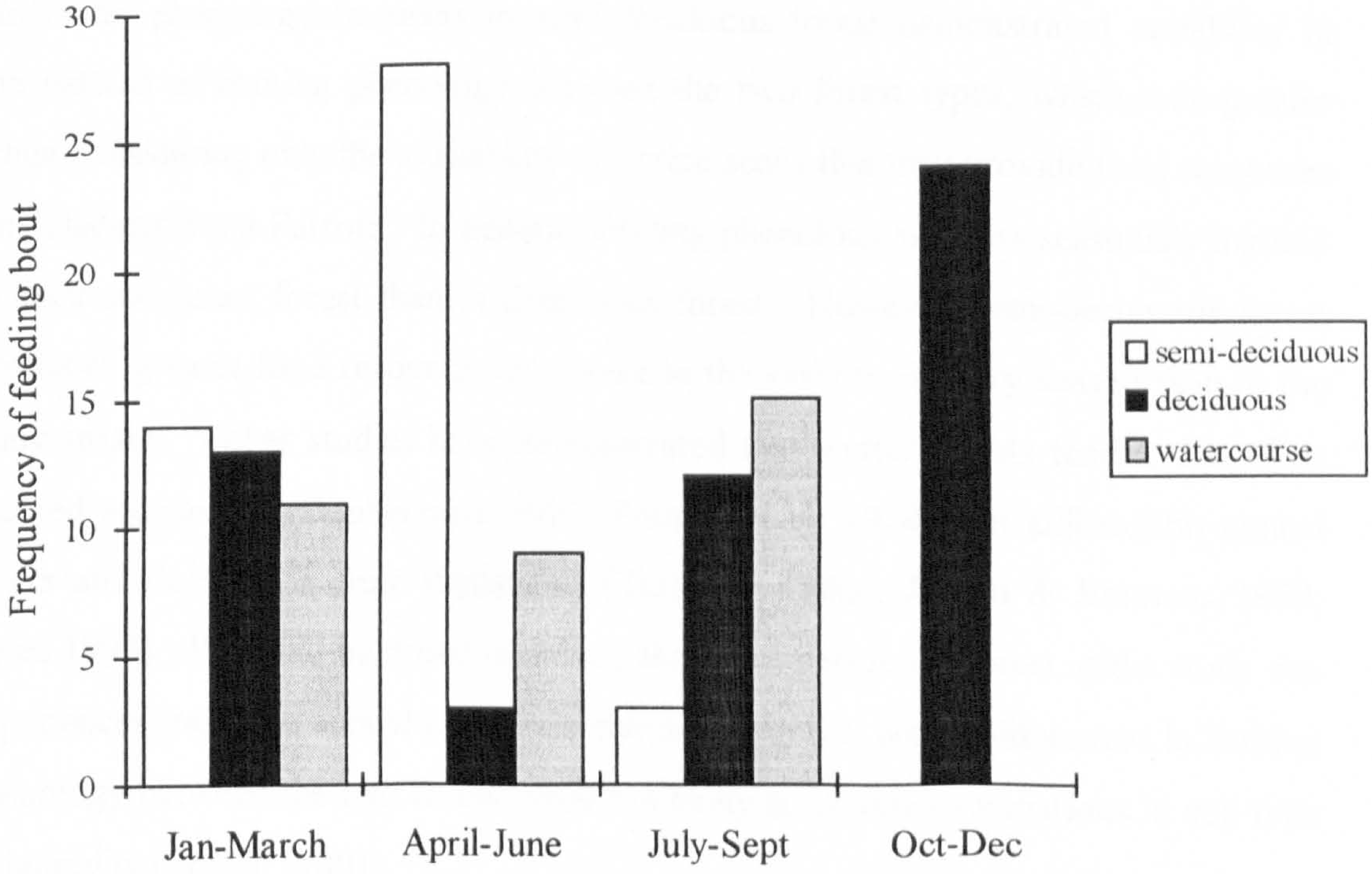


Figure 22: Frequency of feeding bouts by Lilac-crowned Parrots in three habitat types during four periods of the year. $\chi^2 = 74.4$, df = 5, $P < 0.0001$.



3.5. DISCUSSION

3.5.1. FRUITING PHENOLOGY AND RESOURCE AVAILABILITY

Fruiting phenology at the study site demonstrated fluctuations in abundance similar to the seasonality observed in other tropical forests (Janzen 1967; Smythe 1970a; Daubenmire 1972; Frankie et al. 1974; Opler et al. 1980; Foster 1982a; Lieberman 1982; Terborgh 1986a; Bullock & Solis-Magallanes 1990; Janson & Emmons 1990; Guevara et al. 1992; Lugo & Frangi 1993; Murali & Sukumar 1994; Peres 1994; White 1994). The general pattern of fruiting phenology determined in the study corresponds to that observed by Bullock & Solis-Magallenes (1990) for deciduous forest in Chamela. The lowest period of fruit or seed production occurred during the months of May to June at the end of the long dry season, indicating that this is the most critical period in terms of food resource abundance for Lilac-crowned Parrots. The sharp rise in both overall fruiting phenology and food resource abundance during the months of October to December occurred as a response to the rainy season, and corresponds to a similar peak in fruiting phenology in deciduous forest recorded by Bullock & Solis-Magallenes (1990).

However, phenology transects in semi-deciduous forest demonstrated variability in the pattern of fruiting phenology between the two forest types, which was greater when considering only the availability of unripe seeds that may provide food resources for Lilac-crowned Parrots. In general, fruiting phenology was less seasonally marked in semi-deciduous forest than in deciduous forest. However, semi-deciduous forest produced greater food resource abundance in the early to mid dry season than in the rainy season. Other studies have demonstrated that wetter forests tend to have less marked seasonality (Daubenmire 1972; Frankie et al. 1974), but still exhibit annual peaks and declines in fruit availability (Terborgh 1986a; Janson & Emmons 1990; Peres 1994). It should be noted however, that semi-deciduous forest at the study site experiences the same annual rainfall as deciduous forest, hence differences in fruiting phenology between the two forest types are likely to be due to variations in soil type or humidity (Foster 1980).

Habitat types showed less variation in fruiting phenology when considering all species recorded in transects, due to the persistence of ripe fruits on many deciduous forest trees during the early to mid dry season. This pattern corresponded to the extended fruiting period in deciduous forest recorded by Bullock & Solis-Magallenes (1990), and arises as many deciduous forest species commence fruiting during the rainy season, with fruits ripening during the early to mid dry season. However, when considering only food resource abundance for Lilac-crowned Parrots, there was a marked seasonal difference between the two forest types with deciduous forest having significantly lower availability of unripe seeds during the dry season. Hence from the perspective of Lilac-crowned Parrots, semi-deciduous forest is an important source of food during the dry season, which is also the parrot breeding season. In particular, semi-deciduous forest provides essential food resources during the late dry season months of May to June, and may be a key habitat type at this critical time of the year.

Certain tree species may also provide key resources for the animal community due to their characteristic of fruiting in May/June, at the end of the long dry season. These include *Jacaratia mexicana* and *Spondius purpurea* which produce ripe fruit during the dry season. Figs may also provide important food resources throughout the year due to the asynchronous fruiting of individual trees. However, such fruit resources may be of limited value to parrots which are principally granivorous in nature. Tree species such as *Astronium graveolens* may provide essential seed resources, as this species appears to fruit en masse towards the end of the long dry season drought. The habit of *Astronium graveolens* of setting seed during the driest part of year, may mean that this species provides a mainstay food resource for Lilac-crowned Parrots during a critical period of resource scarcity.

In addition to within year variation in fruiting phenology, there was significant variation between years with greater resource abundance during the dry season of 1997 compared to 1996. This may be related to the high rainfall during the preceding rainy season of 1996, and the atypical dry season with rains in March and April of 1997 for the first time in 20 years of recording at the study site (Bullock 1986, 1988; Chapter 2). Foster (1982b) suggests that annual fruiting rhythms of tropical forests may be seriously disrupted only once every 10 years, with mild disruptions occurring once every 5 years. On Barro Colorado Island, excessive rain during the dry season resulted in a crash in fruit production during the second half of the rainy season, with such fluctuations in climate being beneficial to some species of the animal community, but detrimental to others (Foster 1982b). Increased rainfall and fruiting phenology in deciduous forest during the dry season may be of benefit to animal communities during a severe period of the year, though it is unknown what effect this may have on fruit production in deciduous forest during the ensuing rainy season. It is clear however, that annual variations in rainfall in such a markedly seasonal environment may have dramatic impacts on the availability of plant resources, with consequences for the animal community.

Hence, there is significant temporal and spatial variation in fruiting phenology and food resource abundance at the study site. Overall, the critical period of lowest resource abundance occurs during the months of May to June at the end of the long dry season drought. Spatial variation in resource abundance is also demonstrated with greater resource abundance in semi-deciduous forest during the dry season, later increasing in deciduous forest during the rainy season.

The fact that Leguminosae is the largest plant family in the Chamela-Cuixmala forest (Lott 1993), may contribute to the pronounced seasonality of fruiting observed at the study site. Both the Leguminosae and Bombacaceae families contain predominantly dehiscent species, and hence require dry air conditions for dispersal of ripe fruits, leading to a concentration of fruiting activity during the dry season (Janzen 1967). However, in contrast with the tropical dry forest of Costa Rica which exhibits peak fruiting activity at the end of the dry season (Frankie et al. 1974), fruiting in the Chamela dry forest begins in the late rainy season and peaks in the early dry season. The dramatic decline in fruiting activity in the Chamela deciduous forest at the end of the dry season may be due to the extent and strength of the drought at the study site.

The marked seasonality in leaf flush, flowering and fruiting of deciduous forest in Chamela (Bullock & Solis-Magallenes 1990), means that adjacent semi-deciduous forest in low lying areas and larger valleys may form key habitat patches for the animal community during the late dry season. Another important habitat type at the study site may be that of monodominant *Celaenodendron mexicanum* forest (Martijena & Bullock 1994), which was not included in phenology transects due to logistical constraints. However, some areas of *Celaenodendron mexicanum* forest did occur in transects along watercourses in the study site, and contributed to the rise in fruit abundance for watercourses during the rainy season. It is therefore predicted that *Celaenodendron* forest may provide abundant food resources for Lilac-crowned Parrots during the fruiting period of July/August to January.

Foster (1980) suggested that adjacent vegetation types may respond differently to climatic variation, creating environmental patchiness in the availability of plant resources. It is to be expected that animal communities will track these temporal and spatial variations in plant resource abundance either by dietary switching, concentrating on a few key resources, or migrating between forest types (Wiens 1976; Fleming 1992; van Schaik et al. 1993). The present study demonstrates the differential fruiting phenology of semi-deciduous and deciduous forest, and the potential value of semi-deciduous forest to animal communities at the study site during the dry season.

3.5.2. PARROT DIET AND RESOURCE UTILISATION

Observations on the diet of the Lilac-crowned Parrot demonstrate that fruit formed only 10 - 12% of the diet, while immature seeds in particular formed 68% of the diet. In fact, seeds form a major component of the diet for many parrot species (Galetti 1993; Gilardi 1996; Enkerlin-Hoeflich & Hogan 1997), though some parrot species may be primarily frugivorous (Snyder et al. 1987; Wermundsen 1997). Seeds also form a major component of the diet for many Australian parrot species, which have adapted to exploit agricultural crops along the Australian wheatbelt (Saunders 1980; Beeton 1985; Rowley 1990; Rowley & Chapman 1991). Seeds are the most nutritious part of the plant resource being high in protein, minerals, and lipid content, while fruits such as figs are high in calcium and fibre (Gilardi 1996).

The consumption of insect larvae may provide additional protein or fat in the diet, though it did not form a major component of the diet of Lilac-crowned Parrots. Scarlet Macaws in Belize also feed on the leaf gall larvae of *Astronium graveolens* (pers. obs.), while Maroon-bellied Conures have been observed feeding on the gall larvae of *Persea pyrifolia* (Martuscelli 1994). Insect larvae are fairly common in the diet of Australian parrots (Saunders 1980; Rowley 1990; Rowley & Chapman 1991; Smith & Moore 1991), but only occasionally reported for Neotropical parrots (Martuscelli 1994; Gilardi 1996; Enkerlin-Hoeflich & Hogan 1997).

Notably, Lilac-crowned Parrots were not observed consuming flowers. However, flowers are not widely available in deciduous forest during most of the year, with flowering peaks being concentrated at the start of the rainy season between late June to early July (Bullock & Solis-Magallenes 1990). Most other parrot species also consume flowers very infrequently (Snyder et al. 1987; Gilardi 1996; Wermundsen 1997), although flowers formed the second main food item for Scaly-headed Parrots in Brazil (Galetti 1993).

Dry season diets varied slightly when compiled from field observations compared to crop samples, illustrating the potential limitations of field observations. Some food plant species may be eaten in such relatively small proportions that the probability of observing parrots feeding on the resource item may be fairly low. Alternatively, it may be more difficult to observe parrots feeding on some food items than others. An example is *Comocladia engleriana*, which was relatively frequent in nestling diets, but for which there were few observations of parrots feeding on this item. Parrots may be more wary or secretive when feeding on certain food items, particularly where there may be a greater risk of predation in smaller trees which are closer to the ground. Hence, field observations may be limited by inherent biases, however, observations are the only means by which to determine parrot diets throughout the year. Potential bias in field studies of diet should be reduced by conducting regular observations along transects in each habitat type.

A predominantly seed diet means that Lilac-crowned Parrots may need to adjust rapidly to changes in seed availability. Plants may have evolved high synchrony in seed production as a strategy to avoid predation (Janzen 1969, 1971; Augspurger 1981). Hence, pre-dispersal seed predators such as parrots need to be highly mobile and flexible in order to exploit each food resource as it becomes available. This flexibility and adaptability in diet was demonstrated by the between year variations in nestling diets, and the high seasonality in parrot diets within a year.

Nestling diets were more varied in 1997, corresponding with the greater number of fruiting species recorded in phenology transects. However, nestling diets varied little in niche breadth between 1996 and 1997, as there was still the tendency to concentrate on a few main items in the diet. Hence, although Lilac-crowned Parrot nestlings may be fed a variety of food items, only a few of these form a large proportion of the diet. This predominance of a few food items in nestling diets is similar to that observed for other bird species (Lack 1954; Ward 1965; Newton 1967; Banbura et al. 1994; Bancroft & Bowman 1994; Kleintjes & Dahlsten 1994).

However, there was low overlap and similarity in nestling diets between years as the actual food items and proportions consumed varied. The principal variation lay in the switch from *Astronium graveolens* seeds as the main food item for Lilac-crowned Parrot nestlings in 1996, to *Comocladia engleriana* seeds as the main food item in 1997. This switch in nestling diet corresponded with annual variations in the availability of each food species. Furthermore, the fact that there was no significant difference in nestling diet between Lilac-crowned Parrot nests in a given year indicates that changes in diet were general across all nesting pairs.

Dietary switching also occurred within a year, as indicated by the low overlap in diets between the dry and rainy season. This is due to fact that specific food items were only available at certain times of the year. Seasonal variations in diet have been noted for Australian parrots (Saunders 1980; Beeton 1985; Rowley & Chapman 1991), and some Neotropical parrots (Snyder et al. 1987; Galetti 1993; Wermundsen 1997). Seasonal diet switching was also recorded for seed-eating Galapagos finches (Smith et al. 1978; Grant & Grant 1980; Schluter 1982a, b; Boag & Grant 1984; Price 1987), and may occur in response to environmental heterogeneity (Schluter 1981).

The positive correlation between niche breadth value and food species abundance indicates that Lilac-crowned Parrots may exhibit narrower dry season diets in response to resource availability. Hurlburt's indice further demonstrated that while parrots may exhibit a narrower diet during periods of low resource abundance, this is due to the fact that many plant resources are not present throughout the year. Hence the animal community may be restricted to exploiting those few resources which are available.

The present study demonstrates the high flexibility in parrot diets, incorporating dietary switching, as well as niche breadth expansion and contraction, which was closely related to temporal variations in food resource availability. Lilac-crowned Parrots also demonstrated spatial variation in habitat use corresponding to fluctuations in the availability of food resources in different habitat types throughout the year. Finally, an ongoing telemetry study has demonstrated that Lilac-crowned Parrots at the study site make seasonal altitudinal migrations of over 50 km to the mountains during the severe period of resource scarcity in May and June, returning again in July with the start of the rainy season (Renton unpubl. data).

The pattern of resource availability and utilisation by parrots demonstrates the importance of semi-deciduous forest in providing essential food resources during the critical period of resource scarcity in the late dry season. Semi-deciduous forest may be of importance to other animal species at the study site, particularly those which are not equipped to make large-scale movements. However, the dynamics of patch use by the animal community in the tropical dry forest of Chamela is relatively unknown, and requires further investigation to evaluate the impact of habitat fragmentation.

Lilac-crowned Parrots employed all of the strategies proposed for frugivores and nectarivores (Wiens 1976, 1985; Fleming 1992; van Schaik et al. 1993), in order to closely track a seed resource base which exhibited high temporal and spatial variability in abundance. Granivory is relatively uncommon among bird feeding guilds (Poulin et al. 1994a, b), and appears to require high flexibility in diet, spatial scales, and mobility in order to exploit such ephemeral and highly variable resources. However, most parrot species are primarily canopy seed-eaters. The present study indicates that parrot populations may be highly adapted to track food resources, and suggests a close evolutionary relation between parrot seed predators and plant seed resources.

The fact that parrots consume predominantly unripe seeds, and closely track variations in seed abundance, makes them potentially important pre-dispersal seed predators on canopy trees. The tendency for tree species in tropical dry forests to be clumped in distribution (Hubbell 1979; Thorington et al. 1982), and the potential for seed predators such as parrots to significantly impact seed production (Higgins 1979; Janzen 1981; Heithaus et al. 1982; Clout 1989; Galetti & Rodrigues 1992), mean that a highly mobile seed predator may influence forest dynamics. Studies in Central American forests suggest that herbivores play a regulatory role in maintaining forest diversity (Janzen 1970; Dirzo & Miranda 1990, 1991), while Hambäck (1998) presents a model in which an optimally foraging herbivore in a seasonal environment may promote co-existence among plant species. Parrots constitute a high proportion of canopy granivores in tropical forests (Loiselle 1988; Terborgh et al. 1990). This combined with the tendency to form large feeding flocks, high mobility, and a wide range, means that as pre-dispersal seed predators, parrots may play an important regulatory role in maintaining diversity of canopy trees in tropical forests.

CHAPTER 4

NESTING BEHAVIOR OF THE LILAC-CROWNED PARROT[1]

4.1. ABSTRACT

Nesting behavior of the Lilac-crowned Parrot (*Amazona finschi*) was observed at 18 nests in the tropical dry forests of the Chamela-Cuixmala Biosphere Reserve, western Mexico. Nest site characteristics, and the pattern of parental care throughout the nesting cycle are described for a mainland Amazon parrot, and compared with that observed for other Amazon parrot species. Nest sites were located in natural cavities of large mature trees of *Celaenodendron mexicanum* and *Astronium graveolens* characteristic of semi-deciduous forest. There was little variation between nest sites in tree species, tree size, cavity height, and entrance width, indicating that Lilac-crowned parrots may select nest sites based on these characteristics. Lilac-crowned Parrots exhibited a low degree of nest site fidelity regardless of success or failure of nests, which contrasts with the 30 - 40% nest site re-use found for other parrots. Lilac-crowned Parrots were distinct from most other parrot species in the high synchrony of nest initiation, with all eggs laid within 2 weeks at the beginning of February. Lilac-crowned Parrots also exhibited high nest attendance during the incubation phase of the nesting cycle, with the female absent from the nest for a mean of only 39.4 mins per day. Throughout the nesting cycle, females and nestlings were fed on average only twice a day, and nest attendance during feeding visits was short. The infrequent feeding visits and short nest attendance exhibited by Lilac-crowned Parrots corresponds with that found for other mainland Amazon parrots in north-eastern Mexico, but contrasts with the multiple feedings and longer nest attendance observed for island Amazon species. Many of the distinct aspects of nesting behavior of the Lilac-crowned Parrot may be related to environmental factors of predation rate and food resource availability, particularly towards the end of the extreme dry season.

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[1] Prepared for submission to Wilson Bulletin

4.2. INTRODUCTION

The majority of studies on the ecology of Neotropical Amazon parrots have been conducted on species of the Caribbean Islands (Snyder et al. 1987; Gnam 1991; Gnam & Rockwell 1991; Wilson et al. 1995, 1997). A comparative study of three species of mainland Amazon parrot in north-eastern Mexico found distinct variations with island species in some aspects of reproductive behavior and productivity (Enkerlin-Hoeflich 1995). Females and nestlings of three mainland Amazon parrot species were fed only twice a day (Enkerlin-Hoeflich 1995), in comparison with the multiple feedings observed for Caribbean Amazons (Snyder et al. 1987; Gnam 1991; Wilson et al. 1995) and other Neotropical parrots (Lanning 1991; Waltman & Beissinger 1992). Additional studies on mainland Amazon parrots are important to determine whether conclusions from studies on island species are applicable to mainland species. The Amazon parrot species of Mexico are particularly suited to comparison with the *Amazona* species of the Greater Antilles in the Caribbean due to their close evolutionary relation (Snyder et al. 1987; Forshaw 1989). The Lilac-crowned Parrot is endemic to western Mexico, and has a restricted distribution from south-eastern Sonora to Oaxaca (Forshaw 1989). There have been no studies on the ecology of the Lilac-crowned Parrot, and little is known of its breeding biology. This paper presents observations on the nest site requirements and nesting behavior of the Lilac-crowned Parrot in the wild, which is compared with observations for other island and mainland Amazon parrots.

4.3. STUDY AREA AND METHODS

Studies on the breeding biology of the Lilac-crowned Parrot were conducted at the 13,142 hectare Chamela-Cuixmala Biosphere Reserve ($19^0$22'N $104^0$56'W to $19^0$35'N $105^0$03'W), in the state of Jalisco on the Pacific Coast of Mexico. The study site has a dry tropical climate exhibiting a marked seasonality in precipitation, with 85% of the 706.6 mm annual rainfall occurring in June to October, and a prolonged drought from mid-February to late May (Bullock 1986, 1988). The reserve has a hilly topography varying in elevation from 20 m to 520 m above sea level. The dominant vegetation type on the slopes is tropical dry deciduous forest, with semi-deciduous forest in the larger drainages and more humid valleys (Lott et al. 1987; Lott 1993; Rzedowski 1994). Monodominant forests of *Celaenodendron mexicanum* also occur in the reserve as discontinuous patches within the tropical deciduous forest mosaic (Martijena & Bullock 1994).

Observations on the nesting behavior of Lilac-crowned Parrots were conducted from January to June in 1996 and 1997. Nest searches were carried out in February during the nest prospecting and early incubation phases of the parrot breeding cycle. No additional nests were located later in the nesting cycle due to the secretive behavior of breeding pairs which made detection of nest sites difficult. Preliminary observations in February to March 1995 had determined the peak activity period for parrots to be in the early morning and late afternoon. Therefore, nest searches were conducted during the first four hours following sunrise and the last four hours prior to sunset. A cavity was considered a potential nest site if one or both of the adult parrots were observed entering the cavity. The cavity was considered an active nest site if one of the adult parrots remained within the cavity for longer than 20 mins. Nest site fidelity was determined from the incidence of re-use of nest cavities between successive years

Access to nest cavities was achieved using both single-rope ascending (Perry 1978; Perry & Williams 1981), and tree bole-climbing techniques (Donahue & Wood 1995). Nesting requirements of the Lilac-crowned Parrot were determined by measurement of nest cavity dimensions as recommended by Saunders (1979) and Saunders et al.

(1982). The variables measured included: Tree species, diameter at breast height (DBH) of the tree; height above ground of the entrance, width and length of entrance, cavity depth, internal diameter, and circumference at entrance. The map location of each nest site, and where possible, the tree used by the nesting pair for the transfer of food from the male to the female, were obtained using a geographic positioning system (GPS) giving X and Y co-ordinates in the UTM format. The coefficient of variation was determined for each of the mean cavity dimensions to evaluate the variability of characteristics between nest sites.

Behavior of breeding pairs was determined by observations of parrot nests from covered hides using 10x40 binoculars. Continuous dawn to dusk observations were conducted on 30 man-days over 8 nests. No activity was observed at nests during mid-day, therefore additional observations were restricted to the first 4 hours after sunrise and the last 3 hours prior to sunset giving an additional 174 hours of observation over 10 nests. Parental care and investment was evaluated from data on: the number of feeding visits to the nest; arrival time; duration of feeding visit; time spent in the nest cavity; and time spent in the nest area (defined as within 100 m of the nest cavity). All descriptive statistics were presented with means, value ranges, and standard deviations.

4.4. RESULTS

Nest site characteristics

A total of 23 different nest sites were located in 1995 to 1997, all of which occurred in natural cavities. Nest cavities were principally located in live trees of *Celaenodendron mexicanum*, local name 'Guayabillo' (47.8%, n = 11), and *Astronium graveolens*, local name 'Culebro' (34.8%, n = 8). Of the remaining four cavities, 2 were located in dead trees, 1 was located in a *Tabebua* species, and the final cavity was located in an unidentified tree species. There was little evidence of nest site fidelity, with only one instance when a cavity was re-used after an interval of one year.

Mean cavity dimensions for 20 active nest sites are presented in Table 19 - three cavities could not be accessed for safety reasons. The cavity dimensions with least variation between nest sites were height of entrance from the ground, and width of entrance, indicating that parrots may select cavities based on narrow criteria for these two characteristics. Diameter of tree at breast height and circumference of tree at entrance were also relatively consistent between nest sites, and reflect the fact that parrot nest sites were located in large, mature trees. Greatest variability was found in depth of cavity, length of entrance, and distance to nearest active nest, suggesting that these may not be important factors in the selection of nest sites by parrots. Hence, Lilac-crowned Parrots utilised large, emergent trees characteristic of semi-deciduous forest, and may select nest sites on the basis of tree species, size, cavity height, and entrance width.

TABLE 19: CAVITY DIMENSIONS FOR 20 LILAC-CROWNED PARROT NESTS

Nest character	Mean	Standard deviation	Range	Coefficient of variation (s/m)*100
Tree diameter at breast height (cm)	43.63	± 13.34	27.7 - 81.5	30.57%
Cavity height from ground (m)	9.81	± 1.898	7.42 - 14.66	19.34%
Entrance width (cm)	10.01	± 2.26	6.4 - 14.0	22.58%
Entrance length (cm)	17.93	± 11.85	7.5 - 50.0	66.08%
Internal diameter (cm)	20.42	± 7.38	10.5 - 35.0	36.12%
Cavity depth (cm)	71.03	± 56.62	25.0 - 260.0	79.72%
Circumference at entrance (cm)	92.24	± 25.96	45.0 - 135.0	28.14%
Nearest active nest (m)	943.9	± 732.86	184 - 2,419.5	77.64%

Egg-laying and incubation

Timing of egg-laying was highly synchronised between nests with most pairs commencing incubation within 14 days of the first nest being initiated. Mean nest initiation date was 6 February ± 4.63 days in 1996 (range 30 Jan - 13 Feb, $n = 8$), and 15 February ± 5.27 days in 1997 (range 10 Feb - 23 Feb, $n = 6$).

Nest attendance by the female was high during incubation, with the female leaving the nest only twice a day in the morning and afternoon to be fed by the male. During this time the female spent a mean of only 39.4 ± 26.54 mins per day out of the nest over both morning and afternoon feeding sessions (range 15 - 95 mins per day, $n = 20$). Conversely, the male was rarely observed to enter the nest, or perch on the nest rim, apart from at the time of initial egg-laying. Daily activity periods were consistent between nests with the male making an average 2.08 ± 0.29 nest visits per day (range 2 - 3 visits, $n = 35$) to feed the female. The mean arrival times for the morning and afternoon activity periods were respectively 08:36 hours ± 59.54 mins (range 07:21 - 10:08 hours, $n = 26$) and 18:11 hours ± 40.49mins (range 17:15 - 18:53 hours, $n = 25$). Overall, each nest visit by the male lasted an average of 36.14 ± 26.72 mins (range 5 - 113 mins, $n = 40$).

The male usually vocalised loudly on approach to the nest area, and perched in a tree adjacent to the nest cavity making low contact vocalisations until the female emerged. The nesting pair gave a characteristic take-off squawk, or bugle, as the female flew from the nest cavity to join the male. Food transfer from the male to the female usually took place in a regular perch tree located an average 361.8 ± 161.4 m (range 106 - 661 m, $n = 10$) away from the nest cavity. The food transfer session was the only time during the incubation phase when both adults were away from the nest area, and was usually short in duration being an average 9.12 ± 8.62 mins (range 3 - 32 mins, $n = 25$) in the morning, and 12.41 ± 8.74 mins (range 2 - 34 mins, $n = 27$) in the afternoon.

Parental Care

Following hatching of the eggs, females continued to brood nestlings throughout the day until the oldest nestling was 19.6 ± 2.69 days old (range 15 - 23 days, *n* = 9). During this early nestling phase, the male continued to feed the female twice a day, but was not observed entering the nest to feed the young. Later in the nesting cycle when the chicks were larger, both parents entered the nest to feed the young.

The behavior of nesting pairs altered once the female began to forage with the male. Nesting pairs became more secretive around nests, arriving and departing silently, and only using low, almost inaudible vocalisations when in the nest area. Pairs were cautious about approaching the actual nest, and would not do so if they detected the observer or another disturbance. The nesting pair made an average 2.6 ± 0.93 visits per day (range 2 - 4 visits, *n* = 25) to feed the nestlings. Average duration of feeding visits during the nestling phase was 55.64 ± 35.02 mins (range 12 - 143 mins, *n* = 14). However, the nesting pair spent the majority of this time perched in trees around the nest area. Attendance at the nest cavity was short lasting an average of 13.31 ± 10.42 mins, range 1.67 - 27.17 mins, *n* = 14 (total time adult in nest cavity or at nest entrance), with a mean 4.8 ± 3.14 mins per visit (range 0 - 10.37 mins, *n* = 14) actually spent within the nest cavity, and a mean 12.76 ± 11.88 mins (range 0 - 20.55 mins, *n* = 14) perched at the nest rim. This was sufficient time to feed the young, however there was no indication that parent birds ever spent time in the nest preening the young.

Prior to fledging nestlings began to climb to the nest entrance, and were fed at the nest rim. During this stage, nesting pairs spent more time perched near to the nest entrance making low contact vocalisations to the young. Mean age at fledging of nestlings was 64.4 ± 2.44 days (range 60 - 68 days, *n* = 14). Fledging was also highly synchronised between nests with all nestlings fledging within 12 days in 1996 (range 6 - 18 May, *n* = 8), and 17 days in 1997 (range 11 - 28 May, *n* = 7).

4.5. DISCUSSION

The low variability between nest sites in tree species, size, cavity height, and entrance width suggests that the Lilac-crowned Parrot may select nest sites based on these characteristics. Predation rates decrease with increasing height of nest sites from the ground (Nilsson 1984; Wilcove 1985), while the increased size of nest entrance required by large birds may pose greater risks from predation, leading to specificity for entrance dimensions (Christman & Dhondt 1997). Hence, cavities located high above the ground in large, mature trees with a narrow entrance width may prevent the access of predators to the nest, or reduce competition with other cavity nesters. Specificity of nest site characteristics is demonstrated by Amazon parrots in north-eastern Mexico, which appear to select cavities based on tree species, cavity height, and entrance length (Enkerlin-Hoeflich 1995). Australian cockatoos also demonstrate species specific requirements related to body size for entrance dimensions and internal diameter of nest hollows (Saunders et al. 1982). Enkerlin-Hoeflich (1995) suggests that the tendency for parrots to exhibit variability in a number of cavity characteristics combined with narrow specificity for a few key characters may provide parrots with the flexibility to exploit a wide range of available cavities, while maintaining specific criteria to limit predation and competition threats. In addition, the lack of nest site fidelity demonstrated by the Lilac-crowned Parrot is contrary to the 30 - 40% cavity re-use observed for most other parrot species (Saunders 1982; Snyder et al. 1987; Rowley & Chapman 1991; Smith 1991; Enkerlin-Hoeflich 1995), and may help to prevent predators from learning nest site locations (Sonerud 1985, 1989).

The high synchrony of nest initiation exhibited by the Lilac-crowned Parrot is also distinct to that observed for other psittacines, and may be related to environmental factors. Most *Amazona* species have a 3 - 5 week nest initiation period each breeding season (Snyder et al. 1987; Gnam 1991; Enkerlin-Hoeflich 1995). The Monk Parakeet in Argentina extends egg-laying over an average nine week period (Navarro et al. 1992). Australian cockatoos have a similar broad egg-laying period of 5 - 8 weeks in each season, comprising a 15 week nest initiation period over all seasons (Saunders 1982; Smith & Saunders 1986; Rowley & Chapman 1991; Smith 1991).

However, the Lilac-crowned Parrot is notably different to other parrot species in the high synchrony in nest initiation, with all nests commencing within two weeks in each season, and the general nest initiation period comprising the first three weeks in February. In addition, there is no evidence that breeding pairs of the Lilac-crowned Parrot will re-lay after a nest failure, which would also lengthen the nesting period. The nesting season of the Lilac-crowned Parrot may be so sharply defined due to the extreme climatic seasonality in tropical deciduous forest, and the impact this may have on food resource availability. There may be a need for nesting pairs to fledge young prior to the end of the dry season in late May - June when conditions may be most severe in terms of temperature, water availability, and food resource abundance (Bullock & Solis-Magallenes 1990; Chapter 3). Delaying nest initiation over a longer period may result in breeding pairs having to conduct energetically demanding activities of raising young during this environmentally difficult period.

The infrequent feeding visits to the nest per day by breeding pairs of the Lilac-crowned Parrot contrasts with the multiple feedings noted for island *Amazona* species (Snyder et al. 1987; Gnam 1991), but confirms the two nest visits per day observed for three other mainland Amazon parrots in north-eastern Mexico (Enkerlin-Hoeflich 1995). Mean morning and afternoon arrival times for nesting pairs of the Lilac-crowned Parrot were also similar to the three *Amazona* species in north-eastern Mexico (Enkerlin-Hoeflich 1995), with nest visits occuring approximately one hour after sunrise and an hour before sunset. This infrequency of nest visits differs from the feeding pattern observed for most other Neotropical parrots which may be active at the nest throughout the day (Lanning & Shiflett 1983; Lanning 1991; Smith 1991; Waltman & Beissinger 1992; pers. obs.). However, a similar pattern has been noted for large cockatoos in dry areas of Australia, which restrict nest visitation activity to the early morning and late afternoon, spending the hot, mid-day periods resting under the shade of leafy trees (Saunders 1982). Individual Lilac-crowned Parrots at the study site spent the majority of the day from 11:00 - 17:00 hours inactive (Renton unpubl. data), and demonstrate signs of heat stress during the mid-day hours of 12:00 - 14:00 by holding wings away from their bodies, and panting with beaks open (pers obs.). Therefore, restricting foraging and feeding activity to the early morning and late afternoon may enable parrots to conserve energy during high mid-day temperatures, particularly in open or dry habitats.

In addition to being infrequent, attendance at the nest by Lilac-crowned Parrots during feeding visits was also short in duration. Furthermore, Lilac-crowned Parrots conducted the majority of their activity well away from the nest area. Nesting pairs were never observed to forage within the vicinity of the nest, and food transfers from the male to the female took place an average 361 m from the nest site. This contrasts with the behavior observed for island Amazon parrots which may spend longer periods in the nest cavity preening young (Snyder et al. 1987), as well as conduct food transfers and foraging activities within the vicinity of the nest (Snyder et al. 1987; Gnam 1991). These aspects of infrequent visits, short nest attendance, and feeding away from the nest vicinity exhibited by Lilac-crowned Parrots may all serve to limit the amount of activity in the nest area, and hence reduce the risk of attracting predators to the nest. Caribbean Amazons conduct more activity within the nest vicinity, but appear to be more silent and secretive in the nest area (Snyder et al. 1987). Hence, island and mainland Amazon parrots may reduce predation risks either by being more silent and secretive in the nest vicinity, or by limiting the amount of activity conducted in the nest area.

Breeding birds are restricted by competing needs to maintain their own energetic requirements, as well as to protect and nourish the young (Martin 1987). While infrequent, short nest visits may reduce both mid-day energetic expenditures by foraging adults and the risks of nest predation, there is a cost in having to meet the energy demands of the young in a more limited time than adults which may spread energy demands through the day. Hence, the subtle variations in nesting behavior suggest that island and mainland Amazon parrots may be employing differing strategies to meet time constraints in caring for the young.

CHAPTER 5

FECUNDITY AND REPRODUCTIVE OUTPUT

5.1. ABSTRACT

Fecundity and reproductive output was determined for the Lilac-crowned Parrot population in the tropical dry forests of the Chamela-Cuixmala Biosphere Reserve, western Mexico. Overall nest success was low, with only 40% of nests producing fledged young. Major losses in reproduction occurred in both the incubation (28% loss) and nestling (39% loss) phases, and the main cause of failure was natural predation of the nest contents. The high predation rate resulted in a relatively low reproductive output, with Lilac-crowned Parrot females producing on average 1.0 fledglings on their initial investment of 2.5 eggs. The Lilac-crowned Parrot has one of the lowest nest success rates of any other Amazon parrot species, and contrasts with the 60 - 70% nest success rates reported for psittacines in relatively undisturbed habitat. The high predation rate of Lilac-crowned Parrot nests at the study site may be due to the concentration of potential nest predators in small areas of semi-deciduous forest during the dry season. Studies on the breeding biology and reproductive success of parrot populations in disturbed habitats demonstrate that such populations may in fact be reproducing at sub-optimal levels and are vulnerable to decline. Wild populations of the Lilac-crowned Parrot in the tropical dry forests of Chamela-Cuixmala did not demonstrate a reproductive rate which is able to support high levels of pressure for commercial trade.

5.2. INTRODUCTION

Low fecundity is one of the main factors making bird species vulnerable to decline (Bennett & Owens 1997). Data on fecundity and the factors limiting the reproductive output of parrots are of particular importance to determine the ability of wild populations to withstand pressures from trade (Thomsen & Brautigam 1991), evaluate the harvesting potential of species (Beissinger & Bucher 1992a,b), and model population viability (Saunders 1986).

Predation is one of the major factors affecting nest success and limiting the production of young in birds (Lack 1954; Ricklefs 1969; Fogden 1972; Skutch 1976; Gates & Gysel 1978). The need to protect eggs from predators (Bollinger et al. 1990), or to defend nest sites (Beissinger & Waltman 1991), as well as to maintain egg viability (Veiga 1992; Stoleson & Beissinger 1997a), may influence the onset of incubation before egg-laying is complete, resulting in asynchronous hatching for many altricial birds (Clark & Wilson 1981; Stoleson & Beissinger 1997b).

Predation on bird nests is greater in small forest patches than in continuous forest (Ambuel & Temple 1983; Loiselle & Hoppes 1983; Andren et al. 1985; Wilcove 1985; Andren 1992; Keyser et al. 1998). Nest predation is also greater at the edges than the interior of forest patches, and tends to level off at 200 - 500 m from the forest edge (Gates & Gysel 1978; Angelstam 1986; Wilcove et al. 1986; Andren & Angelstam 1988; Fenske-Crawford & Niemi 1997). The increased predation on bird nests in small forest patches may be due to the absence of top predators which require large areas, leading to an increase in medium-sized nest predators (Terborgh & Winter 1980; Wilcove 1985; Terborgh 1988; Sieving 1992), or to edge effects of predators entering forest patches from surrounding areas (Angelstam 1986; Andren & Angelstam 1988; Small & Hunter 1988; Andren 1992; Fenske-Crawford & Niemi 1997).

Cavity nests are less vulnerable to predation than open nests (Alerstam & Hogstedt 1981; Wilcove 1985), while predation rates decrease with increasing height of nest cavities from the ground (Nilsson 1984; Li & Martin 1991). Hence, cavity nesting birds generally have success rates exceeding 60% (Lack 1954; Skutch 1966, 1976; Johnson & Kermott 1994). Most of the early studies on nest success were conducted with nest boxes which may have higher success rates than natural cavities (Nilsson 1986). However, recent studies also provide a 50 - 60% nest success in natural cavities (Johnson & Kermott 1994; Purcell et al. 1997).

The greater safety from predators also enables cavity nesting bird species to raise young over longer development periods than open nesting species (von Haartman 1957; Lack 1968; Saunders et al. 1984; Martin & Li 1992). There may also be selection for exposed, conspicuous foragers to adopt hole-nesting due to the risks of attracting predators to the nest site (Alerstam & Hogstedt 1981). The drawbacks of cavity nesting are a potential lack of available hollows (von Haartman 1957; Raphael & White 1984; Gibbs et al. 1993), and possibly severe competition for nest sites (Minot & Perrins 1986; Gustafsson 1988; Pribil & Picman 1991). This in turn can lead to territorial defence of nesting areas which may limit breeding density (Krebs 1971; Saunders 1982; Village 1983; Gauthier & Smith 1987; Renton 1994).

Most parrot species are secondary cavity nesters, i.e., they do not excavate their own cavities but are dependent on the availability of naturally occurring hollows. Comprehensive, long-term studies on Australian parrots (Saunders 1982, 1986; Rowley 1990; Rowley & Chapman 1991; Smith 1991), and the Puerto Rican Parrot, *Amazona vittata*, (Snyder et al. 1987) demonstrate that small clutches, high parental investment, and fledging of a few offspring is the prevailing reproductive strategy. Most cockatoo species in Australia support the prediction of high success rates for cavity nesters (Saunders 1982, 1986; Rowley 1990; Rowley & Chapman 1991; Smith 1991). However, low reproductive success was recorded for Australian parrot populations in extensively deforested areas (Saunders 1982, 1986, 1990, 1991).

By comparison, there have been few comprehensive studies of Neotropical parrots, though high nest success has been demonstrated for macaws in undisturbed rainforest (Munn 1992) and Caribbean Amazons (Snyder et al. 1987). In contrast, the Bahama

Parrot (*Amazona leucòcephala bahamensis*) exhibits a low 42% nest success, fledging only 0.8 young per breeding pair (Gnam & Rockwell 1991). However, this species is unique among Neotropical psittacines in its habit of nesting in holes in the ground (Gnam 1991). The high reproductive loss is attributed to predation on nests by feral cats, particularly during one unusual year of high cat predation (Gnam & Rockwell 1991).

The majority of studies on the ecology of Neotropical Amazon parrots have been conducted on species of the Carribbean Islands (Snyder et al. 1987; Gnam 1991; Gnam & Rockwell 1991; Wilson et al. 1995, 1997), while studies of mainland Amazon parrots have been limited to evaluations of distribution and status (Ridgely 1981). However, a comparative study of three species of Amazon parrot in north-eastern Mexico, indicated that productivity and nest success was generally lower for the three mainland Amazons than for most Amazon species of the Caribbean Islands (Enkerlin-Hoeflich 1995). Further studies are required on the reproductive ecology of mainland Amazon parrot species in order to evaluate the limitations to wild populations.

During 1979 to 1982 the Lilac-crowned Parrot was the third most captured and exported psittacine species in Mexico (Iñigo-Elias & Ramos 1991), and one of the 15 Neotropical parrot species most frequently imported by the United States (Roet et al. 1981). Although Mexico banned international trade in wildlife in 1982, this did not control domestic trade (Iñigo-Elias & Ramos 1991), and poaching of nestlings for sale in towns and along roadsides continues to be a widespread problem for wild populations (pers. obs.). However, despite this exploitation there have been no studies on the ecology of the Lilac-crowned Parrot in the wild, and information on breeding is only available from anecdotal observations in captivity (Mann & Mann 1978; Forshaw 1989). Hence, data on the fecundity and reproductive output of the Lilac-crowned Parrot are essential to evaluate the ability of the wild population to withstand commercial exploitation.

5.3 METHODS

Reproductive output of the Lilac-crowned Parrot was determined through nest studies, conducted from January to June in 1996 and 1997, at the Chamela-Cuixmala Biosphere Reserve (19^{0}22'N 104^{0}56'W to 19^{0}35'N 105^{0}03'W) on the Pacific Coast of Mexico. Parrot nests were inspected at regular intervals to determine clutch and brood size, and the causes of nest failure. Access to nest cavities was achieved using both single-rope ascending (Perry 1978; Perry & Williams 1981), and tree bole-climbing techniques (Donahue & Wood 1995).

5.3.1. EGGS, CLUTCH SIZE, AND FERTILITY

Care was taken to avoid disturbance around the nest cavity during the incubation phase due to the potential risk of causing nest abandonment by the female. However, cavities were accessed once during incubation in order to determine clutch size and egg fertility. The number of eggs present in the cavity was recorded, and width and length of eggs were measured to the nearest 0.1 mm with dial callipers. Egg volume was calculated using Hoyt's (1979) equation: volume = 0.51 x egg length x (egg width)^2, and egg weight was measured to the nearest 1.0 g with 100 g Pesola scales.

Fertility of eggs was determined by an adapted candling technique in which the egg was placed in a thick black bag and illuminated from behind with a focused beam mini maglight flashlight. If the egg was fertile a darkened mass could be noted at one end, and veins running beneath the egg shell could also be distinguished. These were not noted in eggs that were infertile. Disposable gloves were used when handling eggs to avoid the risk of contaminating the permeable egg shell.

5.3.2. NESTING SUCCESS

Daily survival rates for Lilac-crowned Parrot nests during the incubation, early nestling, and late nestling phases were calculated using a personal computer version of programme Mayfield (Krebs 1989: pp 609-611). This calculates the Mayfield (1975) estimator of daily survival using the Maximum Likelihood Estimate modification of Bart & Robson (1982) to resolve potential biases in survival estimates which arise when nests are inspected at irregular intervals (Johnson 1979).

5.3.3. REPRODUCTIVE OUTPUT

Relative productivity and loss at different stages of the nesting cycle from egg-laying to fledging were calculated following Rockwell et al. (1987) and Gnam & Rockwell (1991). Reproductive output at the major stages of the nesting cycle was determined by total clutch laid (TCL), clutch size at hatching (CSH), brood size at hatching (BSH), and brood size at fledging (BSF). For successful nests, the probability of complete or partial success between stages of the nesting cycle was calculated for egg survival ($P_1 = CSH/TCL$); hatching success ($P_2 = BSH/CSH$), and fledging success ($P_3 = BSF/BSH$). For unsuccessful nests, the probability of complete failure between phases of the nesting cycle was determined as total clutch failure (TCF), and total brood failure (TBF). Hence, as outlined by Gnam & Rockwell (1991), the expected reproductive success of egg-laying females can be expressed as:

$$\text{Expected Reproductive Success} = TCL \times P_1 \times (1 - TCF) \times P_2 \times (1 - TBF) \times P_3$$

Differences between the years in reproductive output were evaluated by two-sample t-test analyses on the productivity measures of total clutch laid, clutch size at hatching, brood size at hatching, and brood size at fledging. All descriptive statistics were presented using means, value ranges, and standard deviations.

5.4. RESULTS

5.4.1. EGGS, CLUTCH SIZE, AND FERTILITY

Average clutch size was 2.5 ± 0.52 eggs (range 2 - 3 eggs, n = 14 nests), and fertility of eggs was 92.3% (24 of 26 eggs examined were fertile). Mean egg length was 36.78 ± 0.89 mm (range 35.8 - 38.7 mm, n = 26), and width was 28.37 ± 0.88 mm (range 27.5 - 30 mm, n = 26). Mean egg volume was 15,110 ± 1082.87 mm^3 (range 14,116 - 16,616 mm^3, n = 26), and the mean egg weight in the final week of incubation was 14.01 ± 2.08 g (range 9 - 16.3 g, n = 24)

5.4.2. NESTING SUCCESS

Finite Maximum Likelihood Estimates of nest survival rates at different phases of the nesting cycle are presented in Table 20. Finite survival of nests during the incubation phase was low at 0.74 probability of survival, although this was higher than the overall 0.54 probability of nest survival during the complete nestling phase of 60 days. However, separating the nestling stage between early and late nestling phases demonstrated that the period of lowest nest survival was the early nestling phase with an overall 0.68 probability of nest survival. Nests may be more vulnerable during the early nestling phase as nestlings are smaller, less developed, and the nest may be left unguarded when the female joins the male on foraging trips. In the late nestling phase, nestlings have approached asymptotic body mass, and therefore may be less vulnerable to predation. Overall, there was a low 40% nest success from egg-laying to fledging.

Table 20: Maximum Likelihood Estimates (MLE) of finite nest success during each phase of the nesting cycle.

Nesting phase	1996	1997	Combined years
Finite nest success during incubation (per 28 days)	0.90	0.59	0.74
Finite nest success during early nestling phase (per 30 days)	0.67	0.83	0.68
Finite nest success during late nestling phase (per 30 days)	0.68	0.81	0.74
Finite nest success during total nestling phase (per 60 days)	0.46	0.67	0.54
Overall: Finite nest success during entire nesting cycle (88 days)	0.44	0.36	0.40

5.4.3. REPRODUCTIVE OUTPUT

The fitness components and productivity of egg-laying females at each stage of the nesting cycle are shown in Table 21. Two-sample t-tests found no significant difference between the years in the productivity factors of total clutch laid, clutch size at hatching, brood size at hatching, or brood size at fledging. Expected reproductive success per egg-laying female was 1.01 fledglings in 1996, 0.97 fledglings in 1997, and 1.0 fledglings over both years combined. Hence, Lilac-crowned Parrot females may expect a return of 1.0 fledglings on their initial investment of 2.5 eggs, with major losses in reproductive output occurring in both the incubation (28% loss) and nestling (39% loss) phases.

The high value of P_2 (Hatching Success), at 0.89 over both years (Table 21), is related to fertility of the population, and indicates that egg loss due to hatching failure (11%

loss) was not a major factor limiting the reproductive output of Lilac-crowned Parrot females. The probability values of both P_1 (egg survival) and P_3 (nestling success) are 1.0 survival of eggs and nestlings in all successful nests (Table 21), as there was no instance of partial loss of reproductive output due to differential mortality of eggs or nestlings in the same nest. Indeed, loss of reproductive output resulted primarily from total clutch or brood failure due to factors which impacted the entire nest such as predation or abandonment.

Table 21: Fitness components and productivity of Lilac-crowned Parrot females at each stage of the reproductive cycle in 1996 and 1997. Values presented as means with standard deviations.

Fitness component	1996	1997	Overall
Total clutch laid (TCL)	2.5 ± 0.55	2.5 ± 0.54	2.5 ± 0.52
Egg survival (P_1)	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0
Probability of total clutch failure (TCF)	0.25	0.3	0.275
Clutch size at hatching (CSH)	2.5 ± 0.55	2.8 ± 0.45	2.64 ± 0.50
Hatching success (P_2)	0.94 ± 0.14	0.83 ± 0.24	0.89 ± 0.19
Brood size at hatching (BSH)	2.33 ± 0.52	2.4 ± 0.89	2.36 ± 0.67
Probability of total brood failure (TBF)	0.43	0.33	0.39
Nestling success (P_3)	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0
Brood size at fledging (BSF)	2.67 ± 0.58	2.67 ± 0.58	2.67 ± 0.52

5.4.4. CAUSES OF NEST FAILURE

During 1996 and 1997, there was complete failure of five nests during the incubation phase, and five nests during the nestling phase of the nesting cycle. Causes of complete nest failure during the incubation phase included two instances of predation, one of which may have involved a reptile predator such as the Indigo Snake (*Drymarchon corais*), Green Iguana (*Iguana iguana*), or the Beaded Lizard (*Heloderma horridum*) which are common at the study site. In the second instance, a body hair of the Virginia Opossum (*Didelphis virginiana*) was found stuck to the half-eaten egg shell. Another instance of total clutch failure resulted from nest abandonment by the incubating female, possibly due to observer disturbance. Finally, two nests failed during the incubation phase from unknown causes, though one was suspected predation.

Causes of nest failure during the nestling phase included two instances of mammal predation identified by claw scratch marks at the outer lip of the nest entrance. In one case, two 28 and 30 day old nestlings were predated from a nest in 1996, and in the second case three 2 - 3 week old nestlings were predated from a nest in 1997. Potential mammal predators which are frequently encountered in the area are the Virginia Opossum (*Didelphis virginiana*), Racoon (*Procyon lotor*), Jaguarundi (*Herpailurus yagouaroundi*), and the White-nosed Coati (*Nasua narica*) which has been noted to take medium-sized vertebrates such as parrots (Smythe 1970b).

The third instance of total brood failure occurred after an ant swarm was noted in the nest tree. On this occasion the ants did not enter the nest cavity, which was inspected immediately afterwards. The single nestling was still present and healthy in the nest at the next inspection four days after the observed ant swarm. However, two days after this second inspection, the 39 day old nestling had disappeared from the nest cavity. A few feather remains were found in the nest cavity and at the base of the tree. Three dead ants which had beak bite marks on the abdomen were also found within the nest cavity. Skutch (1976) also reports that fire ants may be potential predators on nestlings. In the fourth instance of brood failure, two 49 and 51 day old nestlings were noted as healthy at the last nest inspection. However, when the nest was again inspected the following day, the second nestling was found dead within the nest cavity with blood around the nasal area, while the first nestling was absent from the nest cavity and was counted as a mortality. The exact cause of this nest failure is unknown, but is considered a suspected predation. The final instance of total brood failure was due to human poaching of the two 40 and 42 day old nestlings in 1996.

5.4.5. COMPARISON WITH OTHER AMAZON PARROTS

Reproductive success of the Lilac-crowned Parrot (*Amazona finschi*) is compared with that for other *Amazona* parrot species in Table 22. The Lilac-crowned Parrot had the lowest mean clutch size (2.5 eggs) of all *Amazona* species, and a particularly low clutch size and range (2 - 3 eggs) for body size. The closely related Red-crowned Parrot (*A. viridigenalis*) in north-eastern Mexico has a similar body size, but a higher mean clutch size (3.4 eggs) and range (2 - 5 eggs) than the Lilac-crowned Parrot (Table 22). The Lilac-crowned Parrot also had one of the lowest 40% nest success (42% nest success excluding human poaching) of any Amazon parrot species. This was principally due to predation of the entire nest contents, which was the main factor reducing the overall apparant success to 0.94 fledglings per nesting pair.

Table 22: Comparison of reproductive output among *Amazona* species.

Amazona species	Body mass (g)	Mean clutch size (range)	Mean brood size per successful nest	No. of young per egg-laying pair	% egg-laying pairs successful	Source
Island species:						
A. leucocephala caymanensis	295	3.2 (2 - 5)	2.57	1.8	70	Bradley 1986, in Gnam & Rockwell 1991
A. ventralis	228	2.8 (1 - 4)	2.14	2.5	82	Snyder et al. 1987
A. vittata	265	3.0 (2 - 4)	2.41	1.8	69*	Snyder et al. 1987
A. barbadensis	310	3.4 (2 - 5)	1.48	0.89	60	Rojas 1991, in Enkerlin-Hoeflich 1995
A. l. bahamensis	281	3.6 (2 - 6)	1.88	0.8	42	Gnam & Rockwell 1991
Mainland species:						
A. autumnalis	385	2.6 (1 - 4)	2.25	0.94	42	Enkerlin-Hoeflich 1995
A. oratrix	437	2.7 (2 - 3)	1.67	0.82	50	Enkerlin-Hoeflich 1995
A. viridigenalis	316	3.4 (2 - 5)	2.22	1.43	57	Enkerlin-Hoeflich 1995
A. finschi	311	2.5 (2 - 3)	2.36	0.94	40	This study

* Nest success rate obtained under intensive management, real value may be 11 - 26% (N.F.R. Snyder pers. comm.).

Adapted from Gnam & Rockwell (1991)

5.5. DISCUSSION

The impact of nest predation on parrot reproduction is reflected in the finite nest success rates at each stage of the nesting cycle. As with other parrot species (Snyder et al. 1987; Gnam 1991; Waltman & Beissinger 1991; Wilson et al. 1995), Lilac-crowned Parrot females were absent from the nest for less than an hour per day during incubation, and continued to brood nestlings for the first three weeks after hatching (Chapter 4). However, in contrast with the Bahama Parrot (Gnam & Rockwell 1991) which had low incubation loss (17%) and high hatching loss (49%), the Lilac-crowned Parrot had low hatching loss (11%) and high incubation (28%) and nestling loss (39%). The 40% nest success for the Lilac-crowned Parrot was also well below that predicted for cavity nesting species (Lack 1954; Skutch 1976; Martin & Li 1992; Johnson & Kermott 1994). In addition, the lower 0.58 probability of nest survival during the nestling phase compared to the 0.74 probability of nest survival during the incubation phase, may be due to the increased probability of conspicuous foraging adults attracting predators to the nest (Alerstam & Hogstedt 1981).

The high failure rate of Lilac-crowned Parrot nests may be due to a high risk of predation at the study site. Predation of bird nests is greater in small forest patches, and within 200 - 500 m of the forest edge than the forest interior (Gates & Gysel 1978; Ambuel & Temple 1983; Loiselle & Hoppes 1983; Wilcove 1985; Andren et al. 1985; Angelstam 1986; Wilcove et al. 1986; Andren & Angelstam 1988; Andren 1992; Fenske-Crawford & Niemi 1997; Keyser et al. 1998). Lilac-crowned Parrot nest sites were almost exclusively located in semi-deciduous forest, most of which occurs in narrow bands less than 200 m wide along the larger valleys at the study site. During the dry season water is absent from the hills, and environmental conditions can become harsh in the deciduous forest. Densities of small mammals are noted to decline in deciduous forest during the dry season (A. Miranda pers. comm.), while medium-sized mammals such as the Virginia Opossum and the White-nosed Coati preferentially forage in semi-deciduous forest in the valleys rather than in deciduous forest during the dry season (Valenzuela-Galvan 1998). A general decrease in food resource availability for most animal species towards the end of the dry season may also result in a temporal increase in predation risks at this time (Sieving 1992).

Hence, high predation rates may be due to edge effects of predators moving into small patches of semi-deciduous forest from the adjacent deciduous forest during the dry season. This may be compounded by the high deforestation rates for semi-deciduous forest (Miranda 1998), resulting in increasing fragmentation of larger forest patches. Increased predation rates due to an influx of predators to small patches of semi-deciduous forest during the dry season may also limit the reproductive success of other bird communities in this habitat. Despite the long history of research at the study site, very little is known of the dynamics and ecology of vertebrate communities in the deciduous forest. Potentially high predation rates in semi-deciduous forest during the dry season is an aspect which requires further research to evaluate the dynamics of bird communities in deciduous forest, and the potential impacts of habitat fragmentation.

Hence, predation may be the main factor limiting reproduction of the Lilac-crowned Parrot population at the study site, resulting in low nest success and a reproductive output of 1.0 fledglings per egg-laying pair. Predation was also the major factor limiting output of the ground-nesting Bahama Parrot (Gnam & Rockwell 1991), and was a significant cause of nest loss for three Amazon parrot species in north-eastern Mexico (Enkerlin-Hoeflich 1995). Furthermore, the low 40 - 42% nest success for the Lilac-crowned Parrot in the Chamela-Cuixmala reserve does not include human poaching of nests which occurs at greater frequency outside of the protected area (pers. obs.). Hence, nest success and fledgling output is likely to be lower still for parrot populations in the vicinity of local communities.

The low nest success reported for the Lilac-crowned Parrot contrasts with the high success rates of 60 - 70% reported for parrot species in relatively intact forest habitats (Saunders 1982; Munn 1992). Indeed, low reproductive success rates have been reported for most parrot species breeding in disturbed habitats (Saunders 1982, 1986; Enkerlin-Hoeflich 1995). Conversion of forests for agriculture and ranching has proceeded at a rapid rate in Mexico (Masera et al. 1992, 1996; Dirzo & Garcia 1992; Maass 1995), and fragmentation of natural forests is an increasing feature of the landscape. Parrots are adaptable species and are often able to persist in areas modified by man giving an impression of abundant and stable populations. However, increased fragmentation of forest habitats may impact parrot reproduction through food resource limitation (Saunders 1982, 1986), or increased predation pressures (Gnam & Rockwell 1991; Enkerlin-Hoeflich 1995). Studies on the breeding biology and reproductive success of parrot populations in disturbed habitats (Saunders 1982, 1986, 1990, 1991; Enkerlin-Hoeflich 1995), demonstrate that such populations may in fact be reproducing at sub-optimal levels and are vulnerable to decline. Wild populations of the Lilac-crowned Parrot may have declined in recent years due to the dual pressures of capture for trade and destruction of semi-deciduous forest, and do not demonstrate a reproductive rate which is able to support high levels of pressure for commercial trade.

CHAPTER 6

NESTLING GROWTH AND DEVELOPMENT

6.1. ABSTRACT

Studies were conducted on Lilac-crowned Parrot nests in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve in order to describe the pattern of nestling growth, and provide growth rate parameters for a Neotropical Amazon parrot. The early nestling phase was characterised by rapid weight gain and an increase in body size, with nestlings reaching asymptotic body mass half-way through the nestling phase. Development during the second half of the nestling phase consisted principally of feather growth. Growth rates for psittacine species followed the inverse relation with body mass observed for Neotropical land birds, with larger parrot species exhibiting slower growth rates. There was also a marked size hierarchy among Lilac-crowned Parrot siblings, particularly with respect to third-hatched nestlings, which were smaller in size and exhibited slower growth rates than first- or second-hatched nestlings. The differential growth rates for third-hatched nestlings may be due to the greater interval in hatching between second and third eggs, as compared to that between first and second eggs. However, this size hierarchy and differential growth rate did not result in mortality of later-hatched third nestlings. The length of the nestling period, along with food resource abundance, and parental effort, may allow some flexibility in growth, enabling third-hatched nestlings to acquire asymptotic sizes prior to fledging. Finally, there was significant variation between years in nestling sizes and growth rates. In general, nestlings were significantly smaller at hatching, and took longer to acquire asymptotic size in 1996 than in 1997. The increased size and growth rates of nestlings in 1997 may have been due to a greater abundance of food resources, and demonstrates the potential influence of environmental variability on parrot reproduction. It is predicted that third-hatched Lilac-crowned Parrot nestlings may be vulnerable to mortality in years of extreme drought and poor food resource availability which may occur in this habitat.

6.2. INTRODUCTION

Lack (1968) suggested that nestling growth rate is a compromise between rapid growth to reduce predation and slower growth to reduce energy requirements of the young. Open-nesting birds have faster growth rates than hole-nesting species which may reflect a greater need to escape predation pressures (Ricklefs 1968a). However, Neotropical land passarines grow 23% slower than temperate passerines (Ricklefs 1976), even though predation pressures are greater for tropical birds than temperate birds (Ricklefs 1969; Skutch 1976). In addition, precocial birds which may experience greater predation risks also develop at a slower rate than altricial birds (Ricklefs 1979).

In fact, the young of altricial birds develop twice as fast as most altricial mammals (Case 1978). Nestlings of most birds which exhibit rapid growth rates are fed frequently and by both parents, while species exhibiting slow rates of growth tend to be self feeding or fed at infrequent intervals (Case 1978). Reduced growth rates of tropical birds may reflect food limitation via a reduced rate of food delivery by parents (Martin 1987). Hence, growth rate may be adapted to features of the environment, in particular the feeding requirements of the young and availability of food to the parents (Case 1978; Martin 1987).

Nestlings of single broods also develop at a slower rate than nestlings in large broods, and it is suggested that the faster growth of nestlings in larger broods may reflect competition between siblings (Werschkul & Jackson 1979). However, the fact that nestling growth rates are not directly related to the intensity of competition in broods of more than one nestling does not support this hypothesis (Ricklefs 1982; Bortolotti 1986). Instead, slower growth of single brood young may be related to food limitation, and reflect parental fitness, as food delivery times are longer and more variable for single broods (Ricklefs 1982; Bortolotti 1986)

Asynchronous hatching is common in bird species, and frequently produces a growth heirarchy among the young, with later hatched nestlings being smaller than earlier hatched nestlings (Hussell 1972, Bryant 1978a; Zach 1982; Bollinger 1994). Asynchronous hatching may be advantageous in reducing peak feeding loads for adults as energy demands of the young are spread out (Hussell 1972), and there is potential for elimination of the youngest nestling during periods of food limitation (Lack 1954). However, asynchronous hatching does not always lead to brood reduction as later-hatched young may persist in the nest with inadequate feeding, and survive to fledging with no negative effects on growth (Ricklefs 1976; Richter 1984). Hence, position in the brood may only affect survival in particularly poor years (Richter 1984).

In fact, many of the potentially adaptive features of asynchronous hatching may be determined as a result of conditions during the egg-laying and incubation period. Early onset of incubation may arise due to the benefits this offers for the eggs, leading to asynchronous hatching (Clark & Wilson 1981; Bollinger et al. 1990; Stoleson & Beissinger 1997a,b). Food limitation during the laying period may also increase the hatching spread, leading to a greater size hierarchy between nestlings (Bryant 1978a, b; Bollinger 1994).

The influence of food availability on growth has been most easily demonstrated for aerial insectivores, as food supply is highly variable due to weather. Onset of laying, clutch size, and higher nestling growth rates correspond with high insect abundance (Bryant 1975; Quinney et al. 1986; Blancher & Robertson 1987), while natural declines in caterpillar food supply resulted in reduced nestling growth rates and survival for warblers (Rodenhouse & Holmes 1992). Variations in food abundance may have a greater impact on breeding where food resources are not already super-abundant in the environment (Blancher & Robertson 1987).

Young birds may also exhibit flexible growth rates, enabling them to slow development in response to temporary food stress, later recovering growth as food supplies increase (Emlen et al. 1991; Negro et al. 1994). This retardation in growth is greatest in seasons of low food availability (Emlen et al. 1991), and long-term reduction in the food supply leads to significantly slower growth rates, though overall asymptotic weight may remain unchanged (Lacombe et al. 1994).

Breeding birds may also compensate for reductions in the food supply by increasing parental effort to maintain energy requirements of the young (Drent & Daan 1980). Experimental reduction in food supply by Adams et al. (1994) produced no significant effect on nestling growth of sparrows, but resulted in increased parental effort with breeding pairs in experimental plots foraging significantly further from the nest than birds in control areas. In studies of the Pallid Swift, chick growth was found to be independent of daily food availability, while parents of artificially enlarged broods lost more mass than controls indicating increased parental effort to maintain nestling growth (Cucco & Malacaren 1995, 1996). A converse increase in food supply also influences parental effort through reduced foraging flights and shorter times between nestling feedings (Blancher & Robertson 1987). Supplemental feeding of nestling gulls resulted in decreased parental effort, with breeding pairs spending more time in the nest territory, and females conducting shorter foraging trips (Bukacinski et al. 1998). Tveraa et al. (1998) also demonstrated that Antartic petrel parents adjust the amount of food delivered according to the needs of the young, however the ability of parents to respond to the chick's needs was dependent on their own body condition.

Studies on insectivorous bird species have indicated that food resource abundance may influence both nestling growth and parental effort. Nestling parrots hatch asynchronously, are highly altricial, and exhibit slow growth, all of which may increase the potential for growth processes to respond to environmental conditions. Size hierarchies and differential growth rates relating to hatching order have been noted for some psittacine species (Rinke 1989; Smith 1991; Stoleson & Beissinger 1997b). Rinke (1989) found that first hatched young of the Red Shining Parrot (*Prosopeia tabuensis*) were significantly larger in size than second hatched young. In Australia, the youngest nestlings in broods of the Long-billed Corella (*Cacatua pastinator pastinator*) frequently died from starvation within four weeks of hatching (Smith & Saunders 1986; Smith 1991).

However, most studies on nestling growth rates for psittacines have been conducted on Australian parrots (Saunders 1982, 1986; Rowley 1990; Rowley & Chapman 1991; Smith 1991), and very little data exists on nestling growth rates for Neotropical parrot species. Later hatched young of the Green-rumped Parrotlet (*Forpus passerinus*) in Venezuela grew at significantly slower rates than earlier hatched young, and this effect of hatching order was greater in larger broods (Stoleson & Beissinger 1997b). First hatched nestlings of the Monk Parakeet (*Myiopsitta monachus catita*) in Argentina also grew at a faster rate than later hatched nestlings, though this was not found to be significant (Navarro & Bucher 1990).

Little data are available on nestling growth rates for Amazon parrot species, though Enkerlin-Hoeflich (1995) found that the Red-crowned Parrot (*Amazona viridigenalis*) in north-eastern Mexico exhibited rapid weight gain during the first month of the nestling phase, attaining asymptotic size half-way through the nestling phase. No data on growth rates are available for island *Amazona* species, however, incomplete observations on Puerto Rican Parrot nestlings by Snyder et al. (1987) appear to indicate a rapid increase in body mass during the first four weeks of the nestling phase.

Navarro & Bucher (1990) found that growth rates of Monk Parakeet nestlings varied significantly between years, while asymptotic values remained relatively constant, suggesting that growth rate responds to environmental factors. However, no studies of parrots have related variations in growth rate to food resource availability or other environmental conditions. Indeed, most studies relating nestling growth to food supply have been conducted on insectivorous passerine species (Bryant 1975, 1978b; Quinney et al. 1986; Blancher & Robertson 1987; Emlen et al. 1991; Rodenhouse & Holmes 1992; Adams et al. 1994; Cucco & Malacaren 1995, 1996), birds of prey (Lacombe et al. 1994; Negro et al. 1994), or sea birds (Bukacinski et al. 1998; Tveraa et al. 1998). In general, many frugivorous, nectivorous, and granivorous passerine species also consume invertebrates in the diet during the breeding season (Poulin et al. 1992). However, the larger size of parrots may mean they are less likely to rely on an insect diet during reproduction, and may be more susceptible to fluctuations in the availability of fruit or seed resources.

The potential influence of environmental factors on reproduction and nestling growth may be of importance in the conservation of threatened populations of many parrot species. This was demonstrated for cockatoos in the wheatbelt of western Australia where depressed nestling growth rates indicated that breeding birds were experiencing food limitation as a result of extensive loss of native vegetation (Saunders 1982, 1986, 1990, 1991). Hence, data on nestling development are necessary to evaluate the normal pattern of growth, and enable assessment of environmental quality and the viability of wild populations (Bryant 1978b; Saunders 1982, 1986).

6.3. METHODS

The growth and development of Lilac-crowned Parrot nestlings was studied in the tropical dry deciduous forest of the Chamela-Cuixmala Biosphere Reserve (19°22'N 104°56'W to 19°35'N 105°03'W), in the state of Jalisco on the Pacific Coast of Mexico. Nest studies were carried out from January to June in 1996 and 1997. Access to nest cavities was achieved using single-rope ascending techniques with a 25 m caving rope, climbing harness, and ascenders as outlined by Perry (1978), and Perry & Williams (1981). In addition, a tree bole-climbing technique was employed using webbing slings and an etrier as described by Donahue & Wood (1995).

Nestling growth and development

Following hatching of the eggs, nest inspections were carried out 2 - 3 times a week, during the mid-day lull in parental activity. At each inspection, growth of Lilac-crowned Parrot nestlings was evaluated using the variables of length of left wing, and culmen length which were measured to the nearest 0.1 mm with dial callipers. Body mass was also determined by weighing nestlings with a 100 g, 300 g, or 500 g Pesola balance depending on chick size.

Body mass of nestlings is closely related to food intake, and when matched with age, gives a good indication of the condition of nestlings and their chances of survival (Saunders 1986). Growth of the wing and bill are less affected by variations in food intake throughout the nestling phase. Hence, wing length is the most frequently used variable for ageing nestlings (Saunders 1982, 1986), while bill dimensions provide useful cross-checks to evaluate nestling growth (Rinke 1989; Rowley & Chapman 1991).

Measurements were taken of 14 nestlings in 1996 and 9 nestlings in 1997. All growth variables were measured by the same method and researcher in both years, with the exception that in 1996 length of open left wing was measured, while in 1997 it was found more convenient and reliable to measure length of folded left wing. Ectoparasite load of nestlings was evaluated by counting bot-fly larvae, and a visual description was given of plumage development. Each nestling was marked with indelible ink on one foot to identify hatching order. All measurements were conducted at the nest entrance to minimise handling time and potential stress for the nestlings. Disposable gloves and a face mask were used when handling nestlings to avoid potential disease transmission between nestlings and researcher.

Data analysis

Many nestling birds exhibit a pattern of body mass recession prior to fledging due to the loss of water from maturing feathers (Ricklefs 1968b). Complex growth models such as the Richards equation are sensitive to such fluctuations, and small changes in data which affect parameter estimates (Zach 1988). Growth models which have only three parameters require fewer data and are less sensitive to fluctuations. Zach (1988) therefore recommends the use of these simpler growth models, as well as statistical analysis of observed measures to evaluate growth.

Hence, in this study the pattern of nestling growth was described using Ricklefs (1967) logistic equation which has the form:

$$G_t = A / (1 + \exp(-k(\text{age} - t_i)))$$

Where, A = the asymptote (normally the adult value), k = the rate of growth, and t_i = the inflection point of the growth curve (i.e., time to attain 50% of the asymptote). The time interval for growth from 10% to 90% of the asymptote was also used to describe growth and is defined as: $t_{10\text{-}90} = 4.4 / k$ (Ricklefs 1976). It should be noted however, that the growth period parameter of $t_{10\text{-}90}$ only has theoretical value when applied to culmen length, as the culmen of nestlings at hatching is 25% of the asymptote, and is close to the inflection point of the growth curve. This is not the case for either body mass or wing length which are only 5 - 6% of the asymptote at hatching. Growth parameters for the logistic curve were fitted to nestling weights and wing and culmen lengths using the SPSS nonlinear regression procedure (Norusis/SPSS 1994).

Between year differences in nestling size and growth were also analysed by two-sample t-tests on observed values for the growth variables: culmen length of nestlings at 6 days, 40 days, and 60 days after hatching; nestling mass 6 days after hatching; maximum nestling mass; age to attain maximum body mass; mass loss prior to fledging (difference between maximum weight and weight at fledging); body mass at fledging; and nestling age at fledging. As wing length had been measured by slightly different methods in 1996 and 1997 it was not possible to conduct between year comparisons using this growth variable. Finally, general descriptive statistics were presented with means, value ranges, and standard deviations.

6.4. RESULTS

6.4.1. THE PATTERN OF NESTLING GROWTH AND DEVELOPMENT

Lilac-crowned Parrot eggs hatched asynchronously after approximately 28 days of incubation. The mean hatching interval between first and second eggs was 1.78 ± 0.44 days (range 1 - 2 days, n = 9), and between second and third eggs was 4 ± 1.41 days (range 2 - 5 days, n = 4). Average brood size was 2.4 ± 0.67 nestlings per successful nest (range 1 - 3 nestlings, n = 11 nests). Nestlings weighed between 11 - 19 g on hatching, and spent an average of 64.4 ± 2.44 days (range 60 - 68 days, n = 14) in the nest. Nestlings hatched with eye-lids fused together, and only a light covering of feather down. The eye-lids began to unfuse at 18 ± 2.3 days of age (range 15 - 23, n = 15), and were not fully open until 22.5 ± 2.28 days (range 18 - 26 days, n = 15). Nestlings underwent a rapid increase in size and body mass during the first four weeks of the nestling phase (Figs 23 & 24) and completed 90% of their growth in body mass at a mean 32.2 ± 3.94 days after hatching (range 25 - 38 days, n = 15). On reaching an average maximum body mass of 322.38 ± 12.43 g (range 297 - 349 g, n = 16), increase in body mass leveled off, and weight recession occurred 10 - 14 days prior to fledging. Mean body mass of nestlings at fledging was 286.14 ± 24.14 g (range 254 - 325 g, n = 14), which was 11.24% less than the mean maximum body mass.

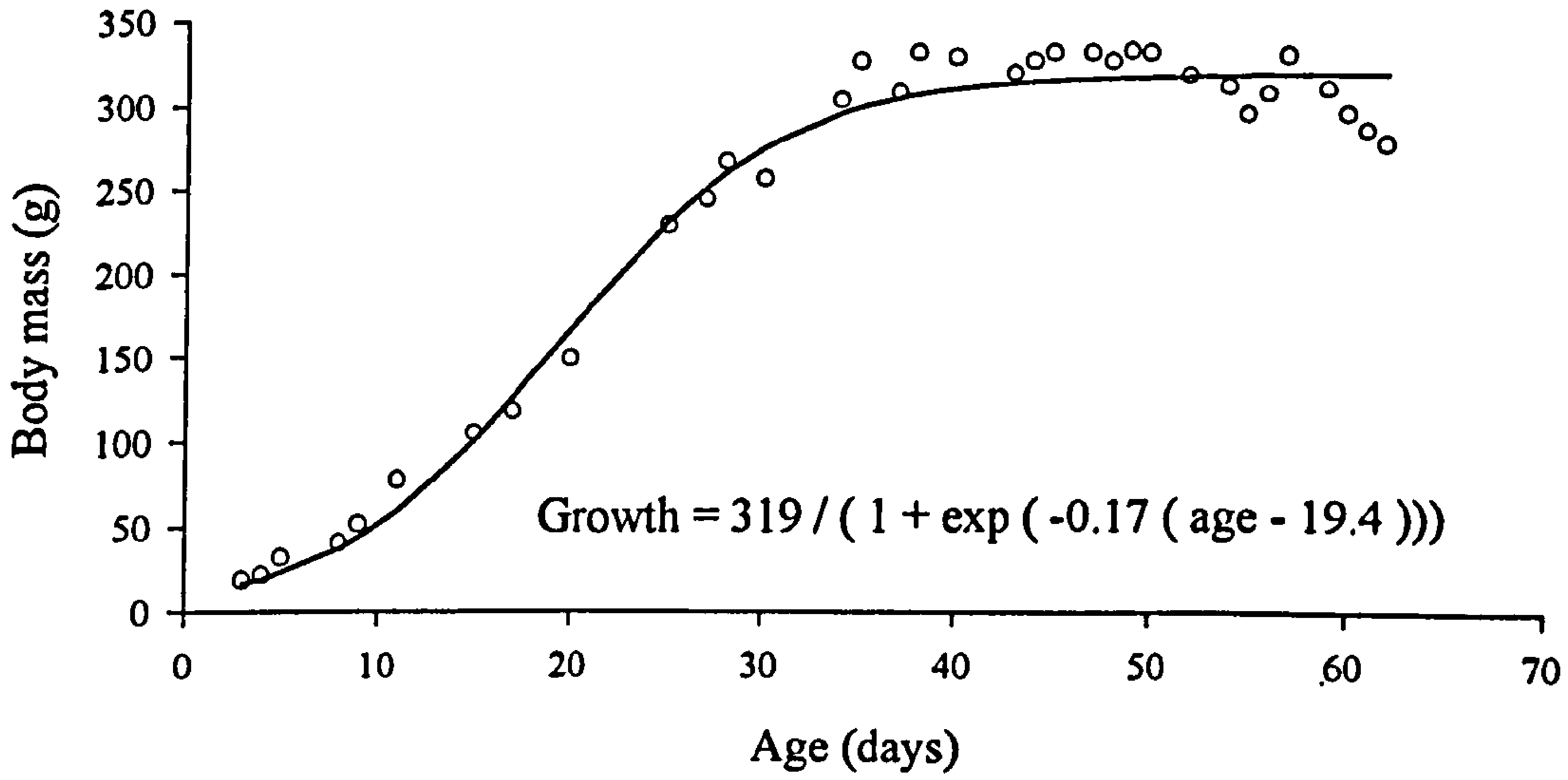
Primary wing feathers erupted by 26.06 ± 1.56 days of age (range 23 - 29 days, n = 17), and development during the second month of the nestling phase consisted principally of feather growth. Increase in wing length was slow during the first 2 - 3 weeks after hatching, but increased linearly once the feather pins began to emerge (Figs 25 & 26). In contrast increase in culmen length was steady during the first 6 - 7 weeks after hatching, but began to level out towards the end of the nestling phase. The most frequent ectoparasites found on parrot nestlings were red mites and bot fly larvae, though the average maximum bot fly load was low with 3.09 ± 4.2 bot fly larvae per nestling (range 0 - 13 larvae, n = 23).

6.4.2. VARIATION BY HATCHING ORDER

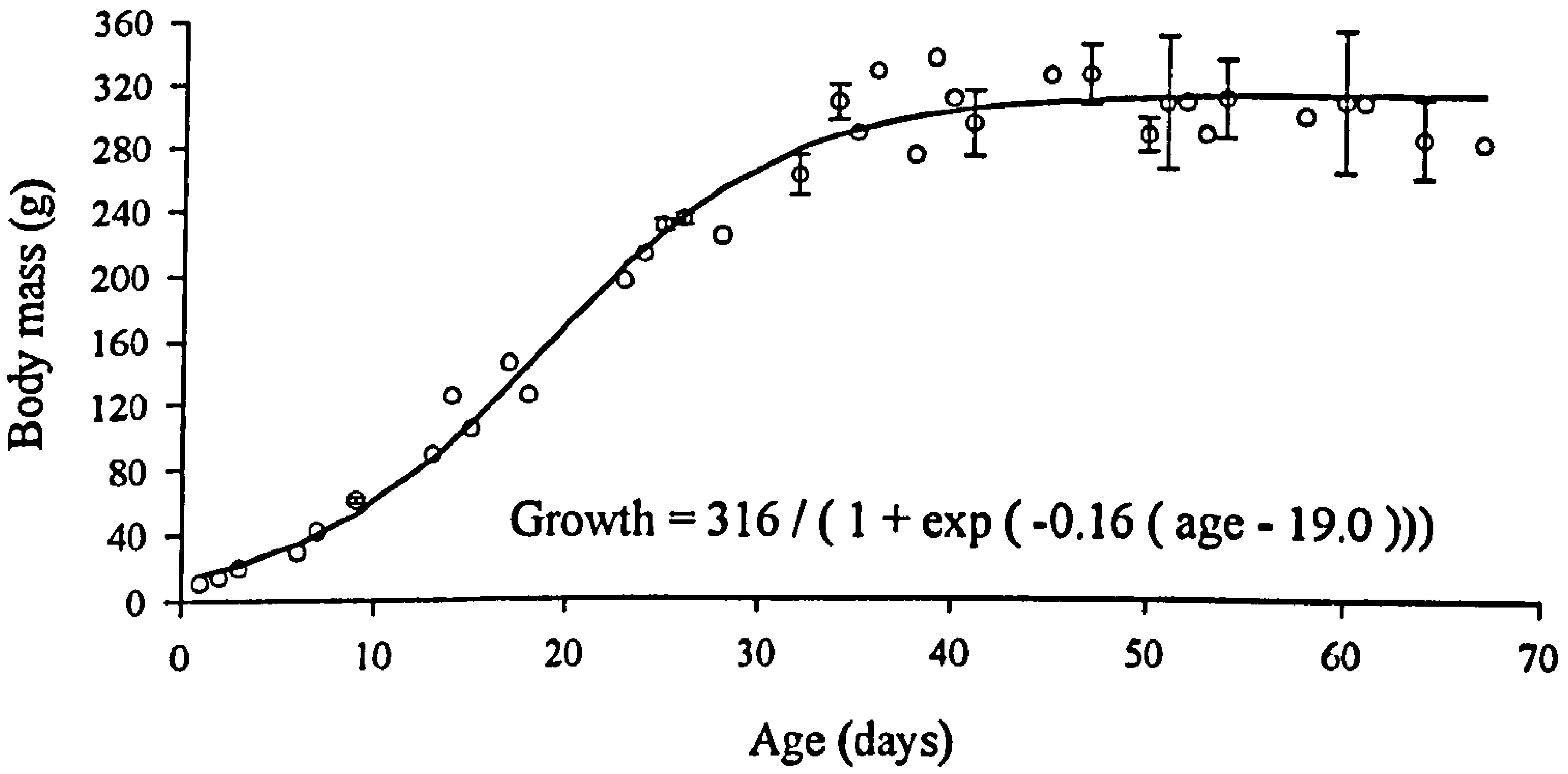
Ricklefs (1967) growth parameters for nestlings in 1996 and 1997 were calculated for body mass (Table 23), wing length (Table 24), and culmen length (Table 25). For all of the growth variables measured there was little difference in growth between first and second hatched nestlings. However, third-hatched nestlings demonstrated a slower growth rate (*k*) and a longer growth period (t_i and $t_{10\text{-}90}$) for both body mass (Table 23, Figs 23 & 24) and wing length (Table 24, Figs 25 & 26). In both 1996 and 1997, third-hatched nestlings were behind older siblings in body mass during the first four weeks of growth, but were able to attain the mass of older siblings in the latter month prior to fledging (Figs 23 & 24). However, while third-hatched nestlings may catch-up in body mass with older siblings, Figures 25 and 26 illustrate that in both 1996 and 1997, third-hatched nestlings were consistently smaller than first- and second-hatched nestlings in wing length, and remained so throughout the period in the nest.

Figure 23: Body mass of Lilac-crowned Parrot nestlings by hatching order (1996). Error bars represent standard deviations of mean weight.

(a) First-hatched, $n = 6$ nestlings.



(b) Second-hatched, $n = 6$ nestlings.



(c) Third-hatched, $n = 2$ nestlings.

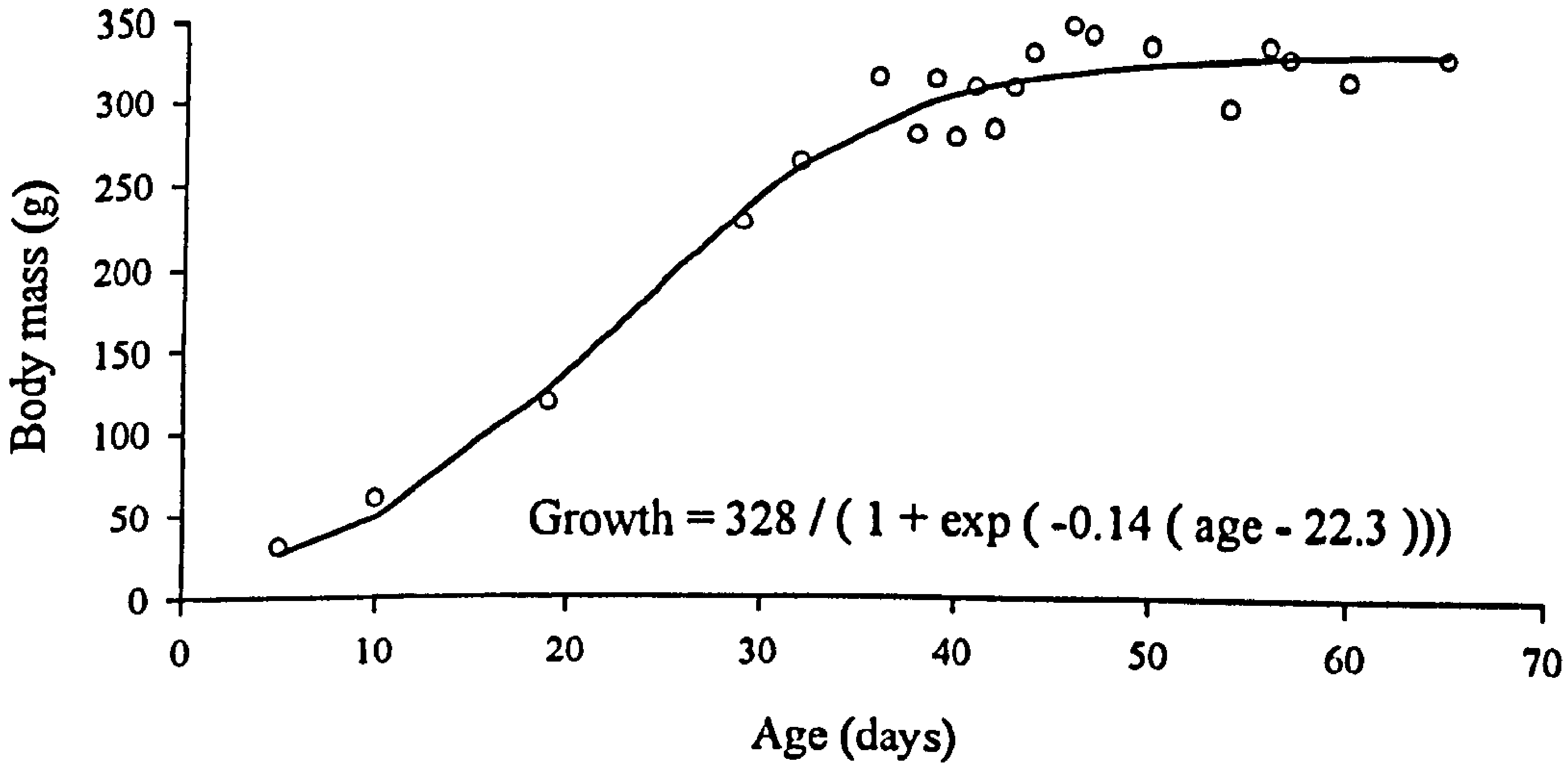
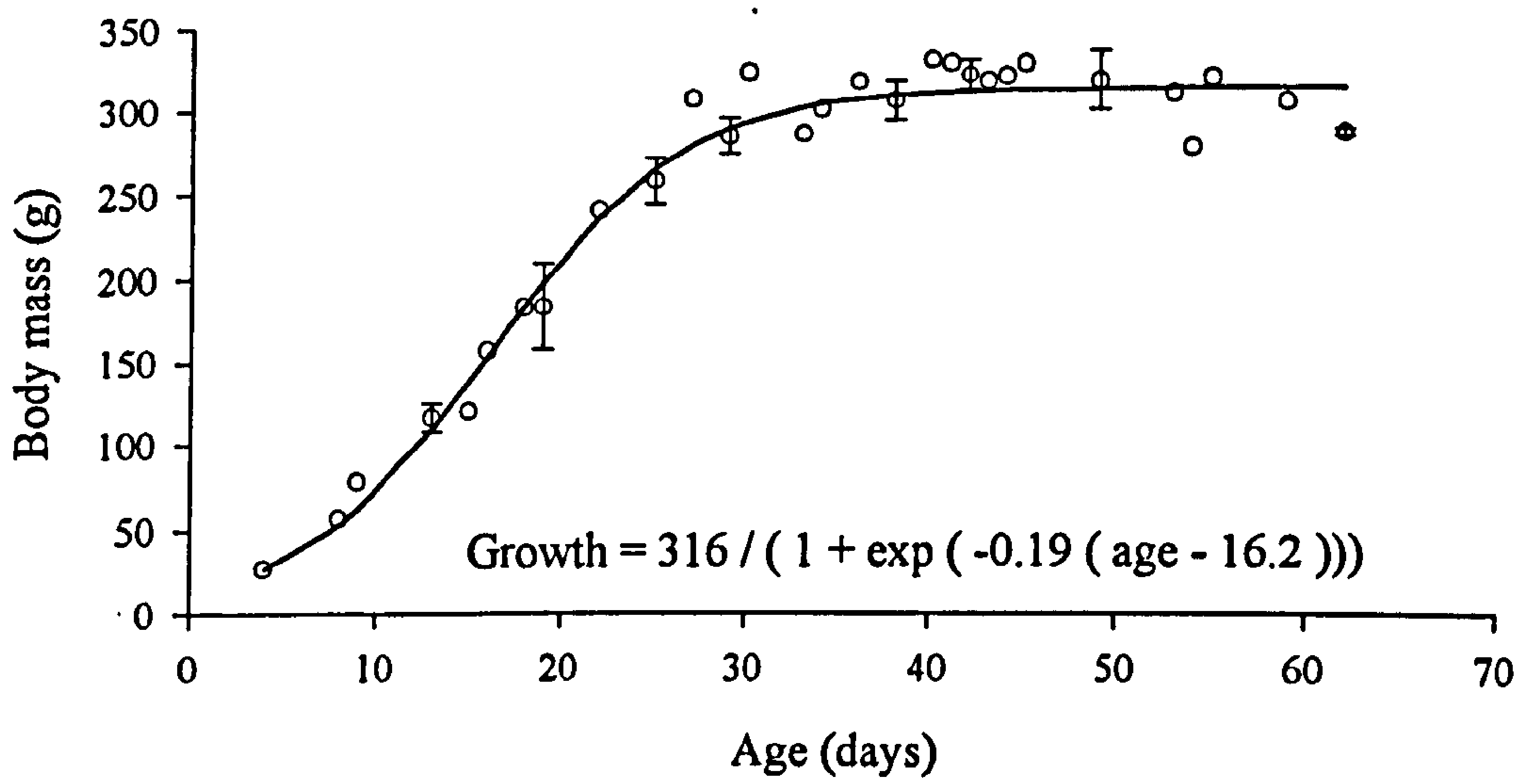
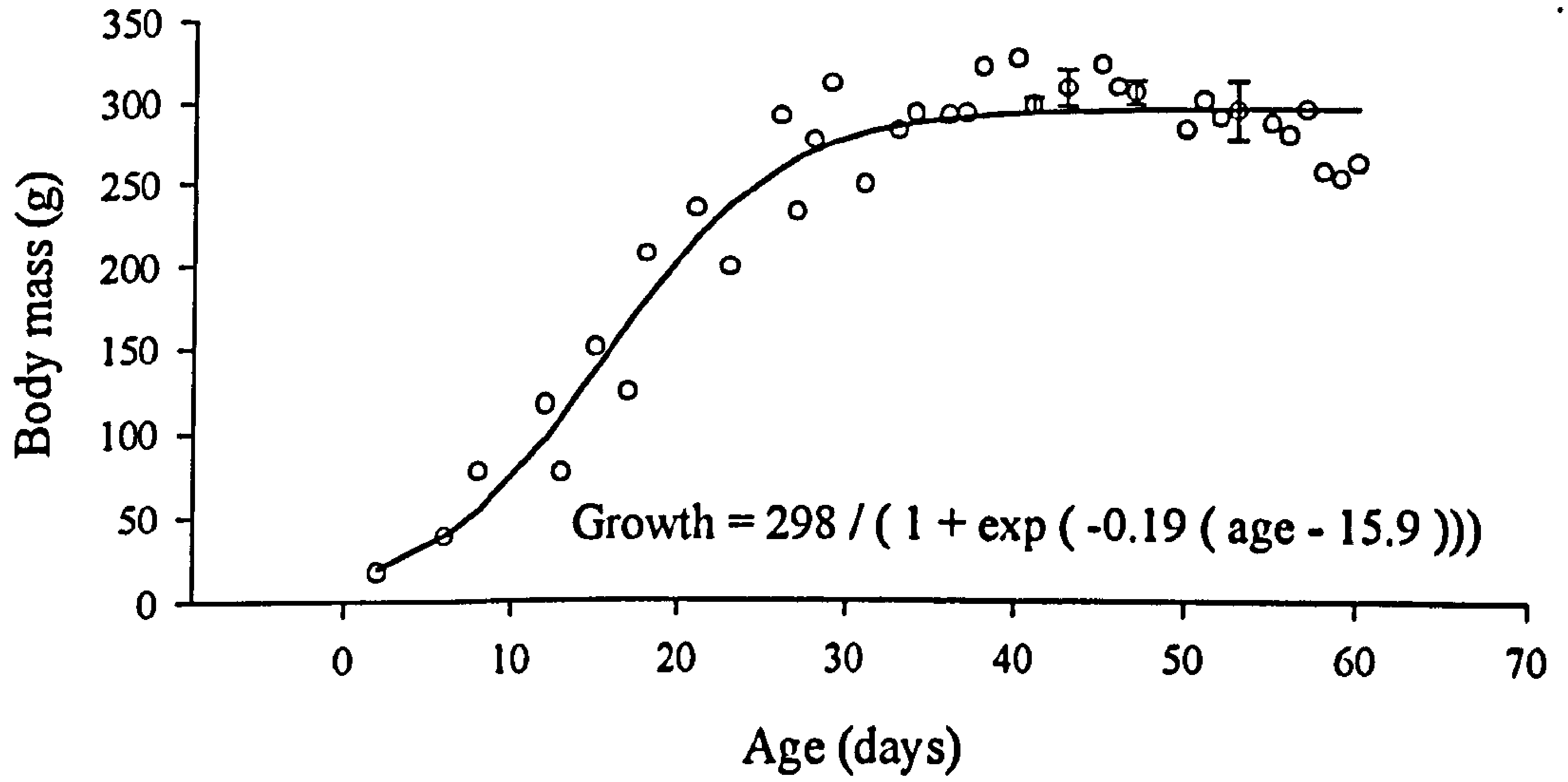


Figure 24: Body mass of Lilac-crowned Parrot nestlings by hatching order (1997). Error bars represent standard deviations of mean weight.

(a) First-hatched, *n* = 4 nestlings.



(b) Second-hatched, *n* = 3 nestlings.



(c) Third-hatched, *n* = 2 nestlings.

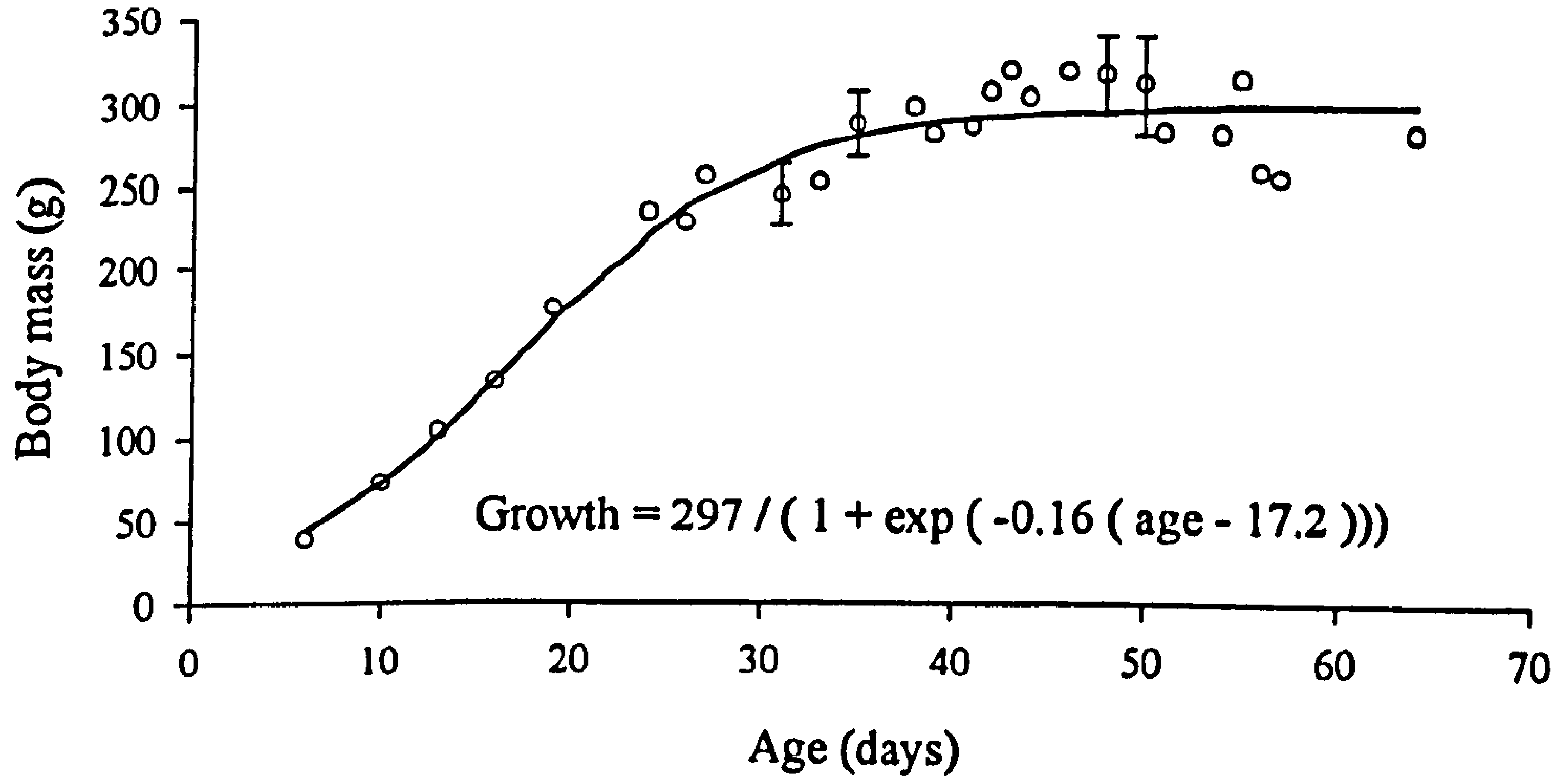
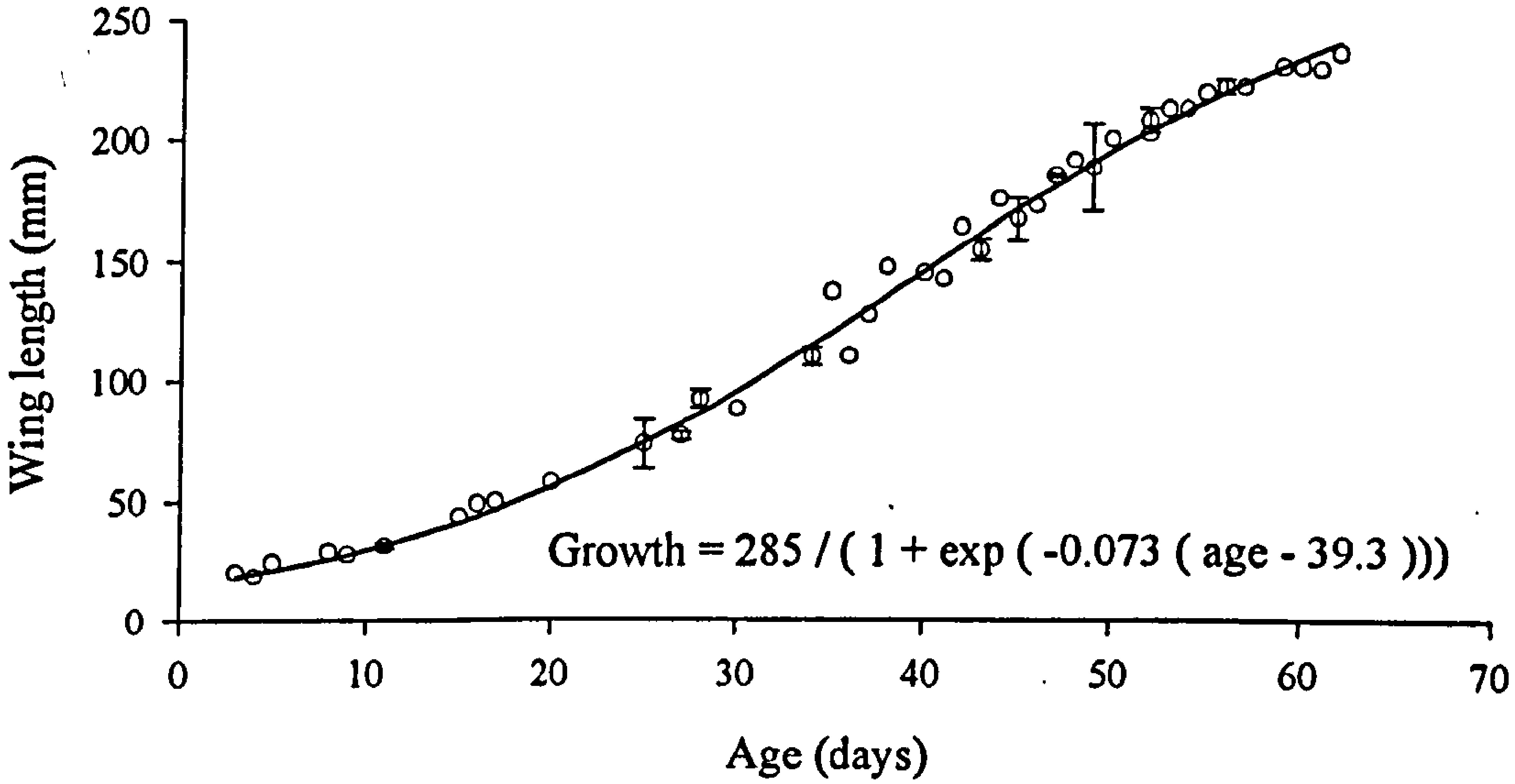
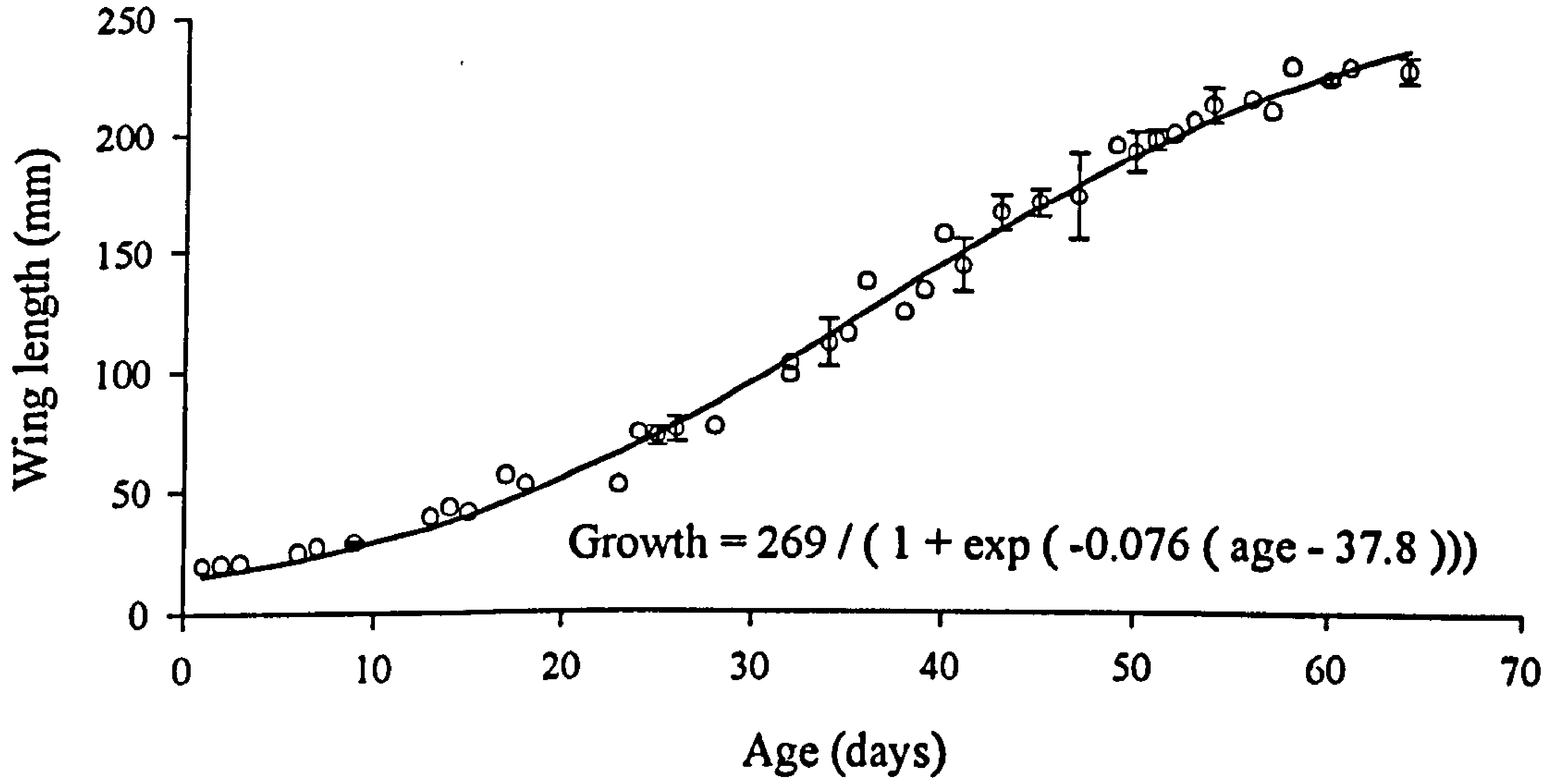


Figure 25: Length of open left wing of Lilac-crowned Parrot nestlings in 1996. Error bars represent standard deviations of mean length.

(a) First-hatched, $n = 6$ nestlings.



(b) Second-hatched, $n = 6$ nestlings.



(c) Third-hatched, $n = 2$ nestlings.

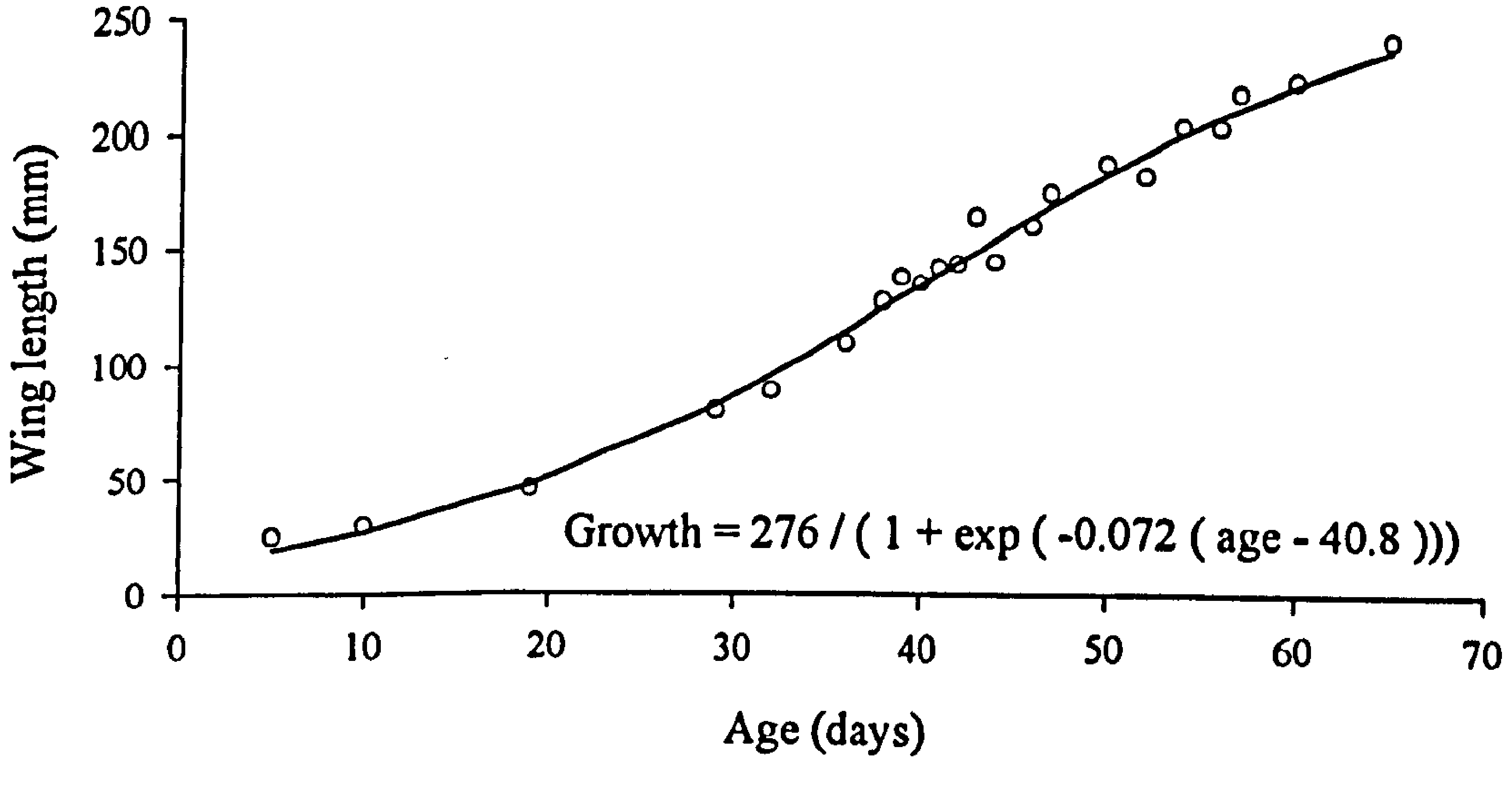
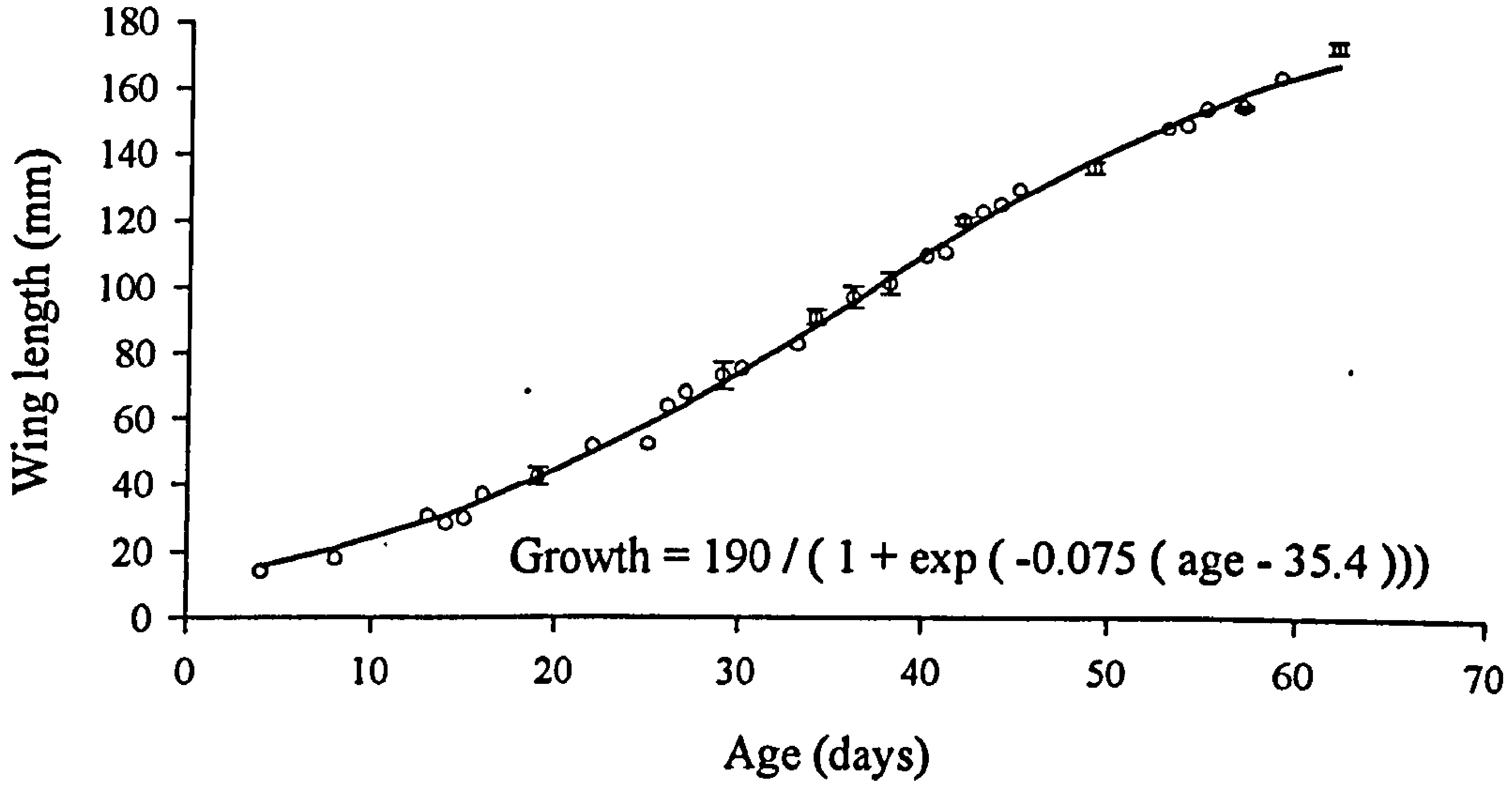
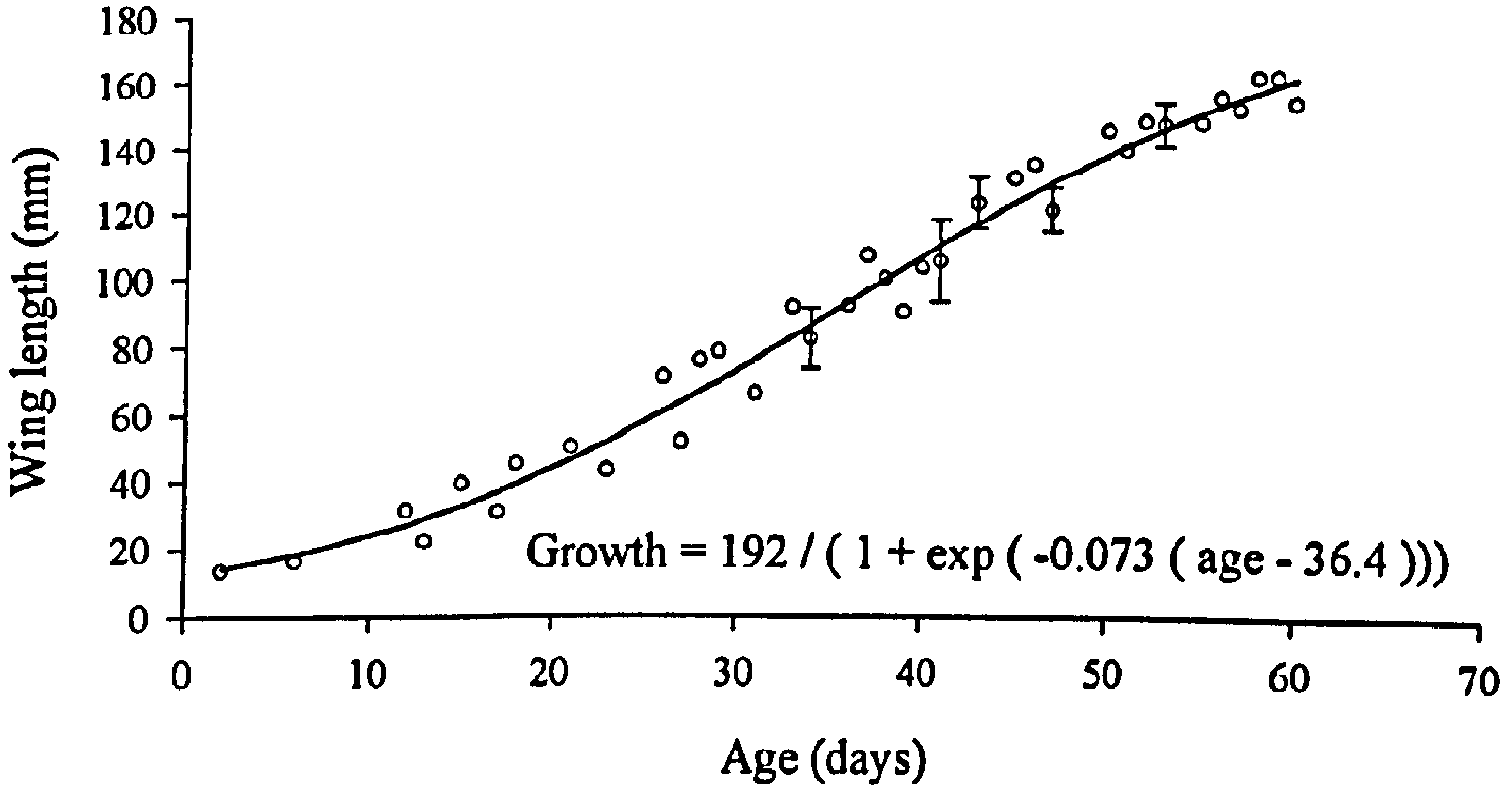


Figure 26: Length of folded left wing of Lilac-crowned Parrot nestlings in 1997. Error bars represent standard deviations of mean length.

(a) First-hatched, *n* = 4 nestlings.



(b) Second-hatched, *n* = 3 nestlings.



(c) Third-hatched, *n* = 2 nestlings.

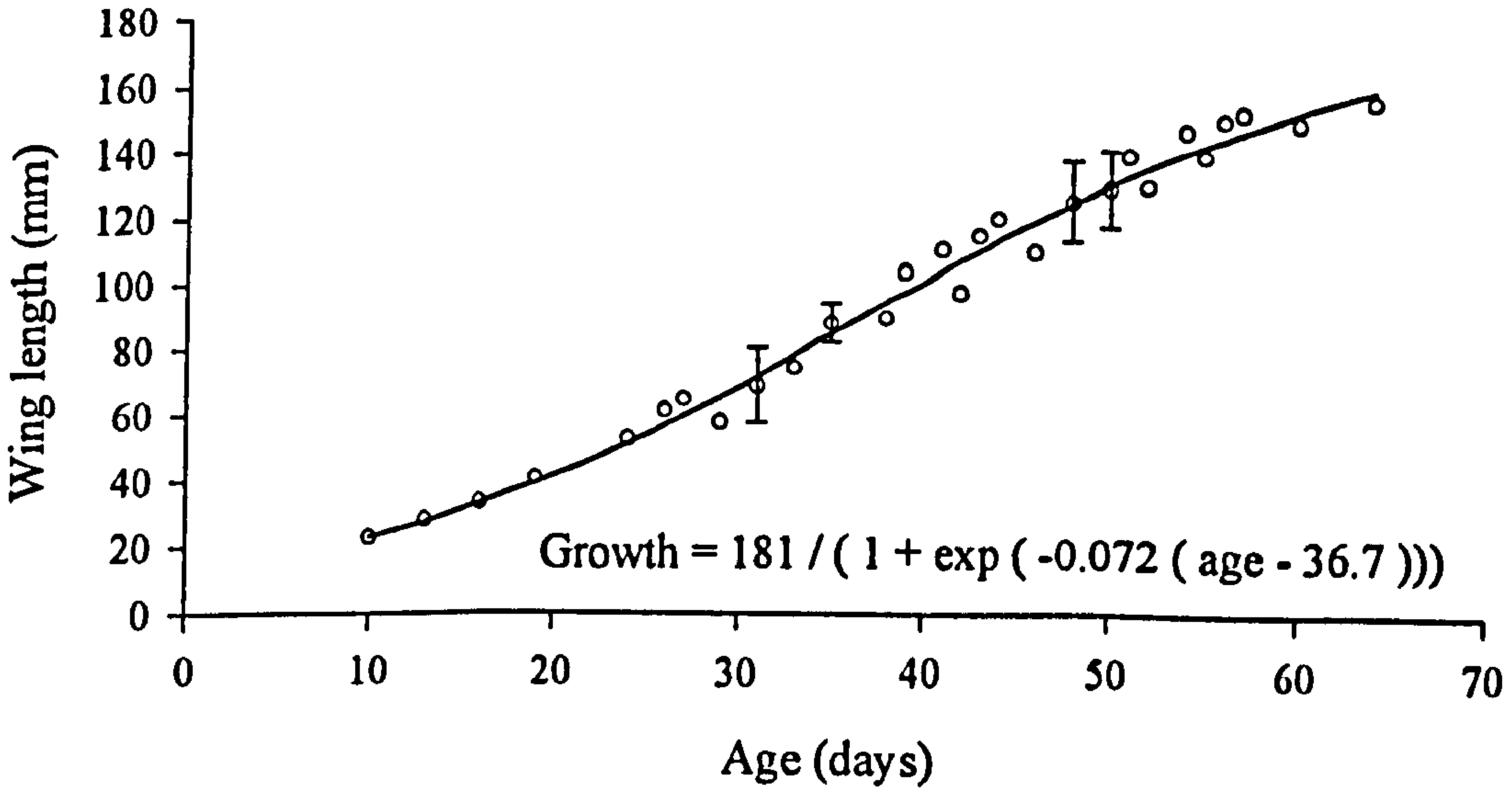


Table 23: Ricklefs (1967) growth parameters for body mass (g) of Lilac-crowned Parrot nestlings by hatching order in 1996 and 1997.

Nestling hatching order	Number of measurements	Asymptote (A)	Growth constant (k)	Inflection point (t_i)	Growth period ($t_{10\text{-}90}$)	Curve fit (r^2)
1996: 1st hatched nestlings	49	319.3	0.174	19.4	25.3	0.979
2nd hatched nestlings	52	315.8	0.158	19.0	27.8	0.954
3rd hatched nestlings	21	328.2	0.14	22.3	31.4	0.967
1st & 2nd hatched nestlings	101	320.2	0.16	19.1	27.5	0.956
1997: 1st hatched nestings	37	315.7	0.193	16.2	22.8	0.97
2nd hatched nestlings	40	297.6	0.191	15.9	23.0	0.929
3rd hatched nestlings	30	296.9	0.155	17.2	28.4	0.932
1st & 2nd hatched nestlings	77	306.2	0.196	16.0	22.4	0.937
Overall: All nestlings 1996	122	320.5	0.16	19.4	27.5	0.955
All nestlings 1997	107	302.5	0.187	16.1	23.5	0.927

Table 24: Ricklefs (1967) growth parameters for wing length (mm) of Lilac-crowned Parrot nestlings by hatching order in 1996 and 1997.

Nestling hatching order	Number of measurements	Asymptote (A)	Growth constant (k)	Inflection point (t_i)	Growth period ($t_{10\text{-}90}$)	Curve fit (r^2)
1996: 1st hatched nestlings	52	285.1	0.073	39.3	60.3	0.991
2nd hatched nestlings	57	268.6	0.076	37.8	57.9	0.989
3rd hatched nestlings	23	275.6	0.072	40.8	61.1	0.99
1st & 2nd hatched nestlings	109	275.2	0.075	38.4	58.7	0.99
1997: 1st hatched nestings	42	189.6	0.075	35.4	57.9	0.995
2nd hatched nestlings	41	191.5	0.0734	36.4	59.9	0.974
3rd hatched nestlings	32	181.2	0.0717	36.7	61.4	0.977
1st & 2nd hatched nestlings	83	190.6	0.0739	35.9	59.2	0.984
Overall: All nestlings 1996	132	275.5	0.074	38.8	59.5	0.986
All nestlings 1997	115	187.3	0.073	36.1	59.9	0.976

Table 25: Ricklefs (1967) growth parameters for culmen length (mm) of Lilac-crowned Parrot nestlings by hatching order in 1996 and 1997.

Nestling hatching order		Number of measurements	Asymptote (A)	Growth constant (k)	Inflection point (t_i)	Growth period ($t_{10\text{-}90}$)	Curve fit (r^2)
1996:	1st hatched nestlings	52	27.4	0.0598	21.1	73.6	0.978
	2nd hatched nestlings	58	28.0	0.0551	21.9	79.9	0.977
	3rd hatched nestlings	23	28.1	0.0508	21.4	86.6	0.99
	1st & 2nd hatched nestlings	110	27.7	0.0572	21.5	76.9	0.977
1997:	1st hatched nestings	43	27.6	0.0638	16.6	69.0	0.99
	2nd hatched nestlings	42	27.7	0.061	16.4	72.1	0.988
	3rd hatched nestlings	33	27.9	0.0596	17.8	73.8	0.99
	1st & 2nd hatched nestlings	85	27.6	0.0624	16.5	70.5	0.989
Overall:	All nestlings 1996	133	27.7	0.0564	21.4	78.0	0.978
	All nestlings 1997	118	27.7	0.0616	16.8	71.5	0.988

6.4.3. BETWEEN YEAR VARIATION IN GROWTH

The growth parameters for body mass (Table 23) and culmen length (Table 25) demonstrate that nestling growth was more rapid in 1997 with a higher growth constant (*k*) and a shorter time to inflection of the growth curve (t_i) compared to 1996. Wing growth could not be compared between the years due to the use of slightly differing methods for measuring wing length in 1996 and 1997. As illustrated in Figure 27, culmen lengths of nestlings were consistently shorter in 1996 than in 1997. Body mass of nestlings was also lower in 1996 compared to 1997 during the first four weeks, however, nestlings in 1996 were able to make up in body mass during the second month of the nestling phase (Fig 28).

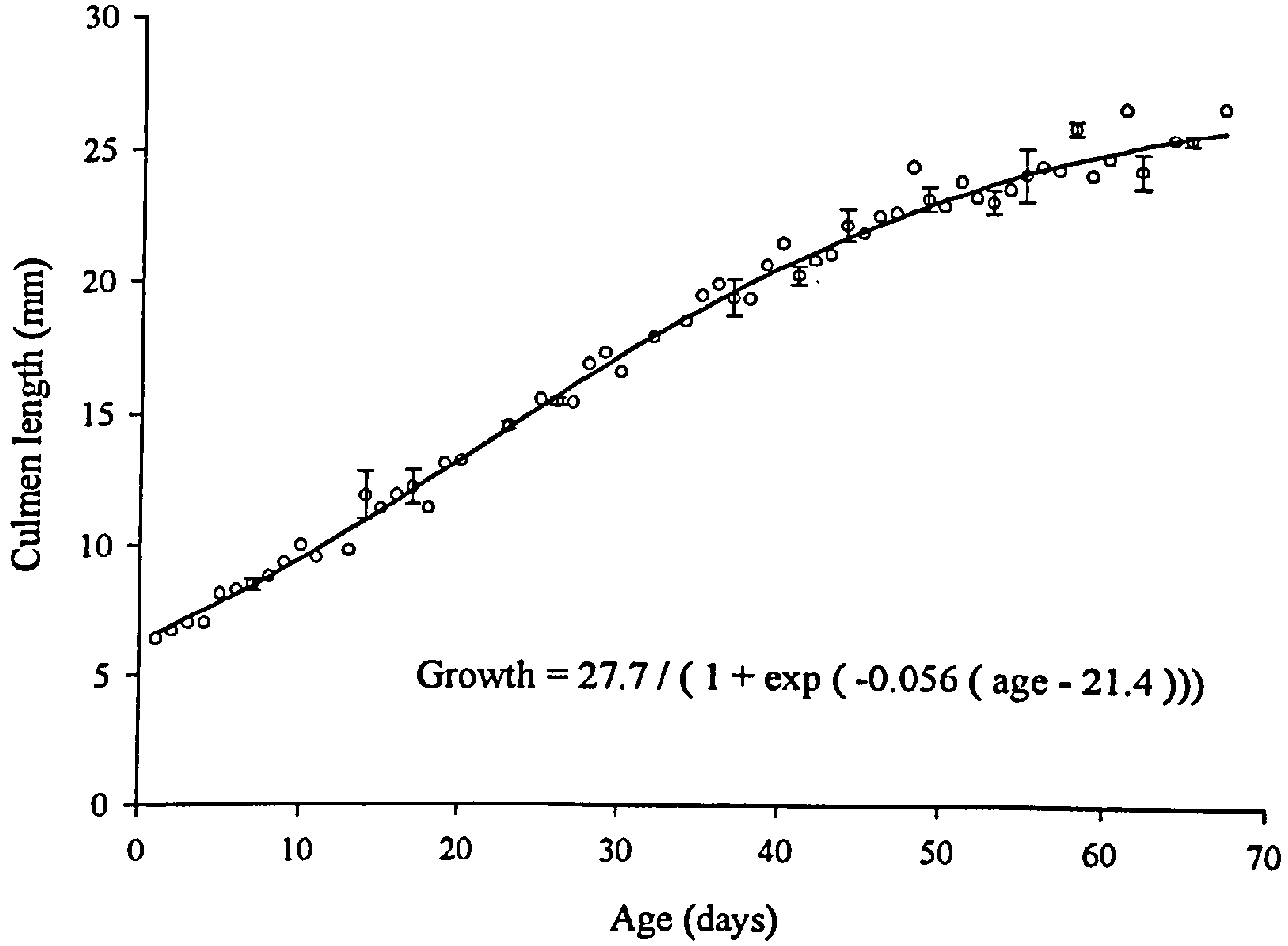
Two-sample t-test analyses on nestling sizes at 6 days, 40 days, and 60 days demonstrated significant differences between 1996 and 1997 (Table 26). Culmen length of nestlings was significantly shorter in 1996 than in 1997 at both 6 days and 40 days after hatching (Table 26). However, by 60 days after hatching there was no difference between the years in culmen length of nestlings, possibly as culmen length reaches an asymptote by the end of the nestling phase.

This size difference was reflected in body mass of nestlings at 6 days after hatching which was significantly lower in 1996 than 1997. The existence of size differences early in the nestling period indicate that nestlings may have been significantly smaller at hatching in 1996 than in 1997. This may be related to differences between years in the nutritional condition of female parrots at the time of egg production. In addition while maximum body mass did not vary between the years, nestlings took significantly longer to attain maximum body mass in 1996 than in 1997 (Table 26, Fig 28).

Finally, while there was no difference between the years in age of nestlings at fledging, there was a significant difference in both mass loss prior to fledging, and fledging mass. The more rapid growth of nestlings during 1997, means that feather maturation may have been more advanced at the time of fledging, resulting in a greater weight recession due to the loss of water from feather tissues than in 1996. Hence, nestlings were significantly smaller at hatching, and took longer to acquire asymptotic size in 1996 than in 1997. However, the length of the nestling period and the rapid growth of nestlings may allow some flexibility, enabling nestlings to acquire asymptotic sizes prior to fledging.

Figure 27: Between year variation in culmen growth of Lilac-crowned Parrot nestlings. Error bars represent standard deviations of mean culmen length.

(a) Culmen growth in 1996, *n* = 14 nestlings.



(b) Culmen growth in 1997, *n* = 9 nestlings

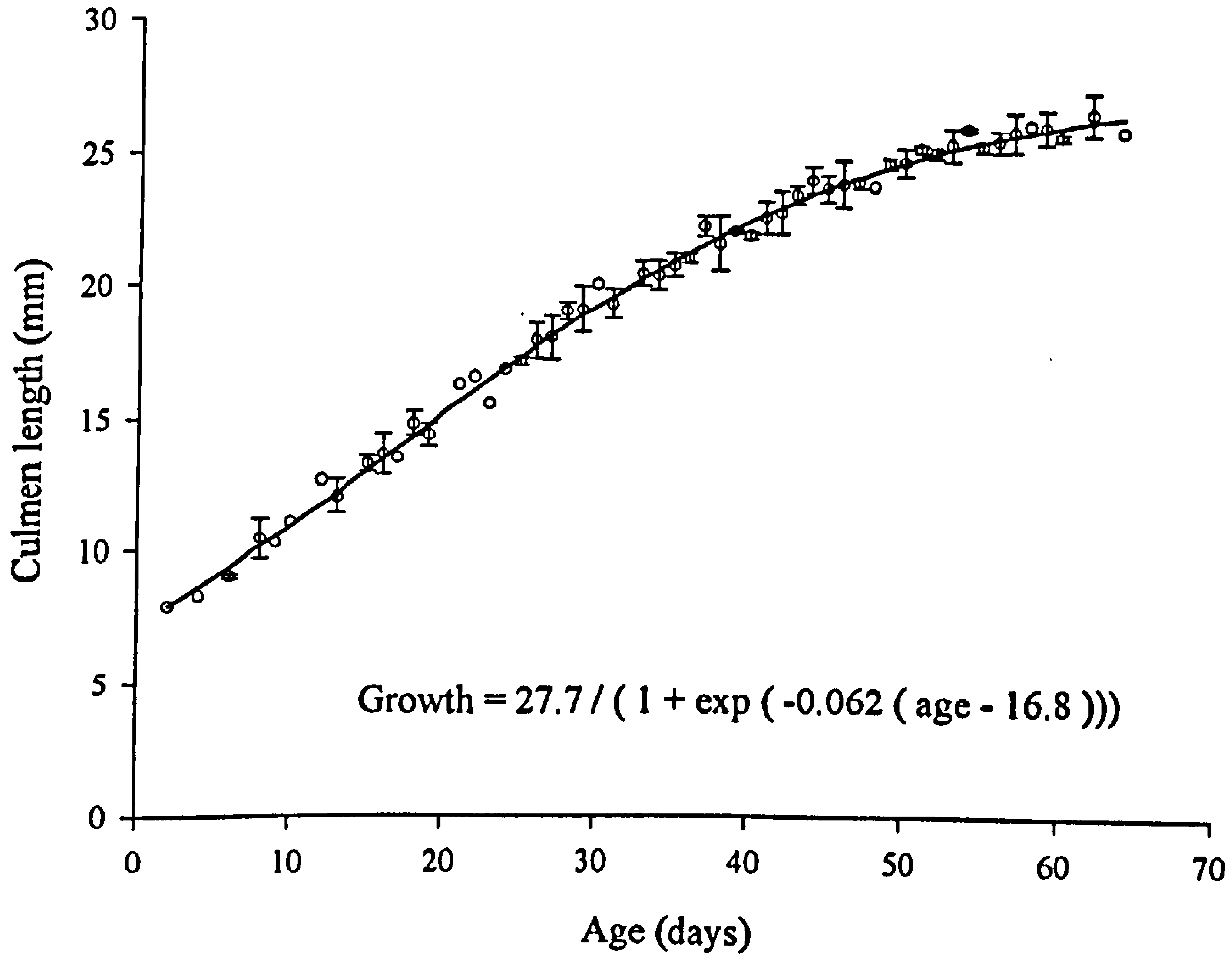
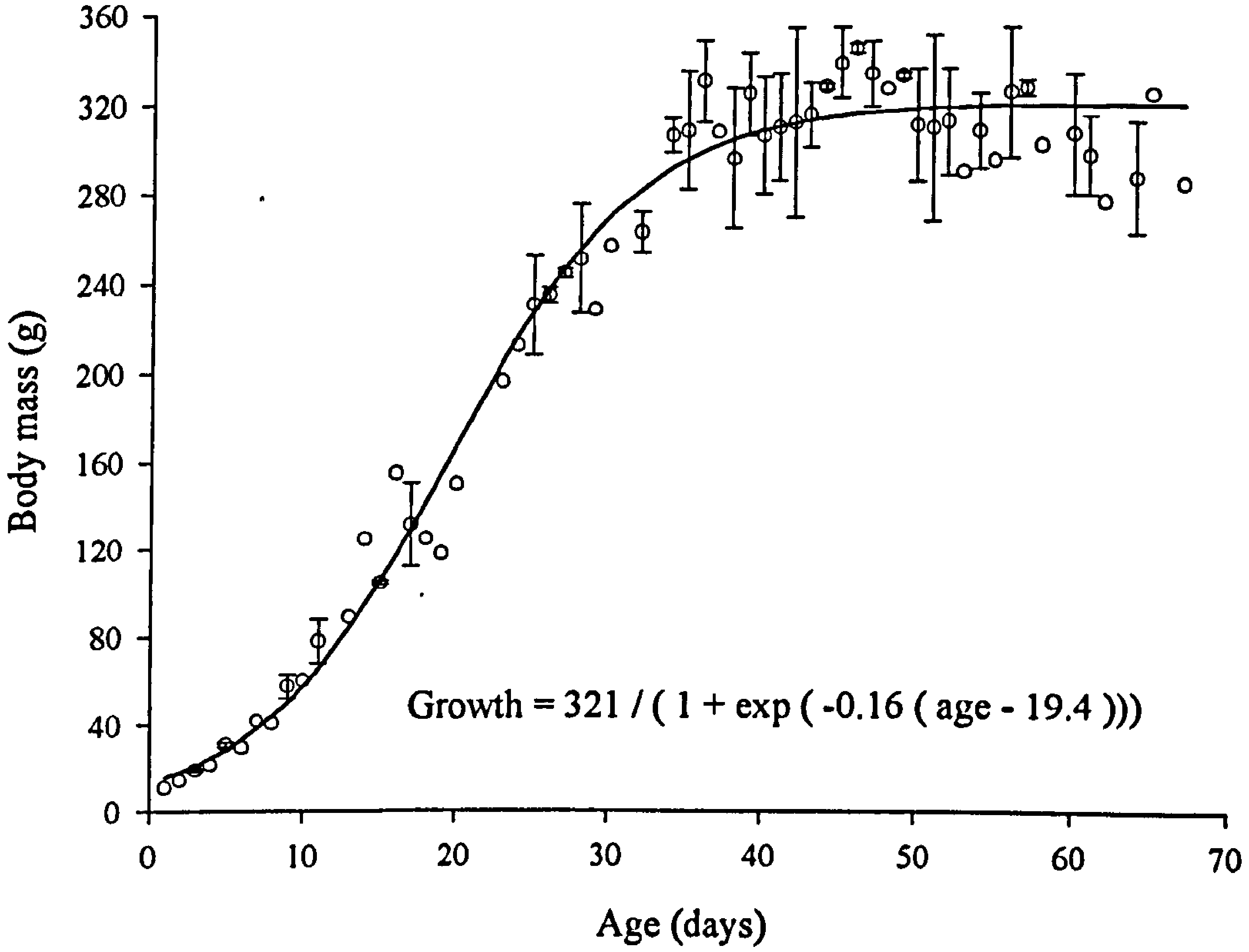


Figure 28: Between year variation in growth of body mass of Lilac-crowned Parrot nestlings. Error bars represent standard deviations around mean body mass.

(a) Body mass 1996, *n* = 14 nestlings.



(b) Body mass 1997, *n* = 9 nestlings.

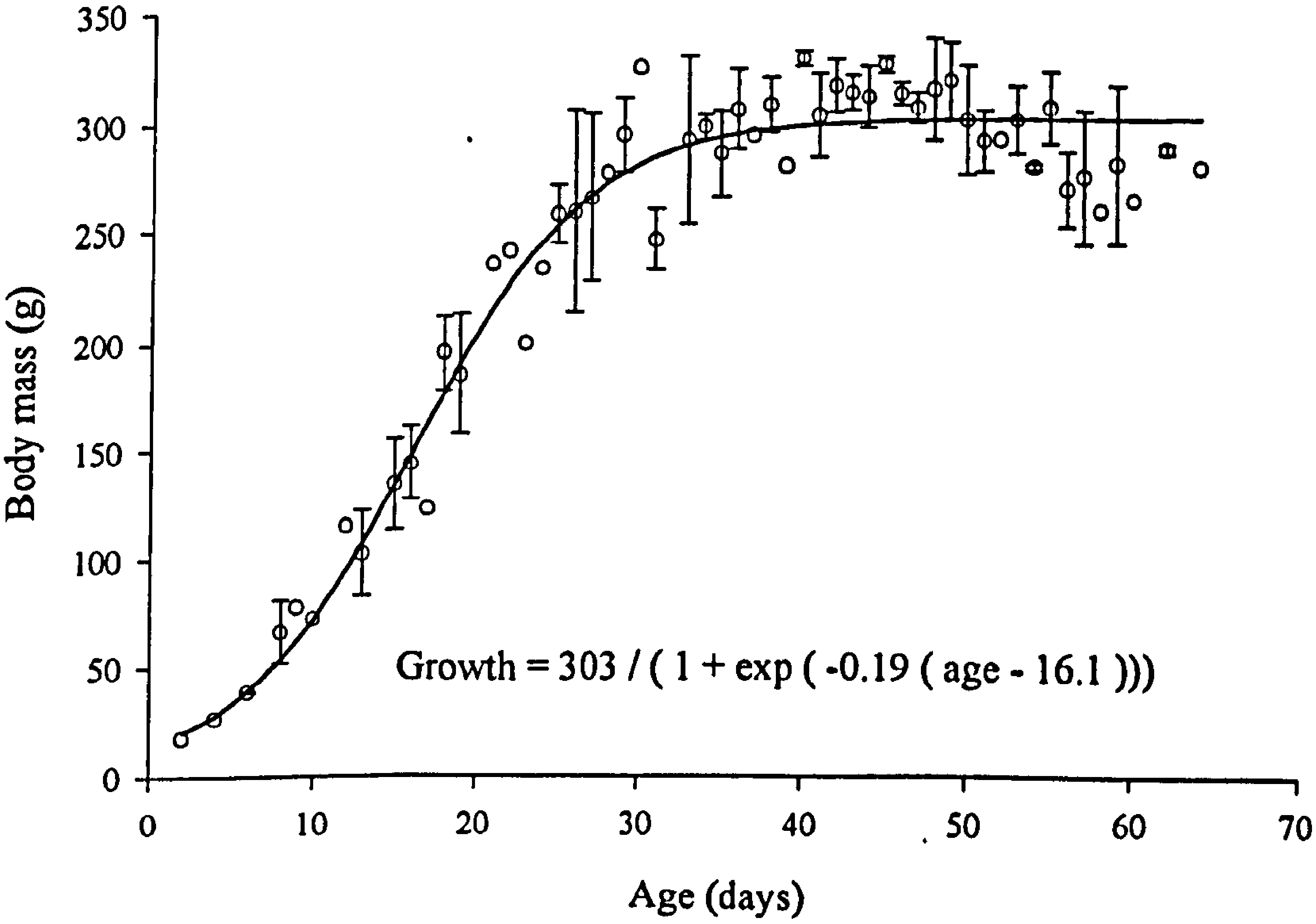


Table 26: Comparison of nestling growth in 1996 and 1997. Results presented with means, standard deviation, value ranges, and two-sample t-test significance level.

Variable	1996 (range)	1997 (range)	Significance test
Culmen length at 6 days (mm)	8.30 ± 0.326 (7.86 - 8.7)	9.16 ± 0.616 (8.45 - 10.15)	$t = 2.96$, df = 9, $P = 0.016$
Culmen length at 40 days (mm)	20.74 ± 1.13 (19.7 - 23.2)	22.07 ± 0.642 (21.15 - 23.05)	$t = 2.89$, df = 14, $P = 0.012$
Culmen length at 60 days (mm)	24.99 ± 1.09 (23.1 - 26.48)	26.07 ± 0.62 (25.4 - 26.7)	$t = 2.15$, df = 12, $P = 0.053$
Mass at 6 days (g)	35.29 ± 3.98 (30 - 40.5)	44.32 ± 8.59 (38.3 - 57.6)	$t = 2.63$, df = 10, $P = 0.025$
Maximum mass (g)	323.75 ± 16.92 (297 - 349)	321 ± 6.37 (312 - 330)	$t = 0.43$, df = 14, $P = 0.67$
Age at max. mass (days)	45.1 ± 3.87 (40 - 50)	41.4 ± 2.67 (39 - 46)	$t = 2.26$, df = 14, $P = 0.041$
Mass loss prior to fledging (g)	27 ± 17.53 (7 - 52)	50.33 ± 12.93 (37 - 68)	$t = 2.74$, df = 12, $P = 0.018$
Fledging mass (g)	298.9 ± 25.1 (270 - 342)	272 ± 15.8 (254 - 290)	$t = 2.29$, df = 12, $P = 0.041$
Age at fledging (days)	65.1 ± 2.17 (62 - 68)	63.3 ± 2.58 (60 - 69)	$t = 1.41$, df = 12, $P = 0.18$

6.4.4. COMPARISON BETWEEN PSITTACINE SPECIES

Ricklefs growth rate constant and asymptotic values for various psittacine species are summarised in Table 27. There was greater variation between parrot species in the growth rate constant (*k*) for body mass (coefficient of variation = 26.8%) than for wing length (coefficient of variation = 11.7%). Growth rate for body mass was also inversely related to adult size ($r^2 = 0.76$, $F_{1,6} = 19.18$, $P < 0.005$), with larger parrot species exhibiting slower growth rates. However, wing growth was fairly constant between parrot species and was not related to adult wing length

Table 27: Comparison of Ricklefs growth rate constant (*k*) for psittacines.

Variable	Asymptote	Growth rate constant (*k*)	Source
Body mass (g)			
Hyacinth Macaw, captive-bred	1,500	0.11	data from Abramson 1991
Scarlet Macaw, Belize	1,135	0.139	Renton (unpubl. data)
Scarlet Macaw, captive-bred	1,111	0.149	data from Abramson 1991
Lilac-crowned Parrot	311	0.173	This study
Red-shining Parrot	277	0.162	Rinke 1989
Long-billed Corella	275	0.23	Smith 1991
Monk Parakeet	103.9	0.24	Navarro & Bucher 1990
Green-rumped Parrotlet	23.7	0.23	Waltman & Beissinger 1992
Length of folded left wing (mm)			
Scarlet Macaw, Belize	399	0.066	Renton (unpubl. data)
White-tailed Black Cockatoo	366	0.074	Saunders 1982, 1986
Long-billed Corella	285	0.087	Smith 1991
Red-shining Parrot	239.5	0.086	Rinke 1989
Lilac-crowned Parrot	190	0.073	This study

6.5. DISCUSSION

The pattern of growth exhibited by Lilac-crowned Parrot nestlings corresponds with that observed for the Red-crowned Parrot in north-eastern Mexico (Enkerlin-Hoeflich 1995), as well as similar sized Australian parrots (Rowley & Chapman 1991; Smith 1991), which reach asymptotic mass half-way through the nestling phase. However, this contrasts with the slow growth exhibited by nestlings of the White-tailed Black Cockatoo in Australia (Saunders 1982), which attain asymptotic body mass only in the last third of the nestling phase. As noted by Ricklefs (1968a), larger bird species tend to have slower growth rates for body mass. This inverse relation between body mass and growth rate is supported for psittacine species ($r^2 = 0.76$), and is similar to the inverse relation obtained by Ricklefs (1976) for tropical land birds ($r^2 = 0.73$).

There was a marked size hierarchy and variation in growth rate between Lilac-crowned Parrot siblings, as has been recorded for a few other parrot species (Rinke 1989; Navarro & Bucher 1990; Smith 1991). However, this difference was only apparent with respect to third-hatched nestlings, while first- and second-hatched nestlings varied little in size or growth rate, regardless of whether they were in a two or three brood nest. The hatching interval was also longer between second and third eggs compared to that between first and second eggs. The delayed hatching of third eggs may have contributed to slower growth rates for third nestlings, which have to compete for food against siblings with a possible 4 - 6 day advantage in age. As hatching spread is influenced by food limitation at the time of laying (Bryant 1978a, b; Bollinger 1994), it is likely that the differential growth rate for third-hatched nestlings may be determined by environmental conditions during the egg-laying period in February.

Though third-hatched nestlings were smaller in size and exhibited slower growth rates than earlier hatched siblings, this did not result in mortality. The lack of differential mortality of Lilac-crowned Parrot nestlings, contrasts with the brood reduction observed for Australian parrots in which later-hatched nestlings frequently died of starvation during the first four weeks after hatching (Saunders 1982; Smith &

Saunders 1986; Smith 1991). Herring gulls also exhibit a 'third-chick disadvantage' in which last laid eggs in broods of three are significantly smaller, and result in smaller third chicks with slower growth rates and higher mortality (Parsons 1970, 1975). Pierotti & Bellrose (1986) suggest that this may arise due to constraints on energy reserves of the female at the time of laying, and where food is abundant the third-chick disadvantage may be reduced or absent.

For the Lilac-crowned Parrot, various factors such as the length of time in the nest, along with food resource availability during the nestling period, and parental effort, may allow some flexibility in growth processes, enabling third chicks to catch-up in body size with earlier hatched siblings. Furthermore, asynchronous hatching and size hierarchies do not always lead to mortality of later-hatched young (Ricklefs 1976; Richter 1984). However, it is predicted from the growth rate analysis that third-hatched Lilac-crowned Parrot nestlings are at a disadvantage compared to earlier hatched siblings, and may be vulnerable to mortality in years of extreme drought and poor food resource availability which may occur in this habitat.

The main period of nestling growth occurred in the mid dry season in March - April, with most nestlings fledging by May. In fact, the nestling period may be timed to coincide with a period of high food resource availability during the mid-dry season, and to enable fledging of young prior to the end of the dry season when there is a dramatic decline in food resource abundance (Chapter 3). A phase of rapid growth during the first month of the nestling cycle would also reduce the vulnerability of nestlings to predation risks which may be greater towards the end of the dry season (Sieving 1992).

The influence of food resource variability on parrot reproduction is suggested by the difference in size and growth rates of nestlings between the 1996 and 1997 breeding seasons. The larger initial size and faster growth rates of nestlings in 1997 may be due to the greater food resource abundance (Chapter 3), as a result of the increased rainfall (Chapter 2). Nestling diets were also more varied in 1997 compared to 1996 (Chapter 3). However, while the nutritional value of different food items in the diet is unknown, it is most likely that Lilac-crowned Parrot nestlings simply received a greater quantity of food in 1997 compared to 1996, leading to increased growth rates. Hence, annual fluctuations in environmental factors may influence nestling condition and survival. This impact may be greater in years with a severe dry season, and a corresponding scarcity of food resources.

The study indicates that growth rate responds to environmental fluctuations in food resource availability. Analysis of nestling growth may therefore serve as a useful tool for monitoring parrot populations, and evaluating both habitat quality and the viability of threatened populations. Food limitation as a result of habitat destruction may have been a principal factor in the poor growth and survival of cockatoo nestlings in agricultural areas of Australia, which eventually led to the extirpation of local populations (Saunders 1982, 1986, 1990, 1991). Between year variations in the growth rate of Lilac-crowned Parrot nestlings corresponded with fluctuations in food resource abundance. Hence, the annual variations in growth rate observed for the Monk Parakeet (Navarro & Bucher 1990) may also be due to fluctuations in environmental conditions, particularly food supply. Very little data are available on the growth rates of Neotropical parrots, or the influence of food resource availability on reproduction, making this is an area which requires further investigation in order to understand the potential impacts of environmental variability on parrot populations.

CHAPTER 7

IMPLICATIONS FOR CONSERVATION

7.1. POTENTIAL IMPACT OF HABITAT FRAGMENTATION

The pattern of food resource availability and utilisation by Lilac-crowned Parrots at the study site, demonstrates the importance of semi-deciduous forest in providing essential food resources during the critical period of resource scarcity at the end of the dry season. Hence, increased fragmentation of semi-deciduous forest could result in food limitation for parrots during the breeding season. Semi-deciduous forest may also provide essential resources for other animal communities in deciduous forest during the dry season.

Breeding birds experience greater food limitation in small forest patches (Burke & Nol 1998), while food limitation due to habitat loss resulted in depressed nestling growth, low reproductive output, and the extirpation of cockatoo populations in agricultural areas of Australia (Saunders 1986, 1990, 1991). The variation between years in growth of Lilac-crowned Parrot nestlings, indicates the potential influence of fluctuations in environmental factors on parrot reproduction. Hence, food limitation as a result of habitat fragmentation may impact nestling growth and reproductive output of the wild population, particularly in extremely dry years of poor food resource abundance.

The high predation rate and low reproductive output of Lilac-crowned Parrot nests may be another consequence of increased fragmentation of semi-deciduous forest. Predation on bird nests is greater in small forest patches (Gates & Gysel 1978; Ambuel & Temple 1983; Loiselle & Hoppes 1983; Wilcove 1985; Andren et al. 1985; Angelstam 1986; Wilcove et al. 1986; Andren & Angelstam 1988; Andren 1992; Fenske-Crawford & Niemi 1997; Keyser et al. 1998), while edge effects of predators entering forest patches from surrounding areas may also lead to increased nest predation (Angelstam 1986; Andren & Angelstam 1988; Small & Hunter 1988;

Andren 1992; Fenske-Crawford & Niemi 1997). Hence, high predation rates on Lilac-crowned Parrot nests may be due to the concentration of predators in small patches of semi-deciduous forest from the adjacent deciduous forest during the dry season. High rates of nest predation may also impact other bird communities at the study site.

The majority of deforestation since the 1950s has occurred in semi-deciduous forest (A. Miranda pers. comm.), and current rates of deforestation are twice as high in semi-deciduous forest than deciduous forest (Miranda 1998). Parrots are highly adaptable in diet, spatial scale, and mobility, and therefore may respond to increasing habitat fragmentation through greater flexibility in diet, utilisation of a large area, and long-distance movements. However, the conservative breeding strategies and low reproductive rates of parrots mean that the combined effects of habitat fragmentation, and nest poaching will heavily impact wild populations.

Conversely, it is not known what effect the loss of parrot populations may have on tropical forest dynamics. The pattern of resource utilisation by Lilac-crowned Parrots suggests a complex inter-action between parrot populations and seed resources. Decreased vegetational diversity in some Central American forests has been associated with the loss of large herbivores, which may play a regulatory role in maintaining forest diversity (Janzen 1970; Dirzo & Miranda 1990, 1991). Parrots are large, highly mobile, pre-dispersal seed predators, with the ability to closely track and exploit temporal and spatial variations in seed resource abundance, and may play an important regulatory role in maintaining diversity of canopy trees in tropical forests.

7.2. IMPLICATIONS FOR SPECIES CONSERVATION

Parrot populations are frequently able to persist in areas disturbed by human activities, giving the impression of abundant and stable populations. However, studies of breeding success and reproductive output of parrot populations in disturbed areas indicate that such populations may be reproducing at sub-optimal levels (Saunders

1986; Gnam & Rockwell 1991; Enkerlin-Hoeflich 1995; Chapter 5). The low nest success and fluctuations in nestling growth of the Lilac-crowned Parrot, as compared with psittacine populations in undisturbed areas (Saunders 1982; Munn 1992), suggest that habitat fragmentation may already be impacting reproduction of the wild population. Hence, the Lilac-crowned Parrot population in the tropical dry forest of the Chamela-Cuixmala reserve does not exhibit a reproductive rate which is able to sustain heavy levels of exploitation for commercial trade.

The temporal and spatial variations in resource utilisation by Lilac-crowned Parrots further demonstrate that parrots require large areas and a variety of habitat types in order to meet their resource needs throughout the year. Added to which, the seasonal altitudinal migration by Lilac-crowned Parrots indicates that parrot populations may depend on entirely different areas and habitat types at critical times of the year. An increase in the abundance of Lilac-crowned Parrots in the Chamela-Cuixmala Biosphere Reserve during the months of August - October (pers. obs.), may also be due to a reverse migration of parrot populations from the mountain foothills to lowland deciduous forest during the rainy season. Hence, the large flocks of Lilac-crowned Parrots observed outside the breeding season (Forshaw 1989), may be comprised of seasonally migrating individuals from various lowland and mountain populations of at least a 50 km radius, and are misleading if taken as an indication of high population densities.

Conservation of threatened populations depends on preservation of the entire habitat range of a species. For the Lilac-crowned Parrot, this may require conservation of sufficient areas of lowland deciduous and semi-deciduous forest, as well as corresponding areas of forest in the mountain foothills. However as a result of deforestation, semi-deciduous forest now comprises only 9.28% of the land area in the Chamela-Cuixmala region (Miranda 1998). Hence, it may no longer be the case that extensive habitat exists for wild populations as stated by Ridgely (1981), particularly in view of the dependence of parrots on semi-deciduous forest during the dry season.

In recent years the Military Macaw has been extirpated from the Chamela-Cuixmala region, and populations of the Yellow-headed Parrot have declined dramatically. The principal cause of this decline has been capture for commercial trade, however, the high rate of deforestation in the region is an additional factor. Indeed, there may no longer be sufficient habitat to sustain large populations of Military Macaws throughout the year, particularly as this species may be more dependent on semi-deciduous forest in low lying areas. Very little is known of the dynamics of habitat use within the animal community of deciduous forest, and such information is essential in order to develop effective strategies for conservation and management of threatened species.

7.3. IMPLICATIONS FOR PROTECTED AREAS

The complex relation between parrot populations and food resources demonstrates the importance of heterogeneity on a temporal and spatial scale for maintaining stability in natural ecosystems (Wu & Loucks 1995). A variety of habitat types may be required to meet the resource needs of animal communities at different times of the year (Foster 1980), as well as a means of maintaining connectivity between resource patches (Merriam 1991; Saunders et al. 1991; Taylor et al. 1993; Wiens 1994).

The Lilac-crowned Parrot covers large areas in its daily and seasonal movements, requires a variety of habitat types, and is sensitive to ecological changes and human disturbance. Hence large parrots, such as the Lilac-crowned Parrot, may be considered focal species in reserve design, being both umbrella species and indicator species (Miller et al. in press). Incorporating the requirements of such focal species in the planning and management of protected areas ensures the preservation of key elements for a healthy ecosystem.

Maintaining a functional ecosystem in the Chamela-Cuixmala Biosphere Reserve (Appendix 1) may require the conservation of sufficient areas of semi-deciduous forest, as well as the dominant vegetation type of deciduous forest. Increased predation pressures and potential food limitation in small forest patches, further demonstrate the importance of preserving large areas of intact forest as opposed to small fragments. The on-going telemetry study has also demonstrated the importance of large hills, such as Cerro Maderas, Cerro Colorado, and Cerro Carayes in the Chamela-Cuixmala reserve, which are used as communal roost sites by Lilac-crowned Parrots (Renton unpubl. data). Hence, bird communities in the Chamela-Cuixmala forest may depend on the maintenance of a mosaic of forest types, providing temporal and spatial diversity in habitats and food resources. However, the high rate of loss of semi-deciduous forest, means that management may be required to maintain and restore areas of semi-deciduous forest in the Chamela-Cuixmala reserve.

Finally, the seasonal altitudinal migration by Lilac-crowned Parrots to the Sierra Cacoma, adjacent to the Sierra Manantlan, indicates the importance of developing connectivity between the Chamela-Cuixmala Biosphere Reserve and the nearby Sierra Manantlan Biosphere Reserve. A potential reverse migration to lowland deciduous forest by parrot populations in the mountains during the rainy season, suggests that bird populations in the Sierra Manantlan Biosphere Reserve may also require the maintenance of sufficient areas of alternative lowland habitat, in order to meet their resource needs throughout the year. Such migratory movements by animal populations strengthen the case for maintaining these two protected areas as functional units within an altitudinal ecosystem, thereby preventing them from becoming isolated by increasing deforestation.

REFERENCES

Abramson, J. 1991. Breeding macaws in captivity: Part 2. Pp 56-72 in Proceedings of the First Mesoamerican Workshop on the Conservation and Management of Macaws. J. Clinton-Eitniear (ed). Center for the Study of Tropical Birds, Texas.

Adams, J.S., R.L. Knight, L.C. McEwen, & T.L. George. 1994. Survival and growth of nestling Vesper Sparrows exposed to experimental food reductions. Condor 96: 739-748.

Alerstam, T., & G. Hogstedt. 1981. Evolution of hole-nesting in birds. Ornis Scandinavica 12: 188-193.

Ambuel, B., & S.A. Temple. 1983. Area-dependent changes in bird communities and the vegetation of southern Wisconsin forests. Ecology 64: 1057-1068.

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73: 794-804.

Andren, H., & P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69: 544-547

Andren, H., P. Angelstam, E. Lindstrom, & P. Widen. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos 45: 273-277.

Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47: 365-373.

Augspurger, C.K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). Ecology 62: 775-788.

Banbura, I., J. Blondel, H. de Wilde-Lambrechts, M.J. Galan, J. Maistre. 1994. Nestling diet variation in an insular Mediterranean population of blue tits *Parus caeruleus*: effects of years, territories and individuals. Oecologia 100: 413-420.

Bancroft, G.T., & R. Bowman. 1994. Temporal patterns in diet of nestling White-crowned Pigeons: implications for conservation of frugivorous columbids. Auk 111: 844-852.

Barba, E., & J.A. Gil-Delgado. 1990. Seasonal variation in nestling diet of the Great Tit, *Parus major*, in orange groves in eastern Spain. Ornis Scandinavica 21: 296-298.

Bart, J. & D.S. Robson. 1982. Estimating survivorship when the subjects are visited periodically. Ecology 63: 1078-1090

Beeton, R.J.S. 1985. The little corella: a seasonally adapted species. Proceedings of the Ecological Society of Australia 13: 53-63.

Beissinger, S.R., & E.H. Bucher. 1992a. Sustainable harvesting of parrots for conservation. Pp 73-117 in New World Parrots in Crisis: Solutions from Conservation Biology. S.R. Beissinger & N.F.R. Snyder (eds). Smithsonian Institution Press, Washington.

Beissinger, S.R., & E.H. Bucher. 1992b. Can parrots be conserved through sustainable harvesting. BioScience 42: 164-173.

Beissinger, S.R., E.C. Steadman, T. Wohlgenant, G. Blate, & S. Zack. 1996. Null models for assessing ecosystem conservation priorities: threatened birds as titers of threatened ecosystems in South America. Conservation Biology 10: 1343-1352.

Beissinger, S.R., & J.R. Waltman. 1991. Extraordinary clutch size and hatching asynchrony of a Neotropical parrot. Auk 108: 863-871.

Bennett, P.M., & I.P.F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings Royal Society of London B. 264: 401-408.

Blake, J.G., & B.A. Loiselle. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. Auk 108: 114-127

Blancher, P.J., & R.J. Robertson. 1987. Effect of food supply on the breeding biology of Western Kingbirds. Ecology 68: 723-732.

Boag, P.T., & P.R. Grant. 1984. Darwin's Finches (*Geospiza*) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. Ecological Monographs 54: 463-489.

Bollinger, P.B. 1994. Relative effects of hatching order, egg-size variation, and parental quality on chick survival in Common Terns. Auk 111: 263-273.

Bollinger, P.B., E.K. Bollinger, & R.A. Malecki. 1990. Tests of three hypotheses of hatching asynchrony in the Common Tern. Auk 107: 696-706.

Bortolotti, G.R. 1986. Evolution of growth rates in eagles: sibling competition vs. energy considerations. Ecology 67: 182-194.

Bryant, D.M. 1975. Breeding biology of House Martins, *Delichon urbica*, in relation to aerial insect abundance. Ibis 117: 180-216.

Bryant, D.M. 1978a. Establishment of weight hierarchies in the broods of House Martins, *Delichon urbica*. Ibis 120: 16-26.

Bryant, D.M. 1978b. Environmental influences on growth and survival of nestling House Martins, *Delichon urbica*. Ibis 120: 271-283.

Bukacinski, D., M. Bukacinska, & A.L. Spaans. 1998. Experimental evidence for the relationship between food supply, parental effort and chick survival in the Lesser Black-backed Gull, *Larus fuscus*. Ibis 140: 422-430.

Bullock, S.H. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. Arch. Met. Geoph. Biocl., Series B 36: 297-316.

Bullock, S.H. 1988. Rasgos del ambiente fisico y biologico de Chamela, Jalisco, Mexico. Pp 5-17 in La Entomofauna de Chamela, Jalisco. M.A. Moron (ed). Folia Entomologica Mexicana 77.

Bullock, S.H., & J.A. Solis-Magallanes. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 22: 22-35.

Burke, D.M., & E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk 115: 96-104.

Calver, M.C., & R.D. Wooller. 1981. Seasonal differences in the diets of small birds in the Karri Forest understorey. Australian Wildlife Research 8: 653-657.

Case, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quarterly Review of Biology 53: 243-282.

Chapman, C.A., L.J. Chapman, R. Wrangham, K. Hunt, D. Gebo, & L. Gardner. 1992. Estimators of fruit abundance of tropical trees. Biotropica 24: 527-531.

Chapman, C.A., R. Wrangham, & L.J. Chapman. 1994. Indices of habitat-wide fruit abundance in tropical forests. Biotropica 26: 160-171.

Christman, B.J., & A.A. Dhondt. 1997. Nest predation in Black-capped Chickadees: how safe are cavity nests? Auk 114: 769-773.

Clark, A.B., & D.S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Quaterly Review of Biology 56: 253-277.

Clout, M.N. 1989. Foraging behaviour of Glossy Black Cockatoos. Australian Wildlife Research 16: 467-473.

Collar, N.J., & P. Andrew. 1988. Birds to Watch: The ICBP World Checklist of Threatened Birds. Technical publication no. 8. ICBP, Cambridge, UK.

Collar, N.J., & A.T. Juniper. 1992. Dimensions and causes of the parrot conservation crisis. Pp 1-24 in New World Parrots in Crisis: Solutions from Conservation Biology, S.R. Beissinger & N.F.R. Snyder (eds). Smithsonian Institution Press, Washington.

Colwell, R.K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55: 1148-1153.

Colwell, R.K., & D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Cucco, M. & G. Malacaren. 1995. Increase of parental effort in an experimentally enlarged brood of the Pallid Swift. Canadian Journal of Zoology 73: 1387-1395.

Cucco, M. & G. Malacaren. 1996. Effect of food availability on nestling growth and fledging success in manipulated Pallid Swift broods. Journal of Zoology 240: 141-151.

Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. Journal of Ecology 60: 147-170.

Dial, R., & S.C. Tobin. 1994. Description of arborist methods for forest canopy access and movement. Selbyana 15: 24-37.

Dirzo, R., & M.C. Garcia. 1992. Rates of deforestation at Los Tuxtlas, a Neotropical area in south-eastern Mexico. Conservation Biology 6: 84-90.

Dirzo, R., & A. Miranda. 1990. Contemporary Neotropical defaunation and forest structure, function, and diversity - a sequel to John Terborgh. Conservation Biology 4: 444-447.

Dirzo, R., & A. Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. Pp 273-287 in Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. P.W. Price, T.M. Lewinsohn, G.W. Fernandes, & W.W. Benson (eds). John Wiley & Sons, Inc.

Donahue, P.K., & T.M. Wood. 1995. A safe, flexible, and non-injurious technique for climbing tall trees. Selbyana 16: 196-200.

Drent, R.H., & S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Emlen, S.T., P.H. Wrege, N.J. Demong, & R.E. Hegner. 1991. Flexible growth rates in nestling White-fronted Bee-eaters: a possible adaptation to short-term food shortage. Condor 93: 591-597.

Enkerlin-Hoeflich, E.C. 1995. Comparative ecology and reproductive biology of three species of *Amazona* parrots in northeastern Mexico. Ph.D. Thesis, Texas A&M University, USA.

Enkerlin-Hoeflich, E.C., & K.M. Hogan. 1997. Red-crowned Parrot, *Amazona viridigenalis*. Birds of North America 292: 1-20.

Enkerlin-Hoeflich, E.C., J.M. Packard, M.D. Schindlinger, & J.J. González-Elizondo. in press. A suite of field techniques for the study of parrots. Journal of Field Ornithology.

Fenske-Crawford, T.J., & G.J. Niemi. 1997. Predation of artificial ground nests at two types of edges in a forest-dominated landscape. Condor 99: 14-24.

Fleming, T.H. 1992. How do fruit- and nectar-feeding birds and mammals track their food resources? Pp 355-391 in Effects of Resource Distribution on Animal-Plant Interactions. M.D. Hunter, T. Ohgushi, & P.W. Price (eds). Academic Press. California.

Fleming, T.H., R. Breitwisch, & G.H. Whitesides. 1987. Patterns of tropical vertebrate frugivore diversity. Annual Review of Ecology & Systematics 18: 91-109.

Fogden, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307-343.

Forshaw, J.M. 1989. Parrots of the World. Third (revised) edition. Lansdowne Editions, Melbourne, Australia.

Foster, R.B. 1980. Heterogeneity and disturbance in tropical vegetation. Pp 75-93 in Conservation Biology: An Evolutionary-Ecological Perspective, M.E. Soule & B.A. Wilcox (eds). Sinauer Associates Inc, Massachusetts.

Foster, R.B. 1982a. The seasonal rhythm of fruitfall on Barro Colorado Island. Pp 151-172 in The Ecology of a Tropical Rainforest: Seasonal Rhythms and Long-term Changes, E.G. Leigh Jr, A.S. Rand, & D.M. Windsor (eds). Smithsonian Institution Press, Washington.

Foster, R.B. 1982b. Famine on Barro Colorado Island. Pp 201-212 in The Ecology of a Tropical Rainforest: Seasonal Rhythms and Long-term Changes, E.G. Leigh Jr, A.S. Rand, & D.M. Windsor (eds). Smithsonian Institution Press, Washington.

Frankie, G.W., H.G. Baker, & P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62: 881-919.

Galetti, M. 1993. Diet of the Scaly-headed Parrot (*Pionus maximiliani*) in a semi-deciduous forest in southeastern Brazil. Biotropica 25: 419-425.

Galetti, M., & M. Rodrigues. 1992. Comparative seed predation on pods by parrots in Brazil. Biotropica 24: 222-224.

Gates, J.E., & L.W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59: 871-883.

Gauthier, G., & J.N.M. Smith. 1987. Territorial behaviour, nest site availability, and breeding density in Buffleheads. Journal of Animal Ecology 56: 171-184.

Gentry, A.H. 1982. Patterns of Neotropical plant species diversity. Evolutionary Biology 15: 1-84.

Gibbs, J.P., M.L. Hunter, & S.M. Melvin. 1993. Snag availability and communities of cavity nesting birds in tropical versus temperate forests. Biotropica 25: 236-241.

Gilardi, J.D. 1996. Ecology of parrots in the Peruvian Amazon: habitat, use, nutrition, and geophagy. Ph.D. Dissertation, University of California, Davis.

Gnam, R.S. 1991. Nesting behaviour of the Bahama Parrot *Amazona leucocephala bahamensis* on Abaco Island, Bahamas. Acta XX Congressus Internationalis Ornithologici 2: 673-680.

Gnam, R.S. & R.F. Rockwell. 1991. Reproductive potential and output of the Bahama Parrot *Amazona leucocephala bahamensis*. Ibis 133: 400-405.

Godfray, H.C.J., L. Patridge, & P.H. Harvey. 1991. Clutch size. Annual Review of Ecology 22: 409-429.

Grant, P.R., & B.R. Grant. 1980. Annual variation in finch numbers, foraging, and food supply on Isla Daphne Major, Galapagos. Oecologia 46: 55-62.

Greenberg, R. 1981. The abundance and seasonality of forest canopy birds on Barro Colorado Island. Biotropica 13: 241-251

Guant, A.S., L.W. Oring, K.P. Abbe, D.W. Anderson, L.F. Baptista, J.C. Barlow, & J.C. Wingfield. 1997. Guidelines to the Use of Wild Birds in Research. Special publication of the Ornithological Council. U.S.A.

Guevara, M., Y. Bergeron, R. McNeil, & A. Leduc. 1992. Seasonal flowering and fruiting patterns in tropical semi-arid vegetation of north-eastern Venezuela. Biotropica 24: 64-76.

Gustafsson, L 1988. Interspecific and intraspecific competition for nest holes in a population of the Collared Flycatcher, *Ficedula albicollis*. Ibis 130: 11-16.

von Haartman, L 1957. Adaptation in hole-nesting birds. Evolution 11: 339-347.

Hambäck, P.A. 1998. Seasonality, optimal foraging, and prey co-existence. American Naturalist 152: 881-895.

Hartshorn, G.S. 1983. Plants: Introduction. Pp 118-157 in Costa Rican Natural History. D.H. Janzen (ed). University of Chicago Press.

Heithaus, E.R., E. Stashko, & P.K. Anderson. 1982. Cumulative effects of plant-animal interactions on seed production by *Bauhinia ungulata*, a Neotropical legume. Ecology 63: 1294-1302.

Higgins, M.L. 1979. Intensity of seed predation on *Brosimum utile* by Mealy Parrots (*Amazona farinosa*). Biotropica 11: 80.

van Horne, B. & A. Bader. 1990. Diet of nestling Winter Wrens in relationship to food availability. Condor 92: 413-420.

Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96: 73-77.

Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299-1309.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Hussell, D.J.T. 1972. Factors affecting clutch size in Artic passerines. Ecological Monographs 42: 317-364.

INEGI (Instituto Nacional de Estadística, Geografía e Informatica). 1973. Fotografía aérea en blanco y negro. Vuelo alto, escala 1:50,000 con gran angular de la zona 16.

Iñigo-Elias, E.E., & M.A. Ramos. 1991. The psittacine trade in Mexico. Pp 380-392 in Neotropical Wildlife Use and Conservation, J.G. Robinson y K.H. Redford (eds). University of Chicago Press, Chicago.

Janson, C.H., & L.H. Emmons. 1990. Ecological structure of non-flying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. Pp 314-339 in Four Neotropical Rainforests, A.H. Gentry (ed). Yale University Press, USA.

Janzen, D.H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21: 620-637.

Janzen, D.H. 1969. Seed-eaters versus seed size, number, toxicity, and dispersal. Evolution 23: 1-27.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501-524.

Janzen. D.H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2: 465-492.

Janzen. D.H. 1981. *Ficus ovalis* seed predation by an Orange-chinned Parakeet (*Brotogeris jugularis*) in Costa Rica. Auk 98: 841-844.

Janzen, D.H. 1982. How and why horses open *Crescentia alata* fruits. Biotropica 14: 149-152.

Janzen, D.H. 1988. Tropical dry forests: the most endangered tropical ecosystem. Pp 130-137 in Biodiversity, E.O. Wilson (ed). National Academy Press.

Janzen, D.H., L.E. Fellows, & P.G. Waterman. 1990. What protects *Lonchocarpus* (Leguminosae) seeds in a Costa Rican dry forest? Biotropica 22: 272-285.

Janzen, D.H., & P.S. Martin. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. Science 215: 19-27.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96: 651-661.

Johnson, L.S., & L.H. Kermott. 1994. Nesting success of cavity-nesting birds using natural tree cavities. Journal of Field Ornithology 65: 36-51.

Karr, J.R. 1976. Seasonality, resource availability, and community diversity in tropical bird communities. American Naturalist 110: 973-994.

Karr, J.R. 1990. The avifauna of Barro Colorado Island and the Pipeline Road, Panama. Pp 183-198 in Four Neotropical Rainforests, A.H. Gentry (ed). Yale University Press, New Haven.

Karr, J.R., & K.E. Freemark. 1985. Habitat selection and environmental gradients: dynamics in the "stable" tropics. Ecology 64: 1481-1494.

Karr, J.R., D.W. Schemske, & N.V.L. Brokaw. 1982. Temporal variation in the understory bird community of a tropical forest. Pp 441-454 in The Ecology of a Tropical Rainforest: Seasonal Rhythms and Long-term Changes, E.G. Leigh Jr, A.S. Rand, & D.M. Windsor (eds). Smithsonian Institution Press, Washington.

Keyser, A.J., G.E. Hill, & E.C. Soehren. 1998. Effects of forest fragment size, nest density, and proximity to edge on the risk of predation to ground-nesting passarine birds. Conservation Biology 12: 986-994.

Kinnaird, M.F., T.G. O'Brien, & S. Suryadi. 1996. Population fluctuation in Sulawesi Red-knobbed Hornbills: tracking figs in space and time. Auk 113: 431-440.

Kleintjes, P.K., & D.L. Dahlsten. 1994. Foraging behavior and nestling diet of Chestnut-backed Chickadees in Monterey Pine. Condor 96: 647-653.

Krebs, C.J. 1989. Ecological Methodology. Harper Collins, London.

Krebs, J.R 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52: 2-22.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen & Co.

Lacombe, D., D.M. Bird, & K.A. Hibbard. 1994. Influence of reduced food availability on growth of captive American Kestrels. Canadian Journal of Zoology 72: 2084-2089.

Lanning, D.V. 1991. Distribution and breeding biology of the Red-fronted Macaw. Wilson Bulletin 103: 357-365.

Lanning, D.V. & J.T. Shiflett. 1983. Nesting ecology of Thick-billed Parrots. Condor 85: 66-73.

Leigh, E.G. Jr., & D.M. Windsor. 1982. Forest production and regulation of primary consumers on Barro Colorado Island. Pp 111-122 in The Ecology of a Tropical Rainforest: Seasonal Rhythms and Long-term Changes, E.G. Leigh Jr, A.S. Rand, & D.M. Windsor (eds). Smithsonian Institution Press, Washington.

Leighton, M., & D.R. Leighton. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pp 181-196 in Tropical Rainforest: Ecology and Management, S.L. Sutton, T.C. Whitmore, & A.C. Chadwick (eds). Blackwell Scientific Press, Oxford.

Levins, R. 1968. Evolution in Changing Environments. Princeton University Press. Princeton.

Levey, D.J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monographs 58: 251-269.

Li, P., & T.E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108: 405-418.

Lieberman, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. Journal of Ecology 70: 791-806.

Lindsey, G.D., W.J. Arendt, & J. Kalina. 1994. Survival and causes of mortality in juvenile Puerto Rican Parrots. Journal of Field Ornithology 65: 76-82.

Lindsey, G.D., W.J. Arendt, J. Kalina, & G.W. Pendleton. 1991. Home range and movements of juvenile Puerto Rican Parrots. Journal of Wildlife Management 55: 318-322.

Loiselle, B.A. 1988. Bird abundance and seasonality in a Costa Rican lowland rainforest canopy. Condor 90: 761-772.

Loiselle, B.A., & J.G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72: 180-193.

Loiselle, B.A., & J.G. Blake. 1992. Population variation in a tropical bird community: implications for conservation. BioScience 42: 838-845

Loiselle, B.A., & J.G. Blake. 1994. Annual variation in birds and plants of a tropical second-growth woodland. Condor 96: 368-380.

Loiselle, B.A., & W.G. Hoppes. 1983. Nest predation in insular and mainland lowland rainforest in Panama. Condor 85: 93-95.

Lott, E.J. 1993. Annotated checklist of the vascular flora of the Chamela Bay region, Jalisco, Mexico. Occasional Papers of the California Academy of Sciences 148: 1-60.

Lott, E.J., S.H. Bullock, & J.A. Solis-Magallanes. 1987. Floristic diversity and structure of upland and arroyo forests of coastal Jalisco. Biotropica 19: 228-235.

Lowman, M.D., & P.K. Wittman. 1996. Forest canopies: methods, hypotheses, and future directions. Annual Review of Ecology & Systematics 27: 55-81.

Lugo, A.E., & J.L. Frangi. 1993. Fruit fall in the Luquillo experimental forest, Puerto Rico. Biotropica 25: 73-84.

Maass, J.M. 1995. Conversion of tropical dry forest to pasture and agriculture. Pp 399-422 in Seasonally Dry Tropical Forests. S.H. Bullock, H.A. Mooney, & E. Medina (eds). Cambridge University Press, Cambridge.

Mann, R.E.H., & P.D. Mann. 1978. Breeding Finch's Amazon Parrot (*Amazona finschi*). The Avicultural Magazine 84: 187-189.

Martijena, N.E., & S.H. Bullock. 1994. Monospecific dominance of a tropical deciduous forest in Mexico. Journal of Biogeography 21: 63-74.

Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology & Systematics 18: 453-487.

Martin, T.E., & J.R. Karr. 1986. Temporal dynamics of Neotropical birds with special reference to frugivores in second-growth woods. Wilson Bulletin 98: 38-60.

Martin, T.E., & P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73: 579-592.

Martuscelli, P. 1994. Maroon-bellied Conures feeding on gall-forming homopteran larvae. Wilson Bulletin 106: 769-770.

Masera, O.R., M.J. Ordóñez, & R. Dirzo. 1992. Volume 4: Carbon emissions from deforestation in Mexico: current situation and long-term scenarios. Carbon Emissions and Sequestration in Forests: Case Studies from Seven Developing Countries, W. Makundi & J. Sathaye (Series eds). Environmental Protection Agency/Lawrence Berkeley Laboratory, USA

Masera, O.R., M.J. Ordóñez, & R. Dirzo. 1996. Carbon emissions from Mexican forests: current situation and long-term scenarios. Climate Change 10: 1-31.

Mayfield, H.F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.

Merriam, G. 1991. Corridors and connectivity: animal populations in heterogenous environments. Pp 133-142 in Nature Conservation 2: The Role of Corridors. D.A. Saunders & R.J. Hobbs. Surrey Beatty & Sons, Australia.

Miller, B., R. Reading, J. Strittholt, C. Carroll, R. Noss, M. Soule, O. Sanchez, J. Terborgh, D. Brightsmith, T. Cheeseman, & D. Foreman. in press. Focal species in the design of reserve networks. Wild Earth 11:

Minot, E.O., & C.M. Perrins. 1986. Interspecific interference competition - nest sites for Blue and Great Tits. Journal of Animal Ecology 55: 331-350.

Miranda, A. 1998. Deforestación y fragmentación del hábitat: consecuencias ecológicas sobre la fauna de mamíferos de la selva tropical estacional. Ph.D. Thesis, Instituto de Ecología, UNAM, Mexico.

Moffet, M.W., & M.D. Lowman. 1995. Canopy access techniques. Pp 3-26 in Forest Canopies, M.D. Lowman & N.M. Nadkarni (eds). Academic Press.

Mulliken, T.A., S.R. Broad, & J.B. Thomsen. 1992. The wild bird trade - an overview. Pp 1-24 in Perceptions, Conservation, and Management of Wild Birds in Trade, J.B. Thomsen, S.R. Edwards, & T.A. Mulliken (eds). TRAFFIC International, Cambridge.

Munn, C.A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. Pp 683-712 in Neotropical Ornithology. Ornithological Monographs No. 36, P.A. Buckley, M.S. Foster, E.S. Morton, R.S. Ridgely, & F.G. Buckley (eds). American Ornithologists Union, Washington.

Munn, C.A. 1992. Macaw biology and ecotourism, or "when a bird in the bush is worth two in the hand". Pp 47-73 in New World Parrots in Crisis: Solutions from Conservation Biology. S.R. Beissinger & N.F.R. Snyder (eds). Smithsonian Institution Press, Washington.

Murali, K.S., & R. Sukumar. 1994. Reproductive phenology of a tropical dry forest in Mudumalai, southern India. Journal of Ecology 82: 759-767.

Navarro, J.L., & E.H. Bucher. 1990. Growth of Monk Parakeets. Wilson Bulletin 102: 520-525.

Navarro, J.L., M.B. Martella, & E.H. Bucher. 1992. Breeding season and productivity of Monk Parakeets in Cordoba, Argentina. Wilson Bulletin 104: 413-424.

Negro, J.J., A. Chastin, & D.M. Bird. 1994. Effects of short-term food deprivation on growth of hand-reared American Kestrels. Condor 96: 749-760.

Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109: 33-98.

Nilsson, S.G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15: 167-175.

Nilsson, S.G. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. Auk 103: 432-435.

NOM-059-ECOL-1994 (Norma Oficial Méxicana). 1994. Que determina las especies y subespecies de flora y fauna silvestres terrestres y acuaticas en peligro de extinción, amenazadas, raras y las sujetas a protección especial, y que establece especificaciones para su protección. Diario oficial de la federación. Lunes 16 de mayo de 1994.

Norusis, M.J./SPSS. 1994. SPSS Advanced Statistics^{TM} 6.1. SPSS Inc., Chicago.

O'Donnell, C.F.J., & P.J. Dilks. 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. New Zealand Journal of Ecology 18: 87-107.

Opler, P.A., G.W. Frankie, & H.G. Baker. 1980. Comparative phenology studies of treelet and shrub species in tropical wet and dry forests in lowland Costa Rica. Journal of Ecology 68: 167-188.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228: 1221-1222.

Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull (*Larus argentatus*). Ibis 117: 517-520.

Pearson, D.L. 1971. Vertical stratification of birds in a tropical dry forest. Condor 73: 46-55.

Peres, C.A. 1994. Primate responses to phenological changes in an Amazonian terra firme forest. Biotropica 26: 98-112.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Perry, D.R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155-157.

Perry, D.R., & J. Williams. 1981. The tropical rain forest canopy: a method providing total access. Biotropica 13: 283-285.

Pierotti, R., & C.A. Bellrose. 1986. Proximate and ultimate causation of egg size and the "third-chick disadvantage" in the Western Gull. Auk 103: 401-407.

Poulin, B., G. Lefebvre, & R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73: 2295-2309.

Poulin, B., G. Lefebvre, & R. McNeil. 1993. Variations in bird abundance in tropical arid and semi-arid habitats. Ibis 135: 432-441.

Poulin, B., G. Lefebvre, & R. McNeil. 1994a. Characteristics of feeding guilds and variation in diets of bird species of three adjacent tropical sites. Biotropica 26: 187-197.

Poulin, B., G. Lefebvre, & R. McNeil. 1994b. Diets of land birds from north-eastern Venezuela. Condor 96: 354-367.

Pribil, S., & J. Picman. 1991. Why House Wrens destroy clutches of other birds - a support for the nest site competition hypothesis. Condor 93: 184-185.

Price, T. 1987. Diet variation in a population of Darwin's finches. Ecology 68: 1015-1028.

Primack, R.B. 1987. Relationships among flowers, fruits, and seeds. Annual Review of Ecology & Systematics 18: 409-430.

Purcell, K.L., J. Verner, & L.W. Oring. 1997. A comparison of the breeding ecology of birds nesting in boxes and tree cavities. Auk 114: 646-656.

Quinney, T.E., D.J.T. Hussell, & C.D. Ankney. 1986. Sources of variation in growth of Tree Swallows. Auk 103: 389-400.

Raphael, M.G., & M. White. 1984. Use of snags by cavity nesting birds in Sierra Nevada. Wildlife Monographs 86: 1-66.

Rathcke, B., & E.P. Lacey. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology & Systematics 16: 179-214.

Renton, K 1994. Seasonal variations in encounter rates and the factors limiting breeding density of macaws, *Ara* species, in the floodplain forest of the Manu Biosphere Reserve, Peru. M.Sc. Thesis, University of Kent at Canterbury, UK.

Rey, P.J. 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. Ecology 76: 1625-1635.

Richter, W. 1984. Nestling survival and growth in the Yellow-headed Blackbird, *Xanthocephalus xanthocepalus*. Ecology 65: 597-608.

Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978-983.

Ricklefs, R.E. 1968a. Patterns of growth in birds. Ibis 110: 419-451.

Ricklefs, R.E. 1968b. Weight recession in nestling birds. Auk 85: 30-35.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Smithsonian Contribution to Zoology 9: 1-48.

Ricklefs, R.E. 1976. Growth rates of birds in the humid New World tropics. Ibis 118: 179-207.

Ricklefs, R.E. 1979. Adaption constraint and compromise in avian postnatal development. Biological Review 54: 269-290.

Ricklefs, R.E. 1982. Some considerations on sibling competition and avian growth rates. Auk 99: 141-147.

Ridgely, R.S. 1981. The current distribution and status of mainland Neotropical parrots. Pp 233-384 in Conservation of New World Parrots: Proceedings of the ICBP Parrot Working Group Meeting, St Lucia 1980, R.F. Pasquier (ed). Smithsonian Institution Press/ICBP Technical Publication No 1.

Rinke, D. 1989. The reproductive biology of the Red Shining Parrot *Prosopeia tabuensis* on the island of 'Eua, Kingdom of Tonga. Ibis 131: 238-249.

Robinson, S.K., & J. Terborgh. 1990. Bird communities of the Cocha Cashu Biological Station in Amazonian Peru. Pp 199-216 in Four Neotropical Rainforests. A.H. Gentry (ed). Yale University Press, New Haven.

Rockwell, R.F., C.S. Findlay, & F. Cooke. 1987. Is there an optimal clutch size in Snow Geese? American Naturalist 130: 839-863.

Rodenhouse, N.L., & R.T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. Ecology 73: 357-372.

Roet, E.C., D.S. Mack, & N. Duplaix. 1981. Psittacines imported by the United States (October 1979-June 1980). Pp 21-56 in Conservation of New World Parrots: Proceedings of the ICBP Parrot Working Group Meeting, St Lucia 1980, R.F. Pasquier (ed). Smithsonian Institution/ICBP Tech. Publ. No 1.

Rowley, I. 1990. Behavioural Ecology of the Galah *Eolophus roseicapillus* in the Wheatbelt of Western Australia. Surrey Beatty & Sons Pty Ltd., Australia.

Rowley, I., & G. Chapman. 1991. The breeding biology, food, social organization, demography and conservation of the Major Mitchell or Pink Cockatoo, *Cacatua leadbeateri*, on the margin of the Western Australian wheatbelt. Australian Journal of Zoology 39: 211-261.

Rzedowski, J. 1994. Vegetación de México. 6th Edition, Limusa Noriega Editores, Mexico.

Sakai, H.F., & J.R. Carpenter. 1990. The variety and nutritional value of foods consumed by Hawaiian Crow nestlings, an endangered species. Condor 92: 220-228.

Saunders, D.A. 1979. The availability of tree hollows for use as nest sites by White-tailed Black Cockatoos. Australian Wildlife Research 6: 205-216.

Saunders, D.A. 1980. Food and movements of the short-billed form of the White-tailed Black Cockatoo. Australian Wildlife Research 7: 257-269.

Saunders, D.A. 1982. The breeding behaviour and biology of the short-billed form of the White-tailed Black Cockatoo *Calyptorhynchus funereus*. Ibis 124: 422-455.

Saunders, D.A. 1986. Breeding season, nesting success and nestling growth in Carnaby's Cockatoo, *Calyptorhynchus funereus latirostris*, over 16 years at Coomallo Creek, and a method for assessing the viability of populations in other areas. Australian Wildlife Research 13: 261-273.

Saunders, D.A. 1990. Problems of survival in an extensively cultivated landscape: the case of the Carnaby's Cockatoo *Calyptorhynchus funereus latirostris*. Biological Conservation 54: 277-290.

Saunders, D.A. 1991. The effect of land clearing on the ecology of Carnaby's Cockatoo and the inland Red-tailed Black Cockatoo in the wheatbelt of Western Australia. Acta XX Congressus Internationalis Ornithologici 2: 658-665.

Saunders, D.A., R.J. Hobbs, & C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5: 18-32.

Saunders, D.A., G.T. Smith, & N.A. Campbell. 1984. The relationship between body weight, egg weight, incubation period, nestling period, and nest site in the Psittaciformes, Falconiformes, Strigiformes and Columbiformes. Australian Journal of Zoology 32: 57-65.

Saunders, D.A, G.T. Smith, I. Rowley. 1982. The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. Australian Wildlife Research 9: 541-556.

van Schaik, C.P., J.W. Terborgh, S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of Ecology & Systematics 24: 353-377.

Schluter, D. 1981. Does the theory of optimal diets apply in complex environments? American Naturalist 118: 139-147.

Schluter, D. 1982a. Seed and patch selection by Galapagos ground finches: relation to foraging efficiency and food supply. Ecology 63: 1106-1120.

Schluter, D. 1982b. Distributions of Galapagos ground finches along an altitudinal gradient: the importance of food supply. Ecology 63: 1504-1517.

Sieving, K.E. 1992. Nest predation and differential insular extinction among selected forest birds of Central Panama. Ecology 73: 2310-2328.

Skutch, A.F. 1966. A breeding bird census and nesting success in Central America. Ibis 108: 1-16.

Skutch, A.F. 1976. Parent Birds and Their Young. University of Texas Press, Austin.

Small, M.F., & M.L. Hunter. 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia 76: 62-64.

Smith, G.T. 1991. Breeding ecology of the Western Long-billed Corella, *Cacatua pastinator pastinator*. Wildlife Research 18: 91-110.

Smith, G.T., & L.A. Moore. 1991. Foods of corellas *Cacatua pastinator* in Western Australia. Emu 91: 87-92.

Smith, G.T., & L.A. Moore. 1992. Patterns of movement in the Western Long-billed Corella *Cacatua pastinator* in the South-west of Western Australia. Emu 92: 19-27.

Smith, G.T., & D.A. Saunders. 1986. Clutch size and productivity in three sympatric species of cockatoo (Psittaciformes) in the south-west of Western Australia. Australian Wildlife Research 13: 275-285.

Smith, J.N.M., P.R. Grant, B.R. Grant, I.J. Abbott, & L.K. Abbott. 1978. Seasonal variation in feeding habits of Darwin's ground finches. Ecology 59: 1137-1150.

Smythe, N. 1970a. Relationships between fruiting seasons and seed dispersal in a Neotropical forest. American Naturalist 104: 25-35.

Smythe, N. 1970b. The adaptive value of the social organization of the coati (*Nasua narica*). Journal of Mammalogy 51: 818-820.

Snyder, N.F.R., F.C. James, & S.R. Beissinger. 1992. Toward a conservation strategy for Neotropical psittacines. Pp 257-276 in New World Parrots in Crisis: Solutions from Conservation Biology, S.R. Beissinger & N.F.R. Snyder (eds). Smithsonian Institution Press, Washington.

Snyder, N.F.R., S.E. Koenig, J. Koschmann, H.A. Snyder, & T.B. Johnson. 1994. Thick-billed Parrot releases in Arizona. Condor 96: 844-862.

Snyder, N.F.R., J.W. Wiley, & C.B. Kepler. 1987. The Parrots of Luquillo: Natural History and Conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles.

Sonerud, G.A. 1985. Nest hole shift in Tengmalm's Owl *Aeogolius funereus* as defence against nest predation involving long-term memory in the predator. Journal of Animal Ecology 54: 179-192.

Sonerud, G.A. 1989. Reduced predation by Pine Martins on nests of Tengmalm's Owl in relocated boxes. Animal Behaviour 37: 332-334.

Stoleson, S.H., & S.R. Beissinger. 1997a. Hatching asynchrony in parrots: boon or bane for sustainable use? Pp 157-180 in Behavioral Approaches to Conservation in the Wild. J.R. Clemmons & R. Buchholz (eds). Cambridge University Press, Cambridge.

Stoleson, S.H., & S.R. Beissinger. 1997b. Hatching asynchrony, brood reduction, and food limitation in a Neotropical parrot. Ecological Monographs 67: 131-154.

Taylor, P.D., L. Fahrig, K. Henein, & G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571-573.

Terborgh, J. 1986a. Keystone plant resources in the tropical forest. Pp 330-344 in Conservation Biology: The Science of Scarcity and Diversity, M.E. Soule (ed). Sinauer Associates Inc, Massachusetts.

Terborgh, J. 1986b. Community aspects of frugivory in tropical forests. Pp 371-384 in Frugivores and Seed Dispersal, A. Estrada & T.H. Fleming (eds). Dr W Junk Publishers, Dordrecht.

Terborgh, J. 1988. The big things that run the world - a sequel to E. O. Wilson. Conservation Biology 2: 402-403.

Terborgh, J., S.K. Robinson, T.A. Parker, C.A. Munn, & N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. Ecological Monographs 60: 213-238.

Terborgh, J., & B. Winter. 1980. Some causes of extinction. Pp 119-133 in Conservation Biology: An Evolutionary-Ecological Perspective. M.E. Soule & B.A. Wilcox (eds). Sinauer Associates Inc., Massachusetts.

Thomsen, J.B. & A. Brautigam. 1991. Sustainable use of Neotropical parrots. Pp 359-379 in Neotropical Wildlife Use and Conservation. J.G. Robinson & K.H. Redford (eds). University of Chicago Press, Chicago.

Thomsen, J.B., & T.A. Mulliken. 1992. Trade in Neotropical psittacines and its conservation implications. Pp 221-239 in New World Parrots in Crisis: Solutions from Conservation Biology. S.R. Beissinger & N.F.R. Snyder (eds.). Smithsonian Institution Press, Washington.

Thorington, R.W., B. Tannenbaum, A. Tarak, R. Rudran. 1982. Distribution of trees on Barro Colorado Island: a five hectare sample. Pp 83-94 in The Ecology of a Tropical Rainforest: Seasonal Rhythms and Long-term Changes. E.G. Leigh, A.S. Rand, & D.M. Windsor (eds). Smithsonian Institution Press, Washington.

Tveraa, T., B.E. Saether, R. Aanes, & K.E. Erikstad. 1998. Regulation of food provisioning in the Antartic petrel: the importance of parental body condition and chick body mass. Journal of Animal Ecology 67: 699-704.

Valenzuela-Galvan, D. 1998. Efectos de la estacionalidad ambiental en la densidad, la conducta de agrupamiento y el tamaño del área de actividad del Coatí (*Nasua narica*) en selvas tropicales caducifolias. Ph.D. Thesis. Instituto de Ecologia, UNAM. México.

Veiga, J.P. 1992. Hatching asynchrony in the House Sparrow: a test of the egg-viability hypothesis. American Naturalist 139: 669-675.

Village, A. 1983. The role of nest site availability and territorial behaviour in limiting the breeding density of kestrels. Journal of Animal Ecology 52: 635-645.

Ward, P. 1965. Feeding ecology of the Black-faced Dioch, *Quelea quelea*, in Nigeria. Ibis 107: 173-214.

Waltman, J.R., & S.R. Beissinger. 1992. Breeding behavior of the Green-rumped Parrotlet. Wilson Bulletin 104: 65-84.

Wermundsen, T. 1997. Seasonal change in the diet of the Pacific Parakeet *Aratinga strenua* in Nicaragua. Ibis 139: 566-568.

Werschkul, D.B., & J.A. Jackson. 1979. Sibling competition and avian growth rates. Ibis 12: 97-102.

Wheelock, W. 1988. Ropes, Knots; and Slings for Climbers. Revised Edition. La Siesta Press, California.

Whitacre, D.F. 1981. Additional techniques and safety hints for climbing tall trees, and some equipment and information sources. Biotropica 13: 286-291.

White, L.J.T. 1994. Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. Journal of Tropical Ecology 10: 298-312.

Whitney, K.D., & T.B. Smith. 1998. Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation. Animal Conservation 1: 107-117.

Wiens, J.A. 1976. Population responses to patchy environments. Annual Review of Ecology & Systematics 7: 81-120.

Wiens, J.A. 1985. Vertebrate responses to environmental patchiness in arid and semi-arid ecosystems. Pp 169-192 in The Ecology of Natural Disturbance and Patch Dynamics. S.T.A. Pickett, White (eds). Academic Press.

Wiens, J.A. 1994. Habitat fragmentation: island *v* landscape perspectives on bird conservation. Ibis supplement 137: S97-S104.

Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1211-1214.

Wilcove, D.S., C.H. McLellan, & A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pp 237-256 in Conservation Biology: The Science of Scarcity and Diversity. M.E. Soule (ed). Sinauer Associates Inc., Massachusetts.

Wilson, K.A., R. Field, & M.H. Wilson. 1995. Successful nesting behavior of Puerto Rican Parrots. Wilson Bulletin 107: 518-529.

Wilson, K.A., M.H. Wilson, & R. Field. 1997. Behavior of Puerto Rican Parrots during failed nesting attempts. Wilson Bulletin 109: 490-503.

Wu, J., & O.L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quaterly Review of Biology 70: 439-466.

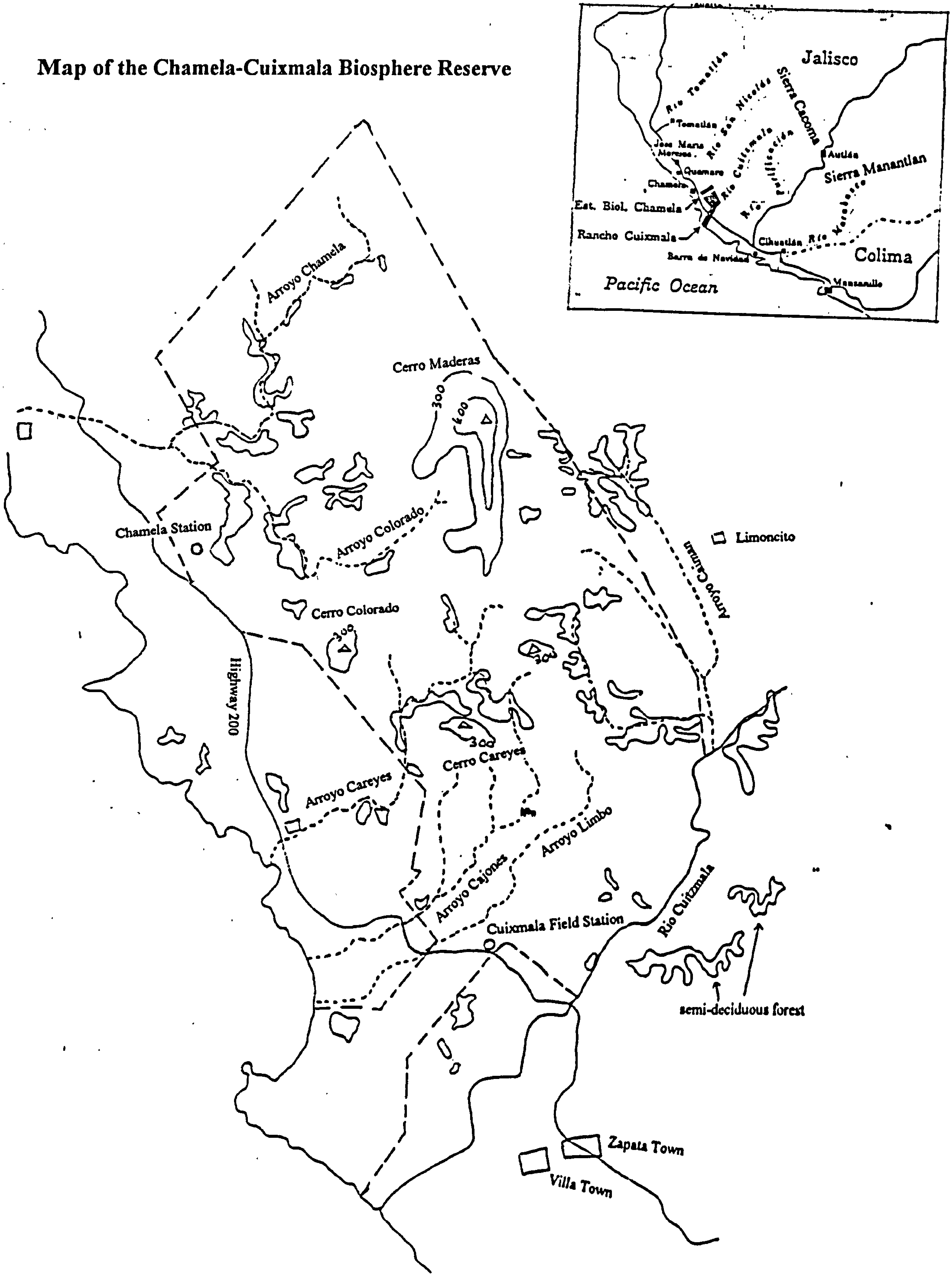
Zach, R. 1982. Hatching asynchrony, egg size, growth, and fledging in tree swallows. Auk 99: 695-700.

Zach, R. 1988. Growth-curve analysis: a critical review. Auk 105: 208-210.

Zar, J.H. 1996. Biostatistical Analysis. Third edition. Prentice Hall International Editions.

APPENDIX 1

Map of the Chamela-Cuixmala Biosphere Reserve



APPENDIX 2

HISTORIA NATURAL DEL LORO CORONA LILA (*AMAZONA FINSCHI*)[2]

El loro corona lila (*Amazona finschi*) es una especie endémica a la costa del Pacifico de México (Forshaw 1989), y está considerada como una especie amenazada (NOM-059-ECOL-1994). Es un loro de tamaño mediano que mide 33 cm de cabeza a cola y con un peso promedio de 310 g. Puede ser dificil observarlo dentro del follaje de los arboles por su plumaje verde, y se caracteriza por su corona de color lila que continua a los lados de la nuca. Las alas miden un promedio 190 mm y solo cuando se despliegan en vuelo se ven las plumas primarias azules y las secundarias rojas.

La época de reproducción para los loros es de febrero a junio y anidan principalmente en cavidades naturales de árboles maduros de *Celaenodendron mexicanum* ('Guayabillo') y *Astronium graveolens* ('Culebro'). Las hembras ponen dos o tres huevos en febrero, y los incuban por un periodo promedio de 28 días. Los huevos eclosionan a principios de marzo y los pollos nacen con los ojos cerrados y sin plumaje. Al eclosionar los huevos, los pollos pesan un promedio de 16 g y tienen un tamaño de ala de 12 mm. Durante los siguentes dos meses los pollos alcanzan su tamaño máximo y desarollan su plumaje adulto antes de dejar el nido. Normalmente dejan el nido a los 60 días después de la eclosión del huevo.

A pesar de que parecen ser muy abundantes en la zona, los loros corona lila en la región de Chamela-Cuixmala, tienen una tasa reproductiva muy baja. Solo 40% de los nidos tienen éxito cada año. El factor principal que limita el éxito reproductivo es la depredación sobre los huevos y pollos. Los depredadores principales incluyen reptiles como el tilcuate (*Drymarchon corais*), la iguana verde (*Iguana iguana*), y el escorpión (*Heloderma horridum*) además de mamíferos como el tlacuache (*Didelphis virginiana*), y los tejones (*Nasua narica*). El hombre también tiene un impacto

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[2] Book chapter submitted to 'La Ecología de Chamela'. S. Bullock, F.A. Noguera, R. Ayala, & A.N. Garcia (eds).

importante sobre el éxito reproductivo de la población silvestre de loros por el saqueo ilegal de los pollos en los nidos.

Después de que abandonan el nido, los depredadores principales de los loros juveniles y adultos son los gavilanes. El período crítico para la sobrevivencia de un pollo juvenil o volantón es las primeras dos o tres semanas después de dejar el nido, debido a que todavía el pollo juvenil no vuela bien y tiene que aprender como evitar a los depredadores. Durante ese período, 25% de los volantones serán depredados por los gavilanes. Debido a esa alta depredación sobre los huevos y pollos juveniles, solo 0.7 pollos por cada pareja que empieza a anidar llegan a su primer año de edad. Los pollos juveniles siguen en sus grupos familiares por un mínimo de tres meses después de dejar el nido. Al separarse de los padres, los juveniles se mantienen juntos en grupos hasta que forman sus propias parejas.

El loro corona lila tiene la costumbre de agregarse en parvadas grandes para dormir en lugares conocidos como dormitorios. Por medio de la técnica de radio-telemetría se ha podido determinar que los dormitorios principales para esta especie se localizan en los cerros más altos de la reserva de Chamela-Cuixmala: el Cerro Maderas; el Cerro Careyes; y el Cerro Colorado. El patrón normal de actividad de los loros durante el día consiste en volar al amanecer de los dormitorios a las zonas de forrageo, principalmente por los arroyos de mayor cauce como Chamela, Careyes, Caiman, Colorado, y Cajones, pero también sobre vegetación subperennifolia al lado del río Cuitzmala y en las zonas planas. Los loros realizan su mayor actividad de forrageo durante las primeras dos o tres horas en la manaña. Apartir de las 11:00 horas hasta las 16:00 horas del día, la actividad de los loros disminuye considerablemente, y se protegen del calor de medio día escondiendose bajo la sombra de las hojas. Los loros forragean un par de horas más por la tarde, antes de volar a los dormitorios comunales un poco antes del anochecer.

La dieta del loro corona lila es muy variable y durante todo el año se ha observado a los loros comiendo semillas, frutos, y hojas de 34 diferentes especies de plantas, aunque el componente principal de la dieta es semillas inmaduras, los cuales forman

70% de la dieta. Tambien, la dieta cambia en relación al patrón de la estacionalidad en la región, y la fenologia de los arboles en los diferentes tipo de selva. Durante la época seca, los loros se alimentan principalmente de semillas de árboles caracteristicas de la selva subperennifolia como *Astronium graveolens*, *Brosimum alicastrum*, y *Celaenodendron mexicanum*, ademas de semillas de *Comocladia engleriana*, y frutos de *Ficus insipida*. Durante la época de lluvias, los loros se alimentan de especies de plantas caracteristicas del bosque tropical caducifolio como *Caesalpinia pulcherrima*, *Esenbeckia nesiotica*, *Jatropha standleyi*, y *Sciadodendron excelsum*.

Con relación al uso que hacen del habitat, se nota que la vegetación subperennifolia es muy importante para mantener a los loros durante el período seco crítico en la zona. Como respuesta a la estacionalidad de la zona, los loros concentran su actividad de forrageo en la selva subperennifolia durante la época seca, aunque durante las lluvias los loros también utilizan el bosque tropical caducifolio, que es la vegetación dominante en la reserva de Chamela-Cuixmala. Otra respuesta a la estacionalidad que tienen los loros es la de hacer una migración altitudinal de aproximadamente 50 km hasta la Sierra Cacoma, cerca de la Sierra de Manantlán, durante los meses más secos de mayo a junio. Esto tiene implicaciones importantes para la conservación de los loros en la región, y para el mantenimiento de la integridad de la reserva de Chamela-Cuixmala como parte de un ecosistema altitudinal.

Se está siguiendo con la investigación a fondo sobre los movimientos de los loros y su uso del habitat durante la migración estacional, para indicar corredores biológicos potenciales que podrían utilizar los loros entre las reservas de Chamela-Cuixmala y Sierra de Manantlán como parte de un ecosistema altitudinal. En conjunto, se está investigando la respuesta de los loros a la estacionalidad al estudiar el cambio de dieta, uso del habitat, y movimientos estacionales. También, hay evidencia que muestra que las variaciones en la disponibilidad de los recursos alimenticios durante la época seca, puede impactar el crecimiento y sobrevivencia de los pollos de los loros, y por ello se están llevando a cabo investigaciones para evaluar el impacto potencial de las fluctuaciones en factores ambientales sobre las poblaciones silvestres de este especie amenazada.

Literatura Citada

Forshaw, J.M. 1989. Parrots of the World. Third (revised) edition. Lansdowne Editions, Melbourne, Australia.

NOM-059-ECOL-1994 (Norma Oficial Méxicana). 1994. Que determina las especies y subespecies de flora y fauna silvestres terrestres y acuaticas en peligro de extinción, amenazadas, raras y las sujetas a protección especial, y que establece especificaciones para su protección. Diario oficial de la federación. Lunes 16 de mayo de 1994.

APPENDIX 3

THE SCARLET MACAW (*ARA MACAO CYANOPTERA*)[3]

Common Name: Scarlet Macaw (English)

Scientific Name: Central American sub-species: *Ara macao cyanoptera*

Order: *Psittaciformes*

Family: *Psittacidae*

Status: Endangered in Mexico (NOM-059-ECOL-1994), Guatemala (Decree 4-89), Belize (Wildlife Protection Act 4-81), Honduras (Law #004-78, 206-82), Nicaragua (Wildlife Law 1983), and Costa Rica (Wildlife Law #7317). Extinct in El Salvador. CITES Appendix I. IUCN category 1 (vulnerable).

Threats: Habitat destruction, and capture for the wildlife trade were principal threats to the species during the 1970s - 1980s. Extensive illegal poaching of wild nestlings continues to be a severe problem for remaining populations in the wild.

Habitat: Tropical humid and dry forests below 1,000 m elevation.

Distribution: Currently restricted to small remnant populations in southern Chiapas, Mexico; western Peten, Guatemala; south-west Belize; north-eastern Honduras; eastern Nicaragua; and the Pacific coast of Costa Rica. Formerly distributed throughout Central America from north-eastern Mexico along the Pacific and Atlantic coasts to Panama.

Description

The Scarlet Macaw is the third largest of the 16 species of macaw in the Neotropics, measuring 85 cm from head to tail. Average adult weight is 1,200 g, with a wing length of 41 cm, and tail length of 53 cm (Forshaw 1989; Wiedenfeld 1994). The general plumage is bright red, with a distinctive yellow band on the wing, which is tipped with blue (Forshaw 1989). The Scarlet Macaw in Central America is considered a separate sub-species to that in South America as there is no green band

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[3] Renton, K. in press. The Scarlet Macaw. in Endangered Animals: Conflicting Issues. R.P. Reading & B.J. Miller (eds). Greenwood Press, USA.

separating the yellow and blue on the wing, and birds from Central America are larger in size than those from South America (Wiedenfeld 1994).

Natural History

Scarlet Macaws are generally seen in bonded pairs, or small family groups with 1 or 2 fledged young, though large groups of 20 - 30 individuals may flock together at feeding trees. The breeding season extends from late November through to the end of May, and nest sites are located in cavities in tall live or dead trees (Marineros & Vaughan 1995; Iñigo-Elias 1996). Scarlet Macaws are highly territorial around nest sites, and may experience pressures from nest site limitation (Iñigo-Elias 1996).

Nesting macaws usually lay 1 - 3 eggs, which the female incubates for approximately 28 - 34 days (Iñigo-Elias 1996). The chicks hatch asynchronously, with eyes fused shut and only a light covering of feather down. The nestlings develop in the nest cavity over 2 - 3 months, and attain adult size and plumage prior to fledging (Iñigo-Elias 1996). Only 20% of the wild population may breed in a given year, with 60 - 70% of nests producing one or two young (Munn 1992; Marineros & Vaughan 1995; Iñigo-Elias 1996). The main cause of nest failure is predation on eggs or young chicks by reptiles, small raptors, and medium-sized mammals, as well as human poachers (Marineros & Vaughan 1995; Iñigo-Elias 1996).

The diet of Scarlet Macaws consists principally of immature seeds from a variety of plant species, though they also consume fruits, flowers, and leaf stems (Munn 1988; Marineros & Vaughan 1995). Scarlet Macaws may be highly adaptable in diet and range widely in search of food resources, but nothing is known of their movements and area requirements.

Historic and Current Threats

Scarlet Macaws were once widespread in the tropical humid and dry forests along the Pacific and Atlantic coasts of Central America from north-eastern Mexico through to Panama (Forshaw 1989; Wiedenfeld 1994). However in the 1970s, government sponsored development and recolonisation policies, such as the National Deforestation Program (Programa Nacional de Desmontes) in Mexico, and the Peten

Promotion and Development Association (FYDEP) in Guatemala, resulted in extensive deforestation. In Mexico, government policy aimed to promote agricultural expansion by donating land and financial subsidies to community groups, known as 'ejidos'. However, in order to maintain ownership, members of the ejido had to demonstrate that they were developing the land. The government definition of development was to deforest land for agriculture, and financial subsidies were provided to encourage this. Added to which, border disputes with Guatemala led to government sponsored recolonisation programs to populate and develop tropical forest areas along the frontier.

By the late 1970s, agricultural development, hard-wood extraction, and recolonisation had resulted in the destruction of tropical forests, and elimination of the Scarlet Macaw, from eastern Mexico, and the Pacific coasts of Guatemala, Honduras, and Nicaragua. In Costa Rica, only 20% of the original macaw habitat still exists, with the remaining Scarlet Macaw populations located in three main areas on the Pacific slope (Marineros & Vaughan 1995). Civil wars in El Salvador and Nicaragua also decimated forests and wildlife of those countries. Natural disasters such as Hurricane Hattie in 1961 and Hurricane Joan in 1988, further impacted Scarlet Macaw populations in Belize and Nicaragua. At present, the impact of the 1998 Hurricane Mitch on Scarlet Macaw populations in Honduras is unknown.

However, the principal threat to wild populations has been the commercial exploitation of Scarlet Macaws for the international wildlife trade. Many of the problems of international trade derive from the disparity between local and international market values, with major profits from trade going to a few middlemen. In Mexico, a local trapper may receive $19 for a Scarlet Macaw, while a trader in the country of origin may receive $450, however once in the United States, a Scarlet Macaw may be sold for as much as $4,000 (Iñigo-Elias & Ramos 1991). Hence, it is at the level of the US importer that the trade becomes most highly organized and profitable, with only four distinct companies controlling 74% of US live bird imports in 1988 (Swanson 1992). The enormous profits which may be made by a few highly organized importers is the major driving force behind international trade.

The Scarlet Macaw was placed on Appendix I of CITES in 1986 which prohibited international trade, but did not control internal trade. CITES is in essence a trade agreement rather than a conservation treaty, hence while CITES may limit legal international trade, it is ineffective against illegal or local trade. Classification of a species under CITES Appendix I may also raise the market value and demand for that species, which is then considered rare. At the local level, enforcement of wildlife laws is hampered by a lack of resources in wildlife departments, and a lack of importance attributed to wildlife laws. Hence, enforcement is frequently non-existent in the remote, rural, or border regions where most macaw populations occur. There remains an extensive and overt illegal commerce in Scarlet Macaws in Guatemala, Honduras, Nicaragua, and Costa Rica, even though the species is protected by national laws in all of these countries. In Costa Rica, traditional Scarlet Macaw nest trees located along roadsides have ladders built into the trunk to aid poachers (Marineros & Vaughan 1995).

The Central American Scarlet Macaw has now been reduced to small, discontinuous populations in Mexico, Guatemala, Belize, Honduras, Nicaragua, and Costa Rica, estimated at a total 4,000 individuals (Wiedenfeld 1994). Conservation of the Scarlet Macaw in Central America therefore involves a number of countries with potentially differing conservation structures, national agendas, and socio-economic profiles, many of which have only recently resolved long-standing disputes over sovereignty. Role players in Scarlet Macaw conservation include various wildlife departments, researchers from different institutions, national and international conservation organisations, and economically poor rural communities around national parks and macaw areas.

Captive breeding and re-introduction of Scarlet Macaws may be an option for conservation. However, captive breeding requires enormous logistical and financial investment, and has potentially detrimental impacts on wild populations through the spread of disease, or genetic inbreeding (Snyder et. al. 1996). In addition, captive-reared individuals frequently lack the behavioral skills required to locate food and evade predators in the wild (Snyder et. al. 1994), hence release programs have been most successful where captive-reared birds are able to join wild populations (Sanz & Grajal 1998).

Above all, captive-breeding and re-introduction do not address the socio-economic problems in Scarlet Macaw conservation. There is an inherent conflict in attitudes between those organisations, institutions, and individuals desiring to protect Scarlet Macaw populations, and poor rural communities which view the Scarlet Macaw as an economic resource to be exploited. Hence, the most effective conservation measures are likely to be those which attack the underlying problem of poaching through education, and work with local communities.

Recommendations

Effective conservation of the Scarlet Macaw must be based on ecological data of population trends and habitat requirements of macaws, and address socio-economic aspects through educational outreach programs and community based development. Field studies demonstrate that Scarlet Macaw populations have low reproductive rates making them vulnerable to decline. However, little is known of the dynamics, resource, and area requirements of wild populations, which is necessary to determine appropriate conservation strategies.

Providing economic benefits to local communities may encourage them to conserve Scarlet Macaw populations. Sustainable harvesting of wild macaws has been proposed as a means of providing an economic incentive for conservation. However, this requires a comprehensive data base on population density, dynamics, and limiting factors (Beissinger & Bucher 1992), which is not available for any Scarlet Macaw population. Scarlet Macaw populations in Central America are also recorded to be in severe decline (Forshaw 1989; Wiedenfeld 1994; Marineros & Vaughan 1995; Iñigo-Elias 1996), rather than stable or increasing, and exhibit conservative breeding strategies, making them unsuitable for sustainable harvesting. Added to which, harvesting of macaws which are destined for international trade is not comparable with harvest programs for local markets, such as iguana farming. High commercial values in international markets drives local harvesting rates. An increasing scarcity in the wild further raises market values, and creates powerful incentives for increased harvesting of declining populations. This type of runaway positive feedback in international trade makes harvesting of threatened species, such as the Scarlet Macaw, inherently unsustainable.

Ecotourism may be the most appropriate non-consumptive use of Scarlet Macaws (Munn 1992; Marineros & Vaughan 1995). Tourism is one of the largest industries in the economies of Mexico, Guatemala, Belize, and Costa Rica, however the majority of that income frequently returns to foreign owned companies (Boo 1990). In Costa Rica, the Carara Biological Reserve receives only 1% of the income generated by tourists, while rural communities around the reserve receive no benefit (Marineros & Vaughan 1995).

The development of community based nature tourism may provide an opportunity for local people to extract economic benefit from the tourist appeal of Scarlet Macaws. Proposals for community based nature tourism in Costa Rica include tourists paying local communities to see macaw nests, and training of local guides (Marineros & Vaughan 1995). In Belize, a community project is also being developed which provides facilities for tourists to view large feeding groups of Scarlet Macaws. However, the success of community based nature tourism depends on effective organization, training, infrastructure, services, and promotion, and should involve all members of the community (Norris et al. 1998). Outreach programs as developed in the Caribbean (Butler 1992), and Belize (Coc et. al. 1998), also need to be implemented to educate schools, local communities, and the visiting public about Scarlet Macaw ecology and conservation.

The dispersed, increasingly isolated nature of the remaining Scarlet Macaw populations, many of which are located close to national frontiers, raises the need for co-operation between different governments, institutions, conservation organisations, and individuals. An initiative is currently underway to develop a regional strategy for conservation of the Scarlet Macaw in the Selva Maya of Mexico, Guatemala, and Belize. However, this will require collaboration between government departments and agencies in each country in order to establish effective policies and procedures for conservation. The challenge will be to develop an integrated approach to conservation of the Scarlet Macaw in Central America, which addresses the socio-economic problems of poaching and habitat destruction, if the species is to be preserved in the region.

Literature Cited

Beissinger, S.R., & E.H. Bucher. 1992. Sustainable harvesting of parrots for conservation. Pp 73-117 in New World Parrots in Crisis: Solutions from Conservation Biology. (eds) S.R. Beissinger & N.F.R. Snyder. Smithsonian Institution Press, Washington.

Butler, P.J. 1992. Parrots, people, pressure, and pride. Pp. 25-46 in New World Parrots in Crisis: Solutions from Conservation Biology. (Eds) S.R. Beissinger & N.F.R. Snyder. Smithsonian Institution Press, Washington.

Boo, E. 1990. Ecotourism: The Potentials and Pitfalls. World Wildlife Fund #72, Maryland.

Coc, R., L. Marsh, & E. Platt. 1998. The Belize Zoo: Grassroots efforts in education and outreach. Pp. 389-396 in Timber, Tourists, and Temples: Conservation and Development in the Maya Forest of Belize, Guatemala, and Mexico. (Eds) R.B. Primack, D. Bray, H.A. Galletti, & I. Ponciano. Island Press, Washington.

Forshaw, J.M. 1989. Parrots of the World (3rd edition). Lansdowne Editions, Melbourne.

Iñigo-Elias, E.E. 1996. Ecology and Breeding Biology of the Scarlet Macaw (*Ara macao*) in the Usumacinta Drainage Basin of Mexico and Guatemala. Ph.D. Dissertation. University of Florida, Gainesville, FL

Iñigo-Elias, E.E., & M.A. Ramos. 1991. The Psittacine trade in Mexico. Pp 380-392 in Neotropical Wildlife Use and Conservation. (Eds) J.G. Robinson & K.H. Redford. University of Chicago Press, Chicago.

Marineros, L. & C. Vaughan. 1995. Scarlet Macaws of Carara: Perspectives for management. Pp. 445-467 in The Large Macaws: Their Care, Breeding and Conservation. (Eds) J. Abramson, B.L. Speer, & J.B. Thomsen. Raintree Publications, California.

Munn, C.A. 1988. Macaw biology in Manu National Park. Parrotletter 1: 821-823

Munn, C.A. 1992. Macaw biology and ecotourism, or "When a bird in the bush is worth two in the hand". Pp. 47-72 in New World Parrots in Crisis: Solutions from Conservation Biology. (Eds) S.R. Beissinger & N.F.R. Snyder. Smithsonian Institution Press, Washington.

Norris, R., J.S. Wilber, & L.O. Morales-Marin. 1998. Community-based ecotourism in the Maya Forest: Problems and potentials. Pp. 327-343 in Timber, Tourists, and Temples: Conservation and Development in the Maya Forest of Belize, Guatemala, and Mexico. (Eds) R.B. Primack, D. Bray, H.A. Galletti, & I. Ponciano. Island Press, Washington.

Sanz, V., & A. Grajal. 1998. Successful reintroduction of captive-raised Yellow-shouldered Amazon Parrots on Margarita Island, Venezuela. Conservation Biology 12: 430-441.

Snyder, N.F.R., S.R. Derrickson, S.R. Beissinger, J.W. Wiley, T.B. Smith, W.D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology 10: 338-348

Snyder, N.F.R., S.E. Koenig, J. Koschmann, H.A. Snyder, & T.B. Johnson. 1994. Thick-billed Parrot releases in Arizona. Condor 96: 844-862.

Swanson, T.M. 1992. Economics and animal welfare: The case of the live bird trade. Pp 43-57 in Perceptions, Conservation, and Management of Wild Birds in Trade. (Eds) J.B. Thomsen, S.R. Edwards, & T.A. Mulliken. TRAFFIC International, Cambridge.

Wiedenfeld, D.A. 1994. A new subspecies of Scarlet Macaw and its status and conservation. Ornitologia Neotropical 5: 99-104.