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THE ECOLOGY AND CONSERVATION OF THE PINK PIGEON *Columba mayeri* IN MAURITIUS.

Kirsty Jane Swinnerton

A thesis submitted for the degree of
Doctor of Philosophy
University of Kent at Canterbury.

January 2001.

This thesis is dedicated to Gerald Durrell (1925 - 1995) whose vision ensured that the pink pigeon survived into the twenty-first century.

"It lay quietly in my hands, without struggling, merely blinking its eyes in what appeared to be mild curiosity at this new experience. The colours seen so closely were vivid and beautiful: the pale chocolates of the wings and the back, the rusty, almost fox-red of the tail and rump, and then the broad breast, neck and head, pale grey flushed with cyclamen-pink overtones. It was a remarkably handsome bird.

Gazing at it, feeling its silken feathering against my fingers and sensing the steady tremor of its heart-beat and its breathing, I was filled with a great sadness. This was one of the thirty-three individuals that survived; the shipwrecked remnants of their species, eking out a precarious existence on their cryptomeria raft...At least with our help, the pink pigeons stood a better chance of survival, even though their numbers were down to such a dangerously low level".

Gerald Durrell, 1977
Golden Bats and Pink Pigeons.

Abstract

The pink pigeon *Columba mayeri* was a critically endangered endemic bird from Mauritius in the Indian Ocean. The species reached its lowest point of between 10 and 20 birds in 1975 and the wild population continued to decline to 9 or 10 birds in 1990. The causes of decline included habitat destruction, seasonal food shortages and predation by introduced mammals. Between 1987 and 1997, 256 captive-reared birds were released on Mauritius at three sites. Free-living birds were intensively managed and between 1988 and 1998, 429 young fledged in the wild. The population numbered 297 birds at the end of 1998.

Factors limiting survival and reproductive success were identified and an assessment of the re-introduction programme made. Mean survival of juveniles (up to one year old) was 68% and adults 83% per year. Median age at egg-laying for females was 10.9 months and fertility 58.6%. Mean annual nest success was 18.4% and productivity 1.2 young per female from 1992. Productivity for males and females peaked in year one and there was large individual variation, 9% of females produced 43% of young. Survival, nest success and productivity varied between sites, were affected by inbreeding and were poorer for released birds than wild-fledged birds. Causes of nesting failure included predation, infertility and disease. Unhatched eggs accounted for 56% of failed nests in a predator-free environment. Disease affected survival of fledged birds and squabs. On Ile aux Aigrettes trichomoniasis affected 49% of squabs. About 10% of all birds suffered from avian pox and 36% of all birds were infected with *Leucocytozoon marchouxi*.

As a result of the programme, the pink pigeon has been down-listed to endangered. With management, survival and productivity are sufficient to contribute to population growth. This programme was considered a good example of the interface between captive-breeding and the recovery of a wild population.

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ACKNOWLEDGEMENTS

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The pink pigeon programme came under the auspices of the Forestry Department and more recently the National Parks and Conservation Service (NPCS) of the Ministry of Agriculture and Natural Resources. I would like to thank the Director of NPCS, Yousoof Mungroo, and Greg Middleton, (previously National Park Manager). In the Forestry Department, I would like to thank the Conservator of Forests, Hans Paupiah. I would also like to thank the officers in the NPCS, in particular Mario Allet and Paul Moolee, who have helped all the pink pigeon staff so much.

The recovery of the pink pigeon, and much of the work presented in this thesis, would not have been possible without all the dedicated and enthusiastic field staff who put up with mud, mosquitoes, rats and foot-rot to find nests and birds. The many staff who worked on the project are too numerous to mention, but those that worked for at least one season or contributed in other ways included: Colin Taylor, Anne-Marie McDevitt, Bridget Griffin, Tim Liddiard, Rupert Hawley, Sarah Paul, Simon Green, Malcolm Nicoll, Stuart Johnston, Jim Groombridge, Roselle Chapman, Kathryn Murray, Tom West, Vicky Jones, Amber Delahooke, Teri-Ann Parry, Daryl Birch, Katherine Dixon, Karen Freeman, Hannah Schellander, Suzannah Doughty, Steve Hurdowar, Frances Beck, Lucy Lindrea, Chris Shaw, Djamila Djeddour, Clinton Eichelberger, Andrew Smart, Polly Phillpot, Lance Woolaver, Sarah McIntyre, Dave Hall, Simon Butler and Colleen Cumming. Some staff worked for several years and contributed greatly to the project with their energy and skills. The release programme would not have been possible without the staff at the Government captive-breeding centre in Black River. I would like to thank in particular Regis Lam

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Chapter 1

Introduction

EXTINCTION OF BIRDS ON ISLANDS

More than one-fifth of the world's bird species are at risk of global extinction (Collar *et al.* 1994) and island birds in particular are at risk. Over 1750 bird species (17% of the world's bird species) are confined to islands and of these, 23% are threatened representing 39% of threatened birds worldwide (Johnson & Stattersfield 1990). Island birds have also suffered 93% of bird extinctions in the last 400 years (King 1985). Diamond (1984, 1989) identified four causes of extinction, of which introduced species (in particular predators and browsers), direct persecution and habitat destruction have been the agents of decline in island birds (Johnson & Stattersfield 1990). Although these factors are still the main threats today, their relative importance has changed. The threat from introduced species, which have contributed to the greatest number of extinctions of island birds (King 1985, Atkinson 1996) may have declined relative to that of habitat destruction (Johnson & Stattersfield 1990). Habitat destruction and degradation is the most important factor threatening island birds today, affecting over 50% of island species (King 1985, Johnson & Stattersfield 1990). Other factors (e.g. hunting and trade) may also contribute to the endangerment of island birds but in most cases are not primary factors. Many island species are at risk simply because of their limited range, 53% of restricted-range species occur on islands (Johnson & Stattersfield 1990, Stattersfield *et al.* 1998).

MAURITIUS

The Mascarene islands (Mauritius, Rodrigues and Reunion) (Figure 1.1) once supported one of the richest vertebrate faunas of any oceanic archipelago, but have also suffered high numbers of extinctions, with at least 28 bird species lost since 1600 (King 1985, Cheke 1987). On Mauritius, 16 species are extinct and seven of the remaining eleven species of land bird are considered threatened. Mauritius ranks tenth in the world for endangered endemic restricted-range birds (Stattersfield *et al.* 1998). The causes of extinction and endangerment for Mauritian birds are well documented (Collar & Stuart 1985, Cheke 1987, Jones 1987, Safford 1997*a*), and are briefly summarised below. Mauritius was almost entirely forested before human colonisation in 1638. The forest remained largely intact until the 1700s, but by 1766, 45% of the island had been conceded to agriculture and the coastal palm savannah had probably already gone (Brouard 1963, Cheke 1987). By the mid-1830s, some 65% of the island remained under forest, mostly in the uplands above 200 m, but severe deforestation followed so that by 1880, virgin forest occupied only 3.6%

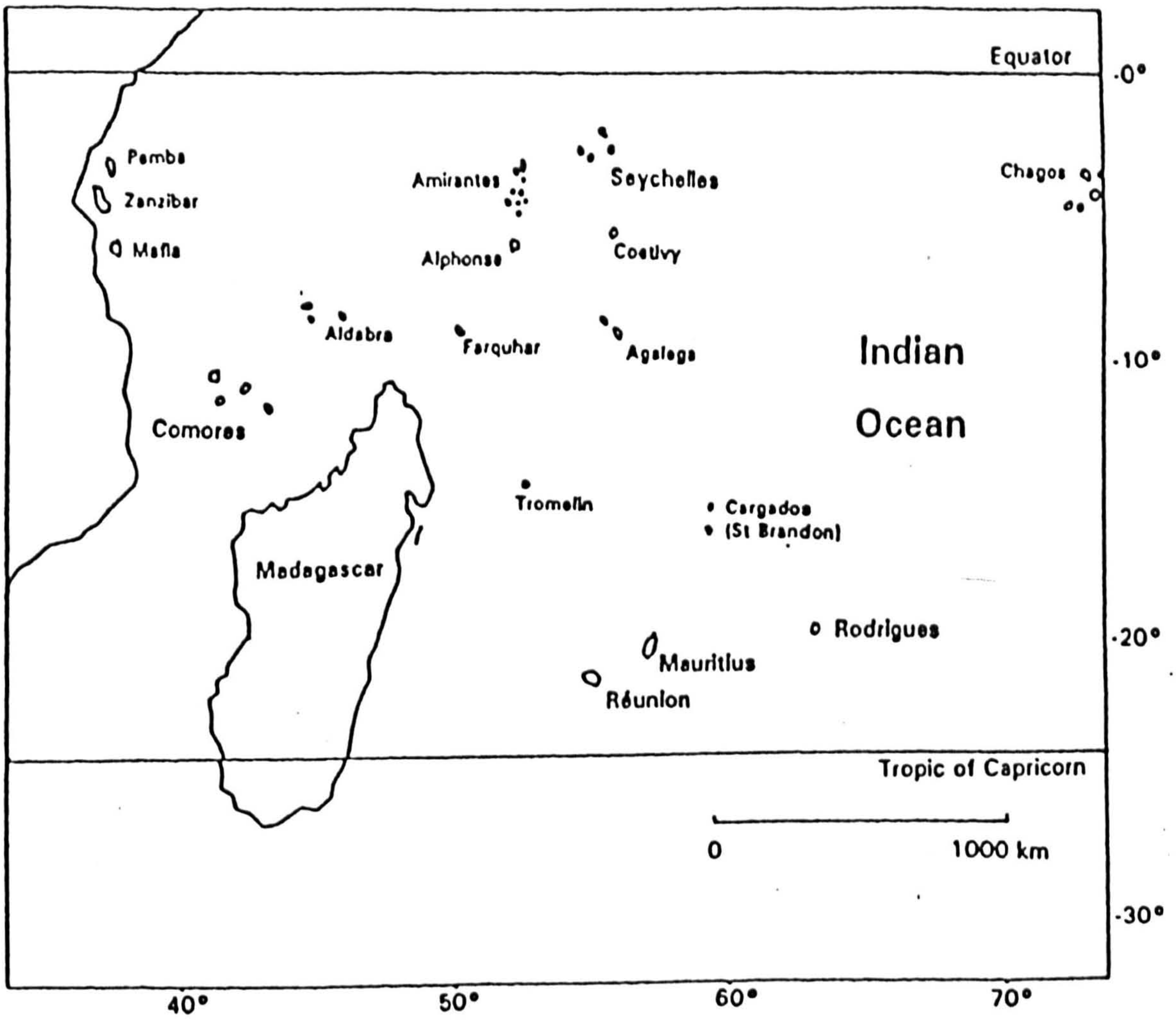

Figure 1.1 Islands and island groups in the Western Indian Ocean.

of the island's area (Vaughan & Wiehé 1937). Timber extraction and its replacement with pine plantations continued into the 20th Century. In the 1970s, the clearance of the upland 'dwarf' forests and marshy scrub at Les Mares (after which the pink pigeon, the 'Pigeon des Mares', was named) delivered the *coup-de-grace* to most of the remaining avifauna, which subsequently declined towards extinction (Jones & Owadally 1985, Cheke 1987). Today, native forest, in variable states of degradation, occupies about 5% of the land area, 63% of which is in the south-west (Safford 1997*b*).

Introduced species have played a major role in past extinctions and remain a threat to surviving species. The effect of mammalian predators, notably the mongoose *Herpestes auropunctatus*, feral cat *Felis catus*, ship rat *Rattus rattus* (and to a lesser extent the brown rat *R. norvegicus*) and the crab-eating macaque *Macaca fascicularis*, on native species is well known (Jones & Owadally 1985, Cheke 1987, Jones 1987, Jones & Owadally 1988, Jones *et al.* 1991, Jones *et al.* 1992, Safford 1997*c*, Carter 1998, Roy 2001). Introduced herbivores, such as the wild boar *Sus scrofa* and Rusa deer *Cervus timorensis*, and invasive exotic plants, such as strawberry guava *Psidium cattleianum*, privet *Ligustrum robustum*, jamrose *Syzigium jambos* and the climber *Hiptage benghalensis*, cause continuing habitat degradation (Lorence & Sussman 1986, Cheke 1987, Lorence & Sussman 1988, Strahm 1993).

The pink pigeon

The pink pigeon *Columba mayeri* (Prévost 1843) was one of the world's rarest and most endangered birds (Collar *et al.* 1994), endemic to Mauritius in the Indian Ocean. The status and distribution of the pink pigeon has been reviewed in detail (Collar & Stuart 1985, Jones 1987, Jones & Owadally 1988, Jones 1995). The pink pigeon was probably once common and widely distributed over Mauritius in both upland and lowland forest. The contraction of its range closely follows the pattern of deforestation described above. By the 1800s, the species was already restricted to upland forest. By the 1930s, its range had contracted to the central plateau from Black River peak, through the dwarf forest of Plaine Champagne, the marsh scrub of Les Mares, the Black River Gorges to Piton du Milieu in the island's centre. The clearance of the upland scrub forests for pine plantations in the 1960s and 1970s and the removal of key habitat between 1973 and 1981 caused a dramatic crash in the pink pigeon population and isolated it from the suitable forests remaining at Macabé and Brise Fer (Jones 1987, 1995). The last sighting in the Brise Fer-Macabé forests was in 1978 (Jones 1987). In 1976, pink pigeons were found breeding in a plantation of *Cryptomeria japonica*, known as Pigeon Wood, on the south-facing scarp

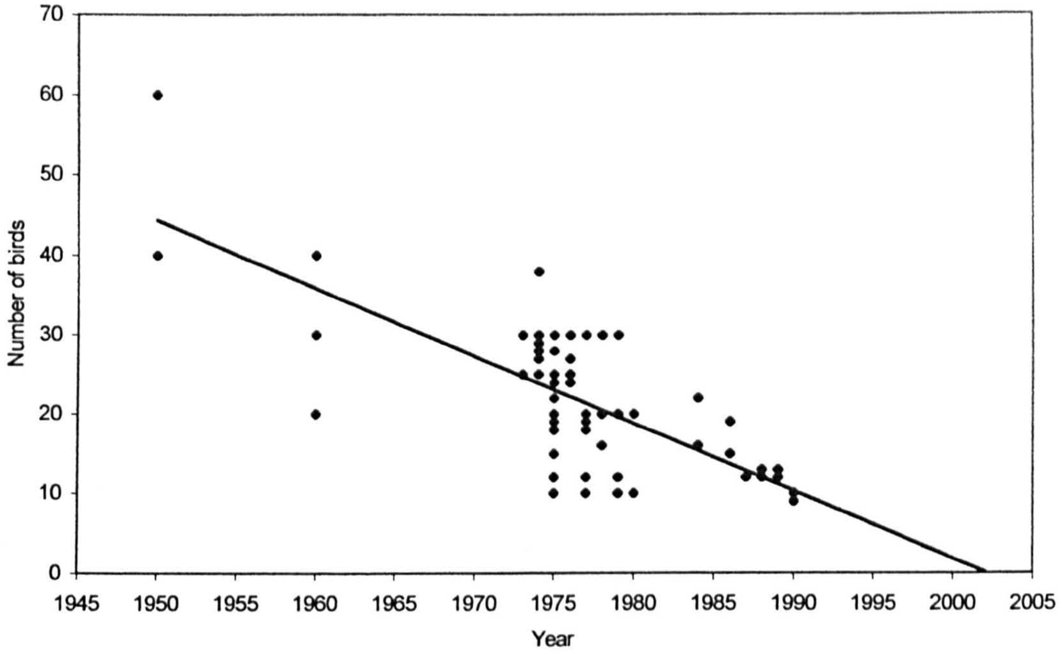

Figure 1.2 Population trend for the wild pink pigeon population, 1950-1990. The data are modified from Jones (1987) and Jones (1995). Projection of the trend suggested that the wild population would have become extinct at about year 2002.

between Piton Savanne and Montagne Cocotte (McKelvey 1976). This remained the only known nesting site until releases occurred in the 1980s. In the early 1980s pink pigeons were restricted to an area of about 30 km^2 in the south-west of Mauritius above the 300 metre contour (Jones 1987). Since 1987 (when this study began) and prior to the establishment of released sub-populations, the wild population ranged along the southern scarp slope from Piton Savanne, Montagne Cocotte, Alexandra Falls, Plaine Champagne and Black River peak (*pers. obs.*). Some birds probably visited the scrub forests around Grand Bassin and the upper half of the Bel Ombre forests (see Chapter 2 for map).

By the turn of the century, the pink pigeon was already rare (see review in Jones 1987). It declined to its lowest numbers (before the captive-breeding programme) after Cyclone Gervaise in February 1975 when the population was estimated at between 10 and 12 birds (Temple 1975) around 12 (Temple 1976*b*), between 12 and 15 (Newlands 1975) or less than 20 (Temple 1976*a*). In the following years the wild population may have made a natural recovery and was estimated at between 20 and 30 individuals in 1977 (Hartley 1977), up to 30 individuals in 1978 (Steele 1979) and in 1979 between 12 and 20 (Jones 1979) and 20 to 30 birds (Jones 1980). Prior to this study there was no subsequent survey and, by the end of the 1980s, it was clear that the wild population had declined to near extinction (Figure 1.2).

The conservation programme

A conservation programme for the pink pigeon has been ongoing since the mid-1970s (Durrell 1977). A captive-breeding programme was established in 1976 on Mauritius by the Government of Mauritius and in 1977 on Jersey by the Jersey Wildlife Preservation Trust (now the Durrell Wildlife Conservation Trust) (Jeggo 1977, 1978, 1979, Hartley 1977, Durrell & Durrell 1980, Jones *et al.* 1983). The Mauritian Wildlife Foundation was established in 1984, and has been the umbrella organisation under which the pink pigeon project has operated (Jones & Hartley 1995). Prior to this study, birds were collected from the wild for the captive programme between 1976 and 1981. A detailed account of the captive history of the species is provided in Jones *et al.* (1983), Jones & Owadally (1988) and Jones (1995). A trial release of captive-bred birds at the Pamplemousses Botanical Gardens in Mauritius (Todd 1984) paved the way for releases into native forest in 1987.

Studies on wild pink pigeons began in 1973 by Temple (1978) and were continued by McKelvey (1976, 1977), who located the remaining birds at Pigeon Wood. From 1977 to 1988, the population was studied opportunistically by several biologists (summarised in Jones 1987 and Jones & Owadally 1988) but no systematic studies of the wild birds were made until 1989 with this study when full-time fieldwork on the Pigeon Wood population began.

SCOPE OF THE THESIS

The aim of the programme was to prevent the pink pigeons' extinction in the wild through captive-breeding, re-introduction and management. When the programme began, the methods for re-introducing birds to the wild were in their infancy and there were few such programmes. Part of this programme's goal was to develop re-introduction and management techniques that would be suitable for other species.

This thesis grew out of the re-introduction and management components of the programme for the pink pigeon. Intensive monitoring of released birds, and later of their progeny, enabled the accumulation of information about the species' ecology together with an assessment of the progress of the re-introduction programme. The intention of this thesis was two-fold: (1) to show that the re-introduction of pink pigeons and the management of free-living birds restored a critically endangered population from near-extinction in the wild; (2) to evaluate factors limiting the population so that future research and management priorities could be identified. Two questions were of particular concern: (1) Has the re-introduction and management programme been a successful conservation tool for the recovery of this species? (2) Does the survival, reproductive ecology and reproductive success of captive-reared released birds differ from wild-fledged birds?

Data were collected from 1987 to 1998 on wild and free-living birds at four study sites in Mauritius, which are described in Chapter 2. Chapter 3 presents data on the survival of wild and released birds and describes the subsequent population trends. This chapter has been presented here as it develops survival analyses methods that are used in Chapters 4, 5 and 7. Also, the interpretation of some data in subsequent chapters is based on survival data. Chapter 4 presents data on aspects of nest site selection and reproductive ecology of the pink pigeon. The analysis focused on the most important aspects for the subsequent analyses and interpretation of nest success and productivity. Chapters 5 and 6 present data on nesting success and the causes of nesting failure, and productivity. There is some overlap between these two chapters, in particular when describing the limiting factors, but the two parameters were considered to be sufficiently important and distinct to warrant independent consideration. Chapter 7 presents data on the effect of pathogens and disease on the survival, nest success and productivity of released and wild birds. Chapter 8 evaluates the success of the pink pigeon recovery project, in the light of similar projects. Based on information gained from this thesis, a prognosis for the continued survival of the pink pigeon is made and some concerns about its genetic viability are raised. Chapter 9 summarises aspects of the pink pigeon re-introduction and management programme that facilitated its success, and that could be used in similar programmes and to develop further the IUCN re-introduction guidelines (1998).

Data on many other aspects of pink pigeon ecology were collected, such as feeding ecology, time-partitioning studies and morphometrics of squabs, juveniles and adults, but were not considered in this thesis. When analysed, these data may offer further insights into the causes of decline, the success of the recovery project and factors currently limiting the population.

DEFINITIONS FOR RE-INTRODUCTION AND TRANSLOCATION

Various terms have been used to describe the release of animals into the wild (translocation, relocation, re-introduction, repatriation, restocking, supplementation, re-enforcement) (Wolf *et al.* 1996, IUCN 1998, Fischer & Lindenmayer 2000) which may reflect the source of the relocated animals and the status and distribution of the wild population. The definition for re-introduction, namely "an attempt to establish a species in an area which was once part of its historical range but from which it has become extirpated or extinct" (IUCN 1998) is limited in its application. Recently, 'translocation' has been used as an inclusive term to describe "the intentional release of animals to the wild, in an attempt to establish, re-establish or augment a population" (IUCN 1987, Griffith *et al.* 1989, Wolf *et al.* 1996, Cade 2000, Fischer & Lindenmayer 2000). This incorporates activities involving the manipulation of captive or wild individuals to boost wild populations, including restocking or augmenting existing populations, island marooning (Williams 1977), introduction into a previously unoccupied range and micro-manipulative techniques such as fostering and chick rescues (Cade 2000). In this study, the term re-introduction was used to describe the method of re-establishment, because the project involved the release of mainly captive-bred birds into areas from which the species had become extirpated. However, wild-bred captive-reared birds were also released, some into their original sub-population and others into a different sub-population, which had themselves originated from captive-bred parents. These types of releases may be defined differently to a re-introduction (IUCN 1998) and illustrate the difficulty of applying specific definitions to a real recovery programme.

DEFINITIONS OF SUCCESS

The success of a re-introduction project has been previously defined as achieving a self-sustaining population (Griffith *et al.* 1989, Fischer & Lindenmayer 2000) of at least 500 individuals or a Population Viability Analysis demonstrating self-sustainability (Beck *et al.* 1994). In a review of 145 re-introductions, Beck *et al.* (1994) reported only 16 projects (11%) that were successful, based on a minimum establishment of 500 self-sustaining individuals. Examples included restocking the American bison *Bison bison* to North America (Campbell 1980), re-introduction of Arabian oryx *Oryx leucoryx* to Oman (Stanley Price 1989) and re-establishment of the peregrine falcon *Falco peregrinus* (Cade *et al.* 1988). Griffith *et al.* (1989) estimated that 38% of projects re-introducing captive-bred animals and 75% of projects translocating wild animals were successful (also based on the creation of a self-sustaining population but criteria for which were not specified). A follow-up study by Wolf *et al.* (1996) suggested that the successful re-introduction of birds was achieved in 63% of projects but that re-introductions of captive-bred birds were less successful (50%) than translocations of wild caught birds (71%). Fischer & Lindenmayer (2000) also reported a lower success rate for captive (15%) than for wild animals (29%). Cade (2000) reported a higher success for raptors than for other bird and mammal species, with at least 75% of projects achieving success.

The determination of a "self-sustaining" population has usually depended on the subjective evaluations of individual researchers and does not account for the problem of time-scale (Cade 2000). For example, Wolf *et al.* (1996) reported that 38% of re-introduction projects had a change in outcome since 1987. More recent projects are likely to have an undetermined success. Fischer & Lindenmayer (2000) reported only 17% of projects from the 1990s were successful but that 51% of projects with an undetermined outcome were from this period. Beck *et al.* (1994) suggested that self-sustaining should be "free of provisioning or other human support". The degree of human support is also highly variable, as it could include intensive species protection as with Arabian oryx *Oryx leucoryx* (Papastavrou 1999) and black rhinos *Diceros bicornis* (Mills 2000), supplemental feeding as with pink pigeons (Jones *et al.* 1992) and kakapo *Strigops habroptilus* (Merton *et al.* 1999), providing nest boxes as with Mauritius kestrels *Falco punctatus* (Jones *et al.* 1991) or habitat management and protection.

Other definitions of success have been suggested which reflect ecological aspects (Lohoefener & Lohmeier 1986). At the 1999 World Conference on Breeding Endangered Species, two criteria for a successful re-introduction were suggested: (1) when released individuals demonstrate appropriate or species-specific behaviours; and (2) when released individuals fulfil their ecological role. This leads to viewing success at two levels: (1) the persistence of released organisms within the environment and (2) the persistence of the species over the long-term. These criteria incorporate the possibility of managed populations but may also be dependent on subjective evaluations of "normal" behaviours and the role an individual plays within the ecosystem. The evaluation of any re-introduction project requires long-term monitoring and an assessment of its success can only be made at that point in time. The re-introduction of the Arabian oryx into Oman was regarded as very successful for the first 10 years but the recent decimation of this population by poachers may deem this project now as unsuccessful (Gorman 1999). The data presented in this thesis was used to help evaluate the success of the pink pigeon recovery programme.

Chapter 2

Study site descriptions and general methods of the recovery project

INTRODUCTION

Mauritius is situated in the south-west Indian Ocean, 840 km east of Madagascar, at longitude 57° 30′ E and latitude 20° 20' S. The island covers 1865 km^2 and is of volcanic origin. The low plains in the north and east rise to a plateau reaching about 700 m in the south-west, where it is dissected by the precipitous Black River Gorges (Figure 2.1). Mauritius is largely surrounded by a fringing reef, which encloses a lagoon and several low coralline islets. The pink pigeon was studied at four sites. Three study-sites, Pigeon Wood, Brise Fer and Bel Ombre, were situated on the mainland in the south-west of Mauritius in the Black River Gorges. The fourth site, Ile aux Aigrettes, was an offshore islet off the south-east coast of Mauritius (Figure 2.1).

THE CLIMATE OF MAURITIUS

Mauritius has a tropical to sub-tropical seasonal climate dominated by the south-east Trade winds which blow throughout the year, but are more persistent in the winter (May-August) (Padya 1989). A warm wet season from December to April and a cooler dry season from June to October are typical with regional variations in temperature and rainfall, the uplands are cooler and wetter than coastal areas. Mean monthly temperatures on the coast range from 20-21°C in August to 26-27°C in January. In the uplands, mean monthly temperatures range from 16 to 23°C. There is no truly dry season but little rain falls on the coast in winter (May to August). In the uplands, rain is continuous throughout the year with September to November drier. Rainfall distribution is affected by the relief of the island, windward slopes and high altitude areas receive more than 5 m of rain a year and the west of the island is in rain shadow. Annual rainfall varies from 900 to 5000 mm, the wettest area being Montagne Cocotte, adjacent to the Pigeon Wood study site. About two-thirds of the rain falls between December and May, often associated with tropical depressions or cyclones. Since 1960, Mauritius has been affected by six cyclones where wind speeds of more than 200 km per hour were recorded, the last one having been Cyclone Hollanda in 1994 (Pathack *in litt.*). During Cyclone Hyacinthe in 1980 a record 1353 mm of rain was recorded. Native fauna and flora have adapted to cyclones and it is the exotic species that are badly affected.

THE VEGETATION OF MAURITIUS

Floristically, Mauritius is relatively well known and its plant communities have been well studied (Vaughan & Wiehé 1937, 1939, 1941, Strahm 1993, Page 1995). Three major

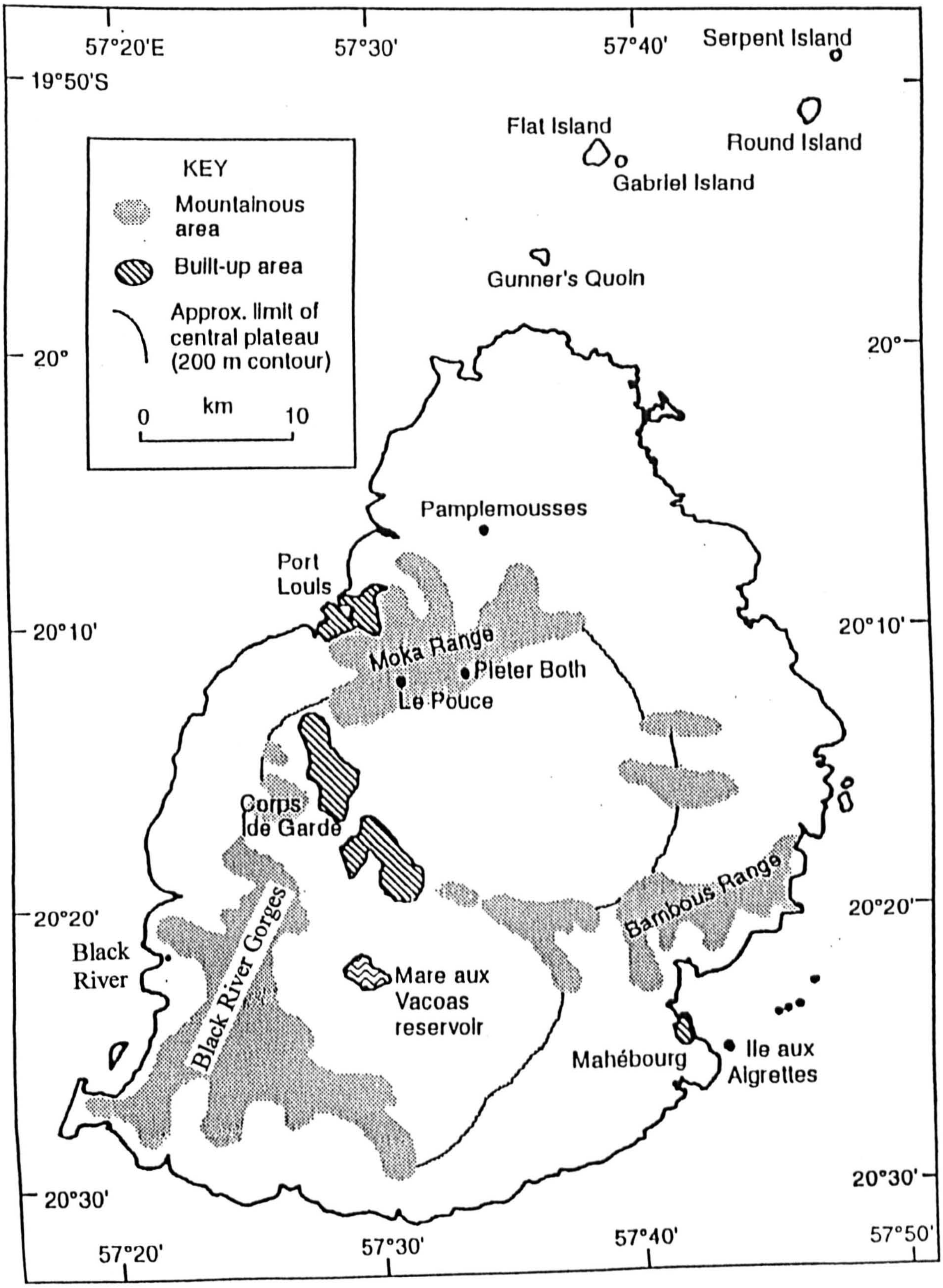

Figure 2.1 Mauritius showing the Black River Gorges and Ile aux Aigrettes.
(Source: Safford 1997*b*).

vegetation types are generally recognised: "upland" lower montane evergreen rain forest, from 500m to 828 m altitude and receiving 2500 mm to 5000 mm rainfall/year; lowland semi-deciduous forest in areas receiving 1000 mm to 2500 mm rainfall/year; and, palm savannah along the coastal areas. The palm savannah is virtually extinct and remnants are found only on offshore islands (Strahm 1993).

The complexity of the upland plant communities are described in Vaughan and Wiehé (1937, 1939, 1941) and five intergrading types of vegetation are recognised. These include a *Pandanus* rich marshy scrub, a *Philippia/Phylica* heath formation, a *Sideroxylon* thicket grading into tall climax forest and a shorter mossy forest in the wettest areas.

In this study pink pigeons were mostly found in upland climax forest, which was generally similar at Brise Fer, Bel Ombre and areas adjacent to Pigeon Wood, although each site suffered varying degrees of degradation. Dominant canopy trees reached 25 m but averaged 18-20 m. Most canopy species belong to several distinctive plant families: the Sapotaceae, Myrtaceae, Burseraceae, Guttiferae and Ebenaceae. Typical species include *Labourdonnasia glauca*, *Sideroxylon grandiflorum*, *Mimusops maxima*, *Calophyllum tacamahaca* and several ebony species, mainly *Diospyros tesselaria* and *D. boutonianum*. The second stratum is usually dense, closed and diverse and may support more than 40 species of woody plants in good canopy forest. They are often linked with numerous lianas and support a high diversity of epiphytes. The third level is nearly continuous with the second but includes taller shrubs, saplings and tree ferns. The lowest stratum is composed of small shrubs, 1-2 m in height and the ground layer comprises herbaceous species, ferns and seedlings. Wetter regions, such as Montagne Cocotte, may support cloud forest and have a higher diversity of mosses, ferns and epiphytes.

Most upland forest types are represented in areas designated as nature reserves or National Park but much of it is heavily invaded by exotic plants and fragmented by plantations. The largest remaining tract of native vegetation is in the south-west of the island, and extends from Petrin and Macabé on the central plateau, south to the forests of Bel Ombre and west into the Black River Gorges. This region was created a National Park in 1993 (Anon 1998) and incorporates 65.7 km^2, in which 41.0 km^2 of native vegetation is protected, comprising 44% of the island's native forest and 70% of the south-western total (Safford 1997*a*). Three study sites, Brise Fer, Pigeon Wood and Bel Ombre, were situated within the boundaries of the National Park.

Brise Fer

Brise Fer was the first release site in native forest for captive-bred pink pigeons (Jones *et al.* 1988). The Brise Fer forest is located on the northernmost spur of the Black River Gorges at the western extremity of the island's central plateau (Figure 2.2). This forest is contiguous with the Macabé forest and the combined area contains 9-15 km^2 of habitat suitable for pink pigeons (Jones *et al.* 1992). Macabé and Brise Fer represent upland climax forest and support some of the best native forest remaining on Mauritius with 80% to 100% native cover (Page 1995). The forest is dense and the main canopy is closed and uniform in height (14-16 m) with occasional large emergents. Floristic composition was similar to areas of native vegetation at Bel Ombre (Lorence & Sussman 1986).

Despite the relative quality of Brise Fer, the forest was patchy and good forest alternated with completely degraded areas. The main study area was located on a small sheltered plateau with a good contiguous canopy but the more exposed slopes were characterised by isolated native canopy trees surrounded by dense stands of invasive exotics, guava *Psidium cattleianum* and privet *Ligustrum robustum*.

In 1987, a 1.3 hectare study plot was fenced and restored by removing invasive plants and supplementary planting with nursery grown plants. Between 1993 and 1997, 24 hectares of additional forest were weeded and fenced, which incorporated the original study plot. This Conservation Management Area included most pink pigeon territories in the Brise Fer forest. A tented field camp was established in 1987 at Plaine Lievre, a natural clearing within the Brise Fer forest, which was replaced by a field station built in 1996. A pigeon release aviary and two supplemental feeding stations were built within the clearing.

Pigeon Wood

Pigeon Wood was the last known breeding site for wild pink pigeons (McKelvey 1976). It is an eight hectare plantation of Japanese red cedar *Cryptomeria japonica* situated on the steep south-facing scarp between Montagne Cocotte and Piton Savanne, and between 500 m and 650 m a.s.l. (Figure 2.2). The plantation resulted from a policy of 'improvement fellings', where dead and dying native species were replaced with plantation trees, between 1903 and 1929 (Koenig 1926, Brouard 1963, Safford 1997*b*). Most pink pigeons bred within the *Cryptomeria* grove but a few birds used adjacent areas, which included native forest, pine plantations and other smaller *Cryptomeria* groves. Under the dense canopy of *Cryptomeria* densities of guava and privet were low, and there was no regeneration of *Cryptomeria* (Safford & Jones 1993). Adjacent to the study site, a patchwork of variably

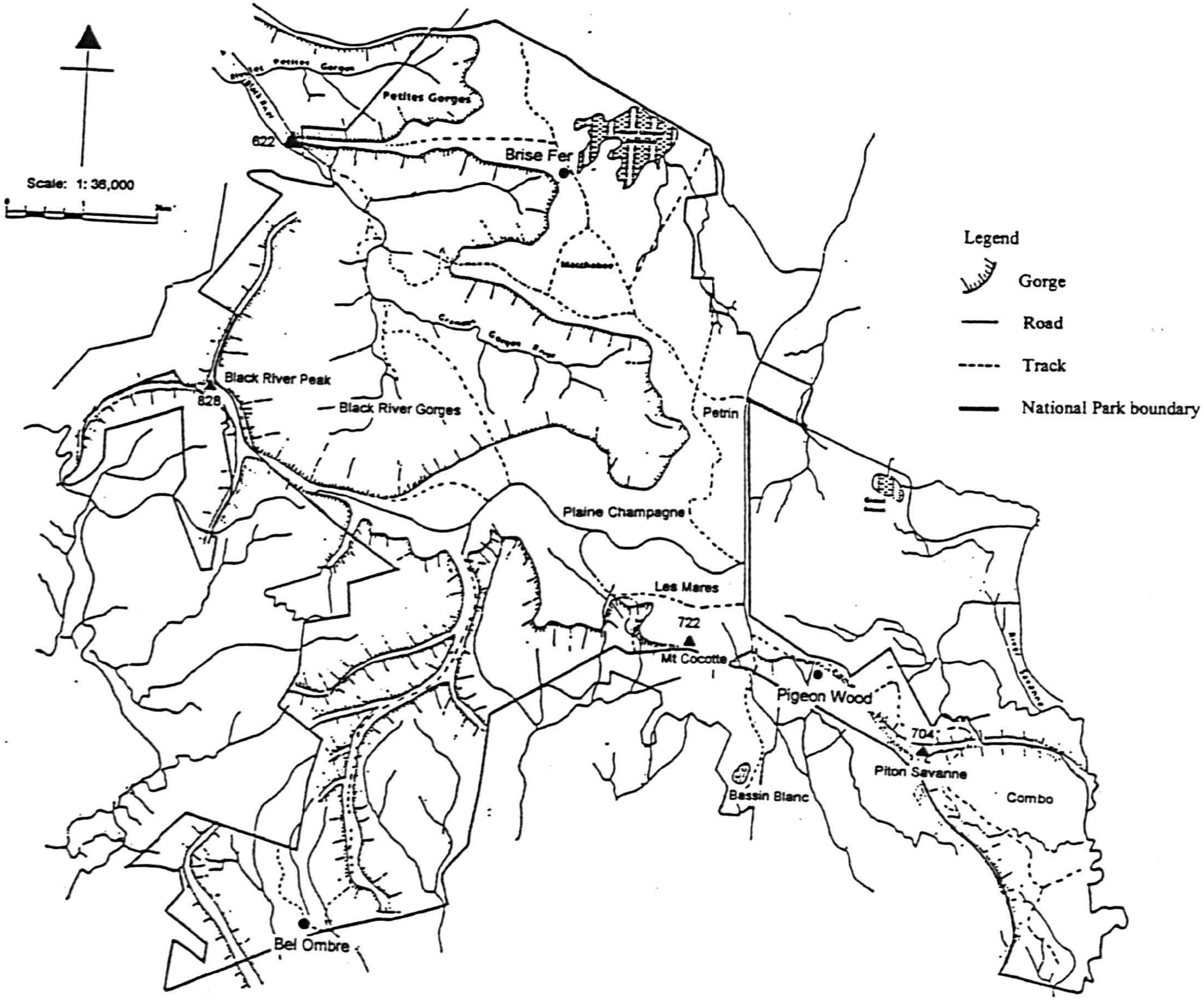

Figure 2.2 South-west Mauritius showing the mainland study sites and localities mentioned in the text.

degraded forest existed with thickets of jamrose *Syzigium jambos*, guava, privet, dense stands of traveller's palm *Ravenala madagascariensis*, groves of *Eucalyptus* spp. and fragments of native forest. Pink pigeons foraged in the adjacent upland mossy forest of Montagne Cocotte, but no breeding was detected there.

Bel Ombre

Releases of pink pigeons began at Bel Ombre in 1994. Bel Ombre forest is located on the southern scarp overlooking the south coast of Mauritius between 200 m and 600 m (Figure 2.2). Most birds were located within 1-1.5 km from the field station, which was in the southernmost part of the forest. The southern portion of Bel Ombre represents a transitional forest where a number of species are common to both upland wet forest and lowland forest (Vaughan & Wiehé 1937). Dominant canopy species were similar to Brise Fer but the native forest was more degraded and pockets of highly degraded forest and plantation trees were found throughout.

Species not commonly found at Brise Fer or Pigeon Wood included mango *Mangifera indica* and a native palm *Dictyosperma album* regenerated from plantations close to the study site. Plantations of pine *Pinus* spp. and tecoma *Tabebuia pallida* occurred, mostly along the main track that ran north to south through the forest, and dense thickets of jamrose were common along watercourses. Two Conservation Management Areas of 4.3 and 2.5 hectares were established at Bel Ombre in 1993 and 1994, though neither sites were much used by pink pigeons. Bel Ombre field station was established in 1994 on the southern boundary of the National Park.

Ile aux Aigrettes

The island of Ile aux Aigrettes has had an introduced population of pink pigeons since 1994. Ile aux Aigrettes is located within the Mahébourg Bay in the south-east of Mauritius (Figure 2.1). It is a calcarenitic, low islet achieving 12 m altitude (Parnell 1989), covering 27 hectares and is about 600 m from the mainland. The islet is a remnant of an old Pleistocene reef that emerged some 30,000 years ago (Montaggioni 1972). The rock is mostly eroded 'champignon' with some 'pavé' in the interior (Stoddart *et al.* 1971) and the entire island is surrounded by an undercut edge.

The island has been extensively deforested and degraded by the introduction of goats *Capra hircus*, ship rats *Rattus rattus*, Indian house shrews *Suncus murinus*, feral cats *Felis catus*, giant snails *Achatina* spp. and a variety of exotic plant species. Although declared a nature reserve in 1965, illegal woodcutting continued until 1987 when the lease was given to the Mauritian Wildlife Foundation. An ongoing restoration programme involving the removal of alien plants and supplemental planting of native species was started in 1985 (Dulloo *et al.* 1997). Goats were eradicated before 1985 and cats and rats had been eradicated by 1988.

The island represents a relict of the eastern coastal dry forest, which has now virtually disappeared on the mainland. Species diversity is low but this is probably due to the island's small size and degradation and, historically, it was probably more diverse (Strahm 1993). Parnell *et al.* (1989) recognised 10 types of natural, semi-natural and alien vegetation. Since then, the restoration programme has changed the vegetation structure of the island and two-thirds of the island has been cleared of exotic vegetation. Two recent vegetation surveys both indicated similar vegetation types (Hosany 1998, Seymore 2000). The following description is taken from Seymore (2000). A continuous canopy forest in the interior occupied about 6% of the island, and consisted mainly of lowland ebony *Diospyros egrettarum*, and an almost continuous ground cover of the fern *Phymatodes scolopendria*. Three vegetation types were transitional between canopy forest and coastal scrub. The first class (Transition 3) represented canopy forest interrupted by large gaps in the canopy and/or fern layer. The second class (Transition 2), shaped by weeding and replanting, was characterised by open areas between small trees, typically *Ehretia petiolaris*, *Tarenna borbonica* and *Dracaena concinna*. The third class (Transition 1) consisted mainly of scrubby coastal vegetation, but included occasional mature trees of *Diospyros egrettarum* and *Gastonia mauritiana*. The remainder of the island comprised dense thickets of scrubby coastal vegetation 2-2.5 m height and monotypic stands of the invasive false acacia *Leucaena leucocephala*. At the very edges of the island was a monotypic vegetation type consisting solely of *Pemphis acidula*, a low-lying perennial less than one metre in height.

The island has had a long history of use and during World War II, a garrison was based on the island. One of the derelict garrison buildings was converted to a permanent field station in 1986. A plant nursery was built in 1996 (previously also in a derelict garrison building) and a visitor and education centre in 1998. Access to the island was by a small boat.

ASPECTS OF PINK PIGEON LIFE-HISTORY

Accounts of the breeding biology of the pink pigeon are given in Jones (1987), Jones & Owadally (1988) and Jones (1995). Much of this information was gained from studies of captive birds and the breeding biology of wild birds was poorly known prior to this study. A brief summary of the life-history of the pink pigeon is as follows. Published accounts of the breeding season were not consistent with each other (see Jones 1987 for a review), or with this study. Climatic seasons on Mauritius vary regionally and according to altitude (see this chapter). The effect of climate on breeding seasonality was investigated in Chapter 4. Captive birds will breed throughout the year with no marked peak in breeding activity (Jones 1987, Lind 1989). The effect of the moult process in the timing of breeding is not clear. Birds in all stages of moult have been seen courting, feeding young or foraging and moult seems to be ungoverned by season or sexual activity (McKelvey 1977). Jones (1987) suggested that moult started between October and January and continued until May or June with few birds moulting during the period of greatest food shortage at the end of 'winter' (July to August). Adults are in heavy body moult during the 'summer' months (January to April) when food is most available in the wild (Jones *et al.* 1992, Jones 1995). Personal observations suggested that birds moulted throughout the year, but there was a period between February and March when birds in all sub-populations appeared to undergo a heavier moult, which may have suppressed breeding (see Chapter 4). The length of this period varied annually, and was sometimes extended at drier sites (e.g. at Brise Fer) or if there had been little rain. Moult data has not been analysed for this thesis.

The incubation period of captive birds has been recorded as 13-14 and 14 days (Jeggo 1977, 1978), 13-15 and 14 days (Jones 1987), and 14 days (Jones 1995). Observations of wild and released birds suggested an incubation period of about 14 days (Jones 1995, and see Chapter 4). Wild-hatched squabs may leave the nest between 18 and 22 days old, but were not independent of parents for crop food until at least 28 days old (Jones 1987). McKelvey (1977) suggested that young first left the nest at 28 days which is nearly one week later than observations on wild and captive birds (Jones 1987, and this study), and later than birds bred at the Jersey Zoo (Jeggo 1979). Captive young are considered independent of foster-parents at about 30 days old. Fledgling pink pigeons showed a prolonged post-fledging dependence upon their parents (McKelvey 1977, Temple 1978, Jones 1995). Juveniles were partly fed by their parents for at least one month after fledging (Jones 1995), and possibly up to six weeks old (McKelvey 1977). Personal observations suggested that juveniles may be fed for longer and may associate with parent birds for up to five months post-fledging. Post-fledging dependence has been reduced to about two weeks with the provision of supplemental food.

Accounts of the growth and development of the fledged captive pink pigeon can be found in Jones (1995). Most bone development has achieved adult size by about 30 days old. Adult size of the head length and width and beak length was achieved at 30 days, the tarsus at fledging (18 to 23 days), the centre toe at 18 to 20 days, the centre claw at 35 to 40 days and the manus length at 40 to 50 days old. At fledging, the manus length is 65% of adult length. Adult mass, however, is not achieved until about 90 to 100 days old. The juvenile flight and tail feathers are fully grown by 40 to 50 days old. Moult from juvenile to adult plumage starts at about two months and is usually finished by six months, but by about 100 days old, the bird is beginning to look like an adult (Jones 1987). McKelvey (1977) suggested that the last juvenile primary was moulted at about eight months and the last juvenile tail feather at nine months. Jones (1995) gave 150 days as the age at which a juvenile bird becomes adult since by then, body mass has stabilised at adult level and most birds will be in adult plumage. However, reproductive maturity is achieved later than this. Jones (1995) gave the median age of females at first egg-laying as 9.79 months, at first fertile egg-laying as 10.5 months, and the median age for males first siring a fertile egg as 14.2 months.

FOUNDER REPRESENTATION IN PINK PIGEONS

Until 1989, the captive population of pink pigeons originated from just eleven founders collected between 1976 and 1981 (Jones *et al.* 1983). Since 1989, eggs removed from the wild population at Pigeon Wood have contributed 12 further founders (referred to here as secondary founders), although one of these (SBN 413) may be in part descended from a captive-bred bird (see Chapter 3).

Figure 2.3 shows the mean founder representation of released birds in each sub-population that laid or sired eggs during this study period. The mean founder representation on Ile aux Aigrettes in 1998 (Figure 2.4) shows how changes have occurred to the distribution of founder representation within the population since the original released birds started breeding and indicates that some founders have become more equally distributed within the population. Between 1987 and 1995, the remaining wild population at Pigeon Wood comprised or were descended from 13 birds, four of which were lost to the wild population by 1993 (Figure 2.5), but three of which have been preserved in released sub-populations. Since 1996, three captive-bred released females that moved from other sub-populations contributed representation of original founders to this sub-population.

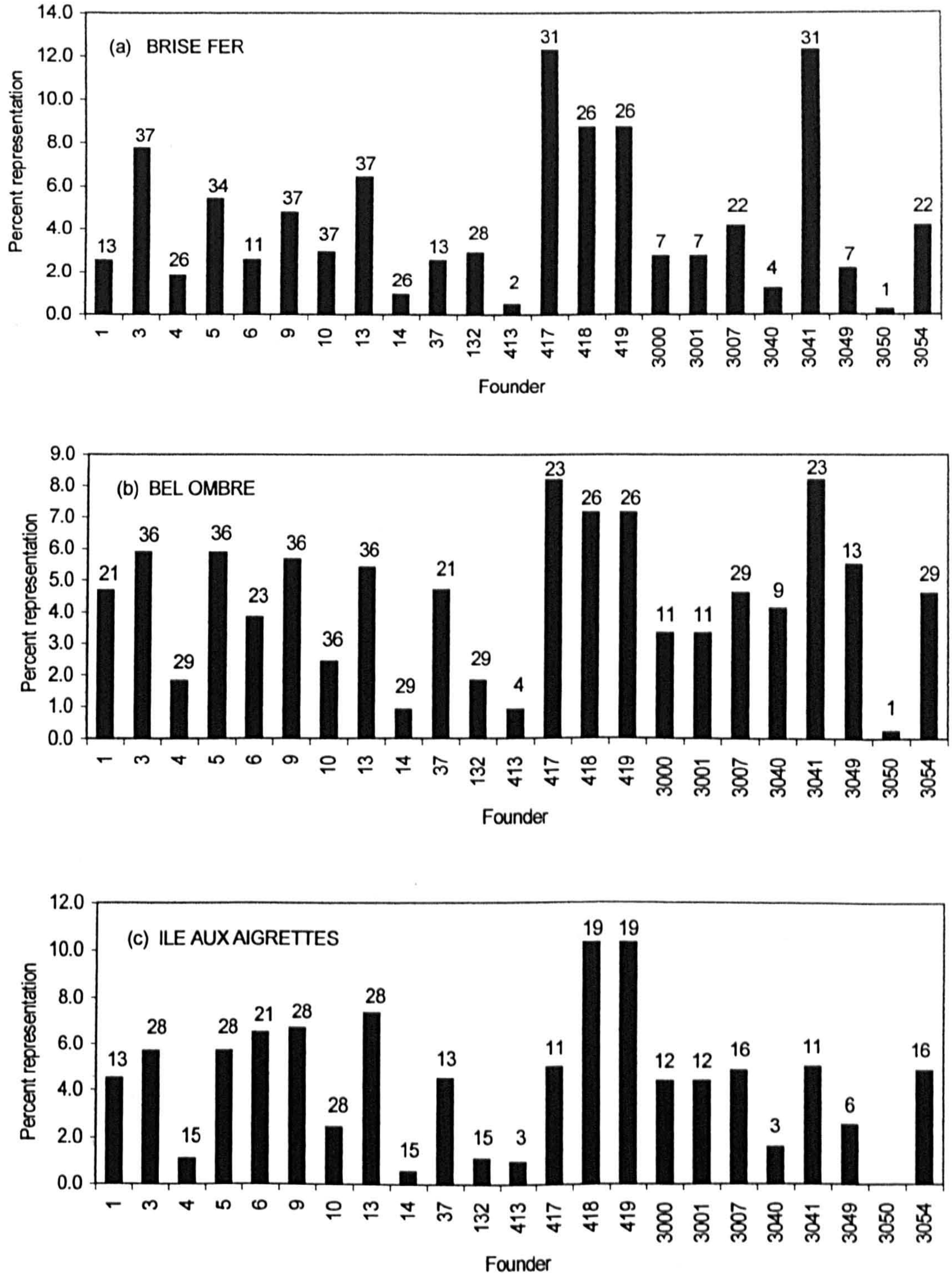

Figure 2.3 Mean founder representation in captive-bred released pink pigeons that laid or sired eggs. Eleven original founders are to the left of the chart and 12 secondary founders are to the right of the chart. Founders 4 and 14 are also poorly represented in the *ex situ* captive populations (Taynton & Lind 1991, Lind 1993). Numbers are the number of birds in which the founder was represented. Sample size: (a) Brise Fer 53, (b) Bel Ombre 49, (c) Ile aux Aigrettes 40. One wild female from Pigeon Wood that contributed a large number of young to Brise Fer was included in the Brise Fer sample.

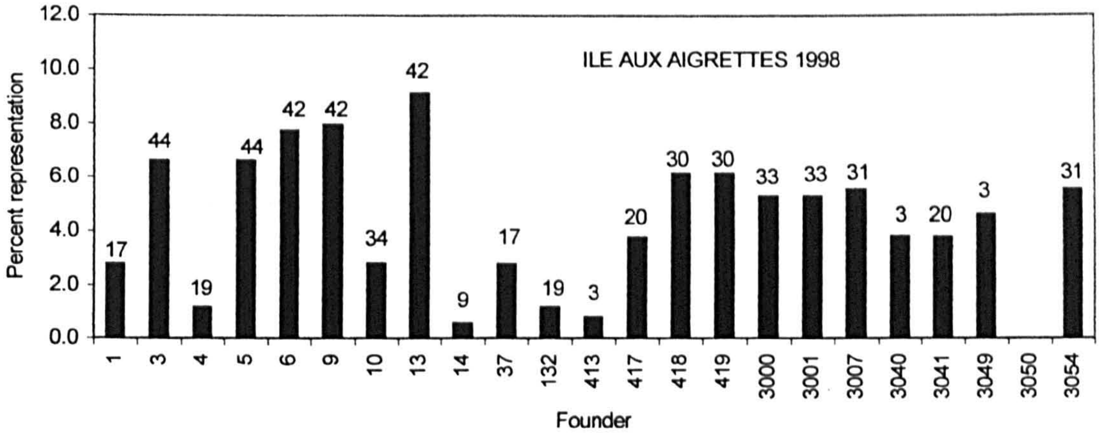

Figure 2.4 Mean founder representation in the Ile aux Aigrettes population at end 1998. Original founders are to the left of the chart and secondary founders to the right. Numbers are the number of birds in which the founder was represented. Sample size 46 birds and excluded 14 birds of unknown pedigree.

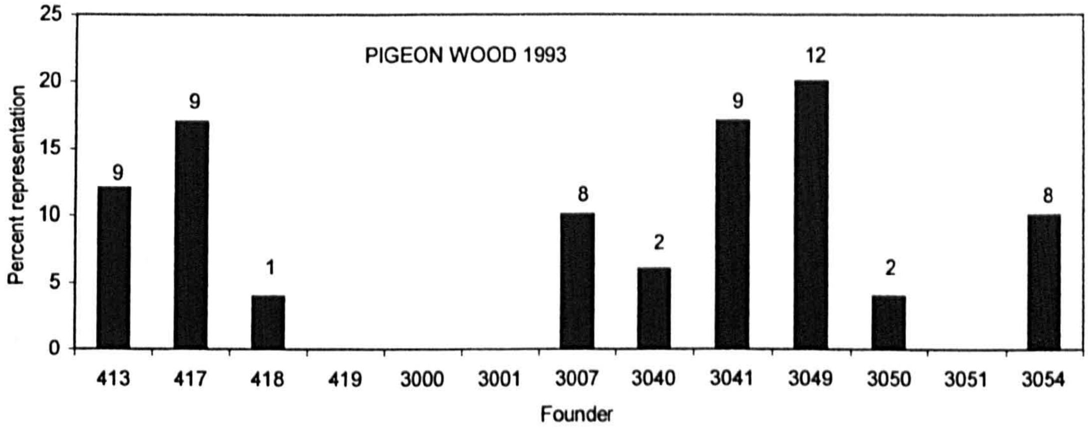

Figure 2.5 Mean founder representation in the Pigeon Wood population at end 1993. Sample size 25 birds. All founders are secondary founders and are likely related to the original founders collected between 1976 and1981. Secondary founders 3000 and 3001 comprised a pair of unringed birds and were only known in the wild in 1990. Secondary founder 3051 did not produce young and died in 1992. Secondary founder 413 is discussed above (see also Chapter 3)

THE FIELD PROGRAMME

The pink pigeon field programme began with one field staff in July 1987. I took over the project in June 1988 and was joined by a field assistant in September 1989. Since then, more than 70 field staff have worked under my supervision, 36 for one season (about six months) and 17 for at least two seasons. Numerous short-term volunteers, local and overseas University students have also been involved. Since 1996, the field team numbered between eight and 11 staff during a season.

Between 1987 and 1994, the programme concentrated on the re-introduction and management of birds at Brise Fer forest and monitoring and management of the remaining wild population. Releases began at Brise Fer in July 1987 (but fieldwork was suspended in March 1988 and resumed in July 1988) and expanded to Ile aux Aigrettes and Bel Ombre in 1994. Full-time work on the wild population at Pigeon Wood started in September 1989 although some monitoring had occurred prior to this.

Fieldwork was year round, initially more intensive between September and February to coincide with the breeding season but when winter breeding was detected, fieldwork became intensive year round. Research teams lived in the field stations located within or close to study sites. Transport to field stations and study sites was by 125cc off-road motorbikes, 4WD vehicle and bicycle. Communication between the field sites and the base camp in the village of Black River was by VHF radio (and later by mobile phones) installed in 1993.

Re-introduction

Release procedure and technique

The methods used for re-introduction have been previously described (Jones *et al.* 1988, Jones *et al.* 1992, Swinnerton *et al.* 1993, Swinnerton *et al.* 2000). The first releases at Brise Fer in 1987 followed the procedure and techniques developed at Pamplemousses Botanic Gardens (Todd 1984), but as releases progressed, 'softer' release methods were developed. After initial release, birds were encouraged to return to the release aviary for food where they were re-trapped. For a period of about one month, birds were allowed liberty for an increasing length of time, until they were eventually given full liberty. This technique allowed the birds to familiarise themselves with their surroundings and with sources of food. It minimised the risk of losing birds in adverse weather and ensured that birds remained in good condition during the release process. As the population around the release sites became established, it was easier to release additional birds into the population and birds were allowed full liberty earlier.

Source of birds

Most released birds were captive-bred in Mauritius at the Black River aviaries (now the Gerald Durrell Endemic Wildlife Sanctuary) and most were reared by foster-parents, domestic barbary doves *Streptopelia risoria*. The foster-parents incubated pink pigeon eggs and reared squabs to about 30 days old, when fledglings would be feeding themselves. Because a fledgling pink pigeon is more than twice the size of its foster-parents, many squabs received some hand-feeding from about 17 days old. Parent-reared squabs were usually hatched by foster-parents and reared by pink pigeons from about four to five days old. Because adult pink pigeons were often poor parents, many parent-reared squabs also received some hand-feeding and some were returned to foster-parents.

Trapping and bird identification

All birds were identified by a unique colour and numbered ring combination fitted on the tarsus. Radio-tags were fitted to 84 birds (31%) and bells fitted to 74 birds (29%) for monitoring post-release. Wild-fledged birds were trapped, in a release aviary or cage trap at a feeding station, and ringed soon after fledging. On Ile aux Aigrettes and at some mainland nests squabs were ringed on the nest. The remaining wild population at Pigeon Wood was ringed between November 1989 and February 1992. Standard guidelines for trapping, handling and ringing techniques were followed (Spencer 1995). The following were recorded from each bird caught: mass, morphometric measurements, moult pattern, signs of disease or injury and general condition. A blood sample for DNA analysis and disease profiling was taken.

Management of birds in the wild

Early studies of the pink pigeon identified predation and seasonal food shortages as factors limiting the population (Jones 1987, Jones & Owadally 1988). Supplemental feeding and predator control were suggested as valuable techniques for the conservation of endangered species (Archibald 1977, Merton 1977) and were applied to the pink pigeon.

Supplemental feeding

Supplemental feeding of released birds began at each site from the first release. Wild birds were supplementally fed from September 1989. At least two feeding platforms were built at each site, close to the release aviary and within breeding sites when breeding birds were established. A mix of cracked maize and wheat was permanently available from a hopper on the platform. The platforms were protected from rats and hoppers excluded exotic doves.

Predator control

Introduced mongooses *Herpestes auropunctatus* and cats *Felis catus* were controlled at release sites, around feeding stations and within breeding areas. At Brise Fer predators were controlled at the release site from 1987 and at Pigeon Wood predator control started in early 1993 (Jones *et al.* 1992, Swinnerton *et al.* 1993). From 1993, predator control intensified and control grids were established at all sites. Cage traps (Veitch 1985) were spaced 100 m apart and surrounded by a peripheral ring of traps to create a core predator free area and to catch immigrant animals (Roy *et al.* 1998). Traps were at higher densities around the release aviary and supplementary feeding stations, and additional traps were placed where field signs of predators were found.

Rats were controlled within breeding areas to reduce predation of eggs and young squabs, and around the release aviary and feeding stations to reduce food spoilage, wastage and the spread of disease. Rats were controlled using an anti-coagulant poison Brodifacoum (0.005%) supplied in commercial wax blocks. Rat poison grids were established at Pigeon Wood at the end of 1991, at Brise Fer between 1992 and 1993 and at the other sites at the start of releases. Poison was placed in bait stations on a 50 m grid that was surrounded by peripheral stations 25 m apart (Dingwall *et al.* 1978).

Data collection and data analyses

Field staff transferred daily observations to data sheets, which were standardised for all field sites. Datasheets were used for data from individual birds, from individual squabs monitored on the nest and for individual nest records. Two daily check sheets were also used, one to record sightings of individual birds and one to monitor the status of individual breeding pairs. Studbook data and breeding records were transferred into Excel spreadsheets. Data quality was variable due to the large number of research staff of differing experience and much of it required 'cleaning' and standardising. Observations in field notes, which were additional to the datasheets, were used to improve the accuracy of the data.

Limitations of the data due to working with an endangered species

The pink pigeons' status as a threatened species limited the research and data collection in two ways. Firstly in the four-year period from 1988 to 1991, the total number of fledged birds available for study was 51, 20 at Pigeon Wood and 31 in the release programme, many of which survived only a few months. Successful nesting attempts were few and the small population size limited statistical analyses. It was not until after 1991, when more birds were available for release and the population increased, that useful data collection and analyses could be carried out. Secondly, owing to the high risk of extinction of the species in the wild at the beginning of the programme, invasive research (trapping and handling birds, accessing nests) was undertaken with extreme caution. The survival of the birds was paramount and data collection always remained secondary to their welfare.

Chapter 3

Survival and population trends

INTRODUCTION

Understanding the factors that cause population decline and limit population growth is essential when developing a successful recovery programme. A number of reasons were suggested as the cause of population decline in the pink pigeon (Collar & Stuart 1985, Jones 1987) but these had not been evaluated, partly owing to the population's small size. The re-introduction and management programme was primarily aimed at preventing the species' extinction in the wild. However, monitoring released and free-living birds has provided data on their population biology and suggested reasons that may have contributed to their original decline. Survival studies were undertaken to assess the success of the release programme and to understand the factors limiting population growth. This was necessary for the future management of the species.

METHODS

Survival studies were conducted between July 1987 and December 1998. Survival of released birds was studied at Brise Fer from July 1987, at Ile aux Aigrettes from March 1994 and at Bel Ombre from November 1994. Survival studies of wild-bred progeny of released birds began at Brise Fer in January 1989, at Ile aux Aigrettes in August 1994 and at Bel Ombre in April 1995. Survival studies of the remaining wild population at Pigeon Wood started in November 1989 when the first bird was ringed.

Age was calculated for all birds as the number of days between hatching and death, or to 31st December 1998 if still alive on this date. Survival was estimated for released birds from 30 days old (when they achieved independence[1]) and for wild birds from fledging (23 days old) using age as the survival time. Post-release survival was also calculated for released birds, where the first day of release represented day one. Two assumptions were made when estimating survival: for released birds that there was no mortality between 30 days old and release and for wild birds that there was no mortality between fledging and ringing.

Hatch dates for captive-bred released birds were obtained from a database and from datasheets for individual squabs. For wild-bred birds, actual hatch dates were obtained for most squabs on Ile aux Aigrettes and some closely monitored nests on the mainland.

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[1] Most captive-bred birds were reared by foster-parents. Independence means the age at which fledglings were feeding themselves and were no longer dependent on their foster-parents.

Where nests were not accessed, or accessed only when containing older squabs, hatch dates were estimated from incubation and brooding behaviour of the parents, and from morphometric measurements and plumage characteristics of the squab. Age was estimated for unringed adults and juveniles when trapped and ringed, using morphometric measurements, moult and plumage colour (see *Aspects of pink pigeon life-history*, Chapter 2). Most unringed juveniles were trapped one to two months post-fledging when they first appeared at a feeding station. On Ile aux Aigrettes most wild-fledged birds were ringed in the nest. The remnant wild population of adult birds at Pigeon Wood were assumed to have fledged in 1987, at least two years prior to ringing.

Where the death date was unknown this was recorded as the date last seen. Most birds were seen at least once a week. Where birds were seen infrequently, once a month or less, death dates were assigned to the month in which the bird was last seen. Survival times for birds which were removed to captivity and not re-released were calculated up to the age when removed, and treated as 'censored' data (see survival analysis). Where birds were re-trapped during the release process and re-released after more than 30 days in captivity, post-release survival was calculated for the subsequent period of release.

Survival of an individual was monitored by its presence at feeding stations, observations in a territory or at a nest or when located in the field, and sightings were kept on check sheets. Some released birds were also radio-tracked or located using bells attached to the tarsus (Chapter 2). Most birds were individually identified by a unique number and colour combination. Eight unringed birds were identified by unique physical characteristics. From 1994 a weekly census was carried out at each feeding station from dawn to dusk over a one or two-day period.

Determining criteria for survival analyses

Released birds were captive-bred or wild-bred and captive-reared. A wild bird was defined as fledged in the wild, and included the remnant population at Pigeon Wood and wild-fledged progeny of released birds. An adult was defined as more than one year old and a juvenile as less than one year old, even though some birds started breeding at less than one year. Using one year as the distinction between juvenile and adult greatly simplified the analysis.

Determining sex

Male and female pink pigeons are not clearly sexually dimorphic, although morphometric measurements and plumage colour differences can help to clarify the sex of most adult birds (Jones 1995). The sex of juveniles was not clear until they reached maturity. Males were identified by territorial and breeding behaviour and by male-specific calls. Owing to the occurrence of male unisexual pairs, females could only be confirmed once eggs were laid.

Calculating inbreeding coefficients

Inbreeding coefficients were calculated in a database previously established for captive pink pigeons. C. Jones and K. Swinnerton designed the database requirements and the system programs were written by R.W. Burn (Burn 1990). The database system is similar to a studbook database but with additions relevant to the pink pigeon research, for example data on eggs, pairings and trial pairings. The database was implemented in the DataEase system, with a program for pedigree analysis (inbreeding and kinship coefficients). The program used for calculating inbreeding coefficients was adapted from an original program written by A.J. Boyce (re-worked to run in Basic) and used an algorithm (the Quaas-Henderson method) in a FORTRAN programme called KINSHIP (see Crow and Kimura 1970 for details of the algorithm). S. Wheeler wrote a separate program in Excel for founder representation, based on an algorithm described by J. Ballou (1983), as this facility on the pink pigeon database was incomplete.

Determining rearing method of released birds

Rearing methods of released birds are described in Chapter 2. Where an individual was both foster and parent-reared, the rearing method that the bird received from 16 days old to independence was chosen for the analysis.

Survival analysis

Survival was investigated using Kaplan-Meier estimates of survivor function (Kaplan & Meier 1958, Cox & Oakes 1984) and life history data. Excel spreadsheets were used to carry out Kaplan-Meier survival estimates and generate survival curves. The Kaplan-Meier method allowed for birds that were still alive at the end of the study or that were removed from the study, by treating them as 'censored' data and accounted for them by adjusting the number of individuals at risk. In the survival analysis there are two functions of central interest, namely the survivor function and the hazard function. The survivor function represents the probability that an individual survives from the time origin t to some time beyond t. The hazard function (the risk or hazard of death) is the probability that an individual dies at time t, conditional on the individual having survived to that time, and represents the instantaneous death rate for an individual surviving to time t.

Cox's proportional hazards model (Cox regression) (Cox 1972, see also Collett 1994) was used in SPSS 9.0 (1998) to investigate the effect of different covariates on survival (e.g. site, sex). In Cox's proportional hazards model, the hazard function is modelled directly. This enables the effect that a covariate has on the hazard of death to be studied as can the effect of a combination of covariates (e.g. site and sex). The proportional hazards model assumes that the hazard of death at any given time for an individual in one group is proportional to the hazard at that time for a similar individual in the other group. If the hazard functions are proportional, the survivor functions for the groups of survival data do not cross one another. In some cases, estimates of survivor function may cross even though the corresponding true hazard functions are proportional (Collett 1994). Crossing is less important at the end of the survival curve where sample sizes are small.

The proportional hazards model provided an overall test statistic (the Wald test was chosen) and a significance probability for the covariate being modelled, for example 'site'. The data had several levels, for example sex had two levels, inbreeding had three levels and site had four levels. Within the model, a test statistic and a significance probability were also obtained for each level relative to one other level. Data that had more than two levels included comparisons between sites and inbreeding effects. Where analyses involved comparisons between sites, survival was compared to that at Pigeon Wood and survival in released sub-populations was compared to that at Bel Ombre. Analyses of inbreeding compared survival of inbred and highly inbred birds to that of non-inbred birds. The overall significance of the test was not necessarily true for each level owing to sample sizes and differences in variation between and within levels. Where the test highlighted significant differences between particular levels, these were investigated more thoroughly by analysing them independently.

Where survival was compared using data pooled from several sites (e.g. a comparison of the survival of released and wild birds) a stratified test was used where data were stratified by site (see Collett 1994 for the calculations). This accounted for the different survival probabilities at each site (i.e. the different baseline hazards) and enabled a more precise summary of the covariate's effect.

Two different sets of survival data were analysed: 'survival' referred to survival from independence (for released birds from 30 days old) or fledging (for wild birds from 23 days old) to death or censoring. For released birds, survival included the pre-release period in captivity. Post-release survival for released birds referred to survival from release to death or censoring as described previously. Kaplan-Meier estimates of survival were determined for each sub-population, for wild and released birds and for juveniles and adults and the survivor function plotted. The effect on survival of different covariates was analysed which included sex, age at release, inbreeding and rearing method of released birds (foster or parent). Data for all sites were pooled when analysing overall effects and analysed for each sub-population where required.

To compare survival between wild and released birds, survival was estimated for birds from the median age or more at release. Released birds were only selected where the age at release was the median age or more in each sub-population. Wild birds were selected only if they had survived up to this median age. Where released and wild birds were compared within sites, the median age at release at each site was used. Where data for released and wild birds from all sites were pooled, the median age at release for all birds was used. To investigate the effect of age at release, survival times were analysed for two cohorts of birds: 150 days old or younger and older than 150 days. To investigate the effect of inbreeding, birds were classified into three categories: non-inbred (inbreeding coefficient of 0), inbred (> 0 and < 0.25) and highly inbred (≥ 0.25). Where sample sizes of highly inbred birds were small, data for inbred and highly inbred birds were pooled.

Kaplan-Meier estimates of annual and seasonal survival were calculated from 1992 to 1998. Cox's proportional hazards model was used to test for differences in annual survival. ANOVA (MINITAB version 8.21, 1991) was used to test for seasonal differences in survival and data were arcsine transformed. Two seasons were defined, a period when breeding activity was low (January to June) and a period when breeding activity was high (July to December). Although some breeding occurred all year around, this distinction simplified the analysis. Actuarial life history tables were constructed in SPSS 9.0 for all birds, for each sub-population, for released and wild birds and for males and females. All mean values are presented with the standard deviation (± SD).

Exclusions

Twenty-two birds were excluded from life history analysis and Kaplan-Meier estimates of survival in different sub-populations. Seven birds were very old for release (mean age at release 8.2 ± 5.6 years). Three released birds were excluded from the Ile aux Aigrettes subset: two birds were old females, had been previously released at Brise Fer and were at liberty for only six days on Ile aux Aigrettes before being re-trapped or death. The third bird could not fly. Twelve birds referred to as 'dispersers' had emigrated from their non-natal sub-population, some moved between all three mainland sites and some bred in two sub-populations. Kaplan-Meier estimates of annual survival for all sites combined included dispersers, but dispersers were excluded from site-specific annual survival. When analysing the effect of rearing method on survival, nine parent-reared birds were excluded from the data because they also received a lot of hand-feeding.

Population Trends

The number of birds alive on the 31st December of each year was calculated for each sub-population together with the number of birds released and wild-fledged during that year. Population figures for each sub-population included immigrants.

RESULTS

Releases

Table 3.1 shows the main parameters of the release programme including birds that were excluded from the analyses. Survival to 30 days post-release (when birds were considered established, i.e. not being re-trapped in the release aviary and at full liberty) averaged 89%. The main parameters of the wild population at Pigeon Wood can be found in Appendices 2 (a) and 2 (c).

Table 3.1 Releases of captive-reared birds from 1987-97. Two birds were released in two sub-populations. Mean size of the release group excluded birds released singly. Median age at release here is for all birds. For survival analyses median age at release at Brise Fer was 85 days, at Ile aux Aigrettes 154 days and for all birds 83 days because some old birds were omitted from the analyses.

	Brise Fer	Ile aux Aigrettes	Bel Ombre	Total
Years released	1987-96	1994-96	1995-97	1987-97
No. captive-bred birds released	107	46	88	239
No. wild-bred birds released	1	9	7	17
No. released Males:Females:unknown	51:37:20	27:22:6	35:43:17	113:100:43
No. survived 30 days post-release	94	52	84	230
% survived 30 days post-release	87	95	88	89
Mean size of release group	4	7	6	5
Median age at release (days)	88	171	72	86
Mean no. days in release aviary	31	48	15	29
No. birds fitted with radio-tag:bell	56:26	14:7	14:41	84:74

Kaplan-Meier estimates of survival

Table 3.2 shows a summary of the significant effects of different covariates on survival. Further details of these results are presented in the following sections.

Influence of site on survival

Survival of birds varied significantly between sites (Figure 3.1). Survival was highest at Pigeon Wood and poorest at Ile aux Aigrettes. Survival differences between Pigeon Wood and Ile aux Aigrettes were highly significant ($P < 0.0001$) and for Brise Fer were significant ($P < 0.01$). Survival of birds at Bel Ombre was not significantly different to Pigeon Wood but the small sample size together with a short study period at Bel Ombre may have influenced the results.

Table 3.2 Results of Cox's proportional hazards model showing significant effects on survival. An overall test statistic is presented for each covariate where significant. Where data involved more than two levels, the test statistic is also presented for each level where significant (see Methods). The results are presented in the order in which they are cited in the text. Abbreviations: vs = compared to, BF = Brise Fer, IAA = Ile aux Aigrettes, Wald is the test statistic, df = degrees of freedom, P = probability.

Covariate	Parameter on which covariate was significant	Wald	df	P
Site	Survival - all birds	42.28	3	0.0000
	- Ile aux Aigrettes	31.48	1	0.0000
	- Brise Fer	8.53	1	0.0030
Site	Post-release survival			
	- Brise Fer only	4.45	1	0.0348
	- first year post-release at BF	5.16	1	0.0232
Site	Survival - wild birds	57.78	3	0.0000
	- Ile aux Aigrettes	46.51	1	0.0000
	- Brise Fer	5.99	1	0.0140
Released vs wild	Survival - all birds			
	- adult survival after adjusting for sex	4.07	1	0.0436
	- Ile aux Aigrettes only	14.20	1	0.0002
Released vs wild	Survival from median age at release	4.97	1	0.0259
	- Brise Fer only	5.37	1	0.0205
Age at release	Post-release survival – released birds	3.82	1	0.0510
Inbreeding	Survival - all birds	9.96	2	0.0069
	- released females	4.71	1	0.0300
	- released adult females	4.51	1	0.0337
Inbreeding	Post-release survival			
	- all females	4.59	1	0.0322
	- adult females	4.11	1	0.0426
Site	Juvenile survival			
	- Ile aux Aigrettes only	23.84	1	0.0000
	- wild juveniles, Ile aux Aigrettes	42.55	1	0.0000
	- released juveniles at IAA vs BF	3.89	1	0.0484
Released vs wild	Juvenile survival – Ile aux Aigrettes	21.94	1	0.0000
Inbreeding	Juvenile survival	6.58	2	0.0372
	- highly inbred	5.77	1	0.0163
	- inbred (inbreeding coefficient >0)	4.06	1	0.0438
Site	Adult survival	8.67	3	0.0340
	- Brise Fer	7.63	1	0.0057
	- Ile aux Aigrettes	6.14	1	0.0132
	Post-release adult survival			
	- Ile aux Aigrettes vs Bel Ombre	4.84	1	0.0277
Site	Wild adult survival			
	- Brise Fer only	5.63	1	0.0176

Influence of site on survival of released birds

Survival of released birds was not significantly different between release sites ($P > 0.05$, $n = 242$). However, post-release survival of birds at Brise Fer was significantly poorer than at Bel Ombre ($P < 0.05$). This was largely due to poor survival during the first year post-release at Brise Fer which was significantly poorer than subsequent years ($P < 0.05$). Survival after the first-year post-release was not significantly different between release sites. Poorer post-release survival at Ile aux Aigrettes was suggested (see Table 3.5) but the small number of birds released may have influenced the results.

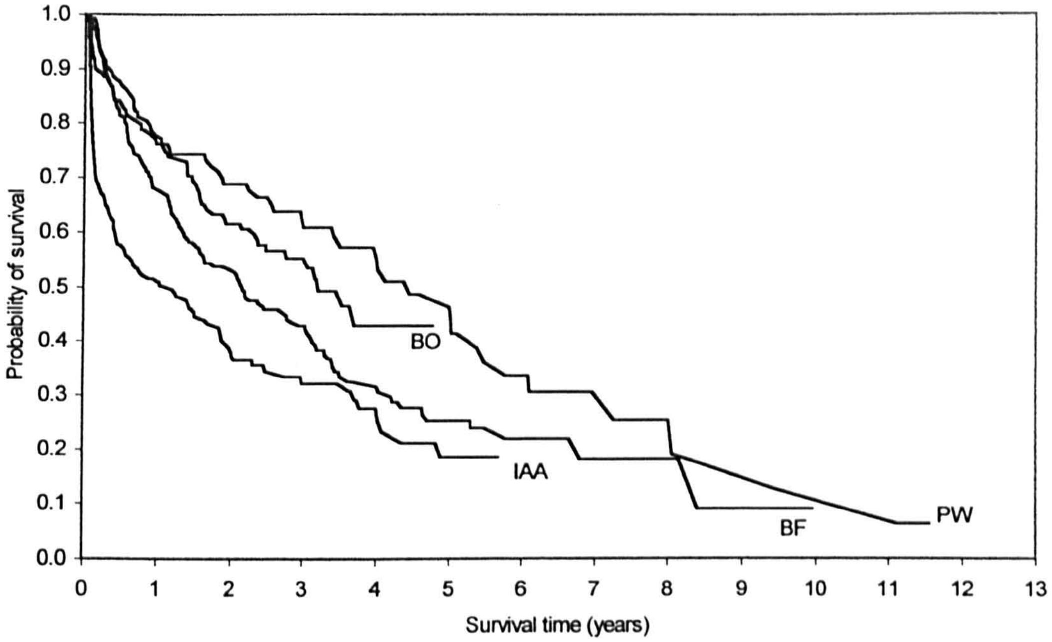

Figure 3.1 Survival curves for pink pigeons in different sub-populations, 1987-98. Survival from 30 days for released birds and from fledging (23 days) for wild birds. Data for released and wild birds were pooled. Kaplan-Meier estimates of survivor function are plotted. PW = Pigeon Wood, BO = Bel Ombre, BF = Brise Fer, IAA = Ile aux Aigrettes. Sample size: PW 132, BO 139, BF 230, IAA 176 (44% censored). Survival was significantly different between sites ($P < 0.0001$).

Influence of site on survival of wild birds

Survival of wild birds was significantly different between sites ($P < 0.0001$) and the pattern of survival was the same as in Figure 3.1. Compared to the birds at Pigeon Wood, survival of wild birds was significantly poorer at Ile aux Aigrettes ($P < 0.0001$) and at Brise Fer ($P \cong 0.01$).

Survival of released and wild birds

When data for released and wild birds from all sites were pooled, there was no overall significant difference between survival of released and wild birds ($P > 0.05$, $n = 677$). However, when data were pooled from all sites for adult birds and survival was adjusted for the variation caused by sex, survival of released adults was significantly poorer than wild adults ($P < 0.05$). This effect could not be repeated for individual sites or when data from mainland sites were pooled.

When survival of released and wild birds were compared within sites, survival of wild birds was significantly poorer than released birds at Ile aux Aigrettes ($P < 0.001$). When data from all sites were pooled and survival of released and wild birds was compared from the median age at release, released birds showed significantly poorer survival than wild birds (Figure 3.2). When survival was compared within release sites from the median age at release, survival of released birds was only significantly poorer than survival of wild birds at Brise Fer ($P < 0.05$) ($n = 161$). The differences seen in survival of released and wild birds at Ile aux Aigrettes were not significant when comparisons were made from the median age at release. At Bel Ombre, poorer survival of released birds was suggested (see Table 3.4) but was not significant. A small sample size ($n = 91$) and short time-span for wild birds at this site may have accounted for this.

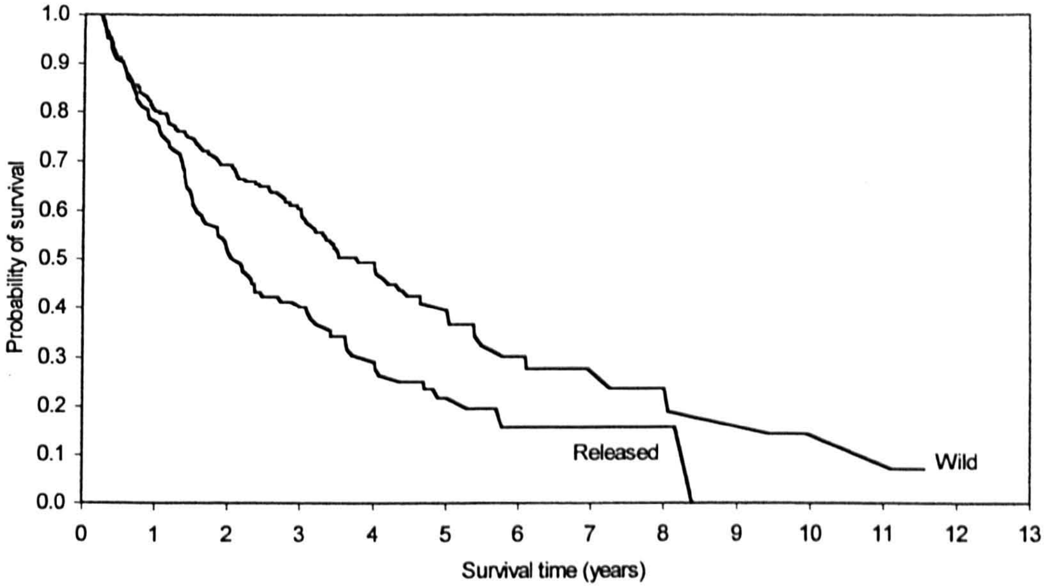

Figure 3.2 Survival curves for released and wild birds from the median age at release, all sites 1987-98. Kaplan-Meier estimates of survivor function are plotted. Sample size: released birds 123, wild birds 322 (50% censored). Survival of released birds was significantly poorer than survival of wild birds ($P < 0.05$).

Influence of sex on survival

There was no significant difference between the survival or post-release survival of adult males and females when data from all sites were pooled (survival $P > 0.05$, post-release survival $P > 0.05$, $n = 225$). Survival probabilities of juvenile males and females were not true estimates and were biased towards birds that survived to breed (Table 3.3). The sex of only 50 (23%) juveniles that died at less than one year old was confirmed.

Age at release

Birds older than 150 days at release showed almost significantly poorer survival than younger birds when data from release sites were pooled (Figure 3.3). The median age at release for younger birds was 76 days (n = 196) and for older birds was 206 days (n = 52).

Rearing method of released birds

When data from release sites were pooled, the method of captive-rearing in released birds (foster-reared or parent-reared) did not significantly affect survival or post-release survival, although some effect was suggested (Figure 3.4).

Influence of inbreeding on survival

Inbreeding significantly affected survival when data from all sites were pooled (Figure 3.5). This effect was mainly seen in juveniles (see *Effect of inbreeding in juvenile survival*) and in released adult females. Overall, inbreeding (when data for inbred and highly inbred were pooled) did not significantly affect the survival of adult birds ($P > 0.05$, $n = 225$). Mean age at death of non-inbred adults was 2.6 ± 1.5 calendar years ($n = 45$) and 2.2 ± 1.2 calendar years for inbred adults ($n = 56$). Inbreeding coefficients for fledged birds are shown in Appendix 4.

When data were pooled for wild and released birds, inbreeding did not significantly affect the survival of males or females (males $P > 0.05$, $n = 133$; females $P > 0.05$, $n = 115$) nor for only adult males and females (adult males $P > 0.05$, $n = 113$; adult females $P > 0.05$, $n = 102$). However, when the survival of released birds was analysed independently, inbreeding significantly affected the survival and post-release survival of released females which was poorer for inbred birds than for non-inbred birds (Figure 3.6). Results were also significant for adult released females (survival $P < 0.05$, post release $P < 0.05$). Post-release survival of released males was not significantly affected by inbreeding. The sample sizes of wild-fledged males and females with known inbreeding coefficients were too small to analyse independently.

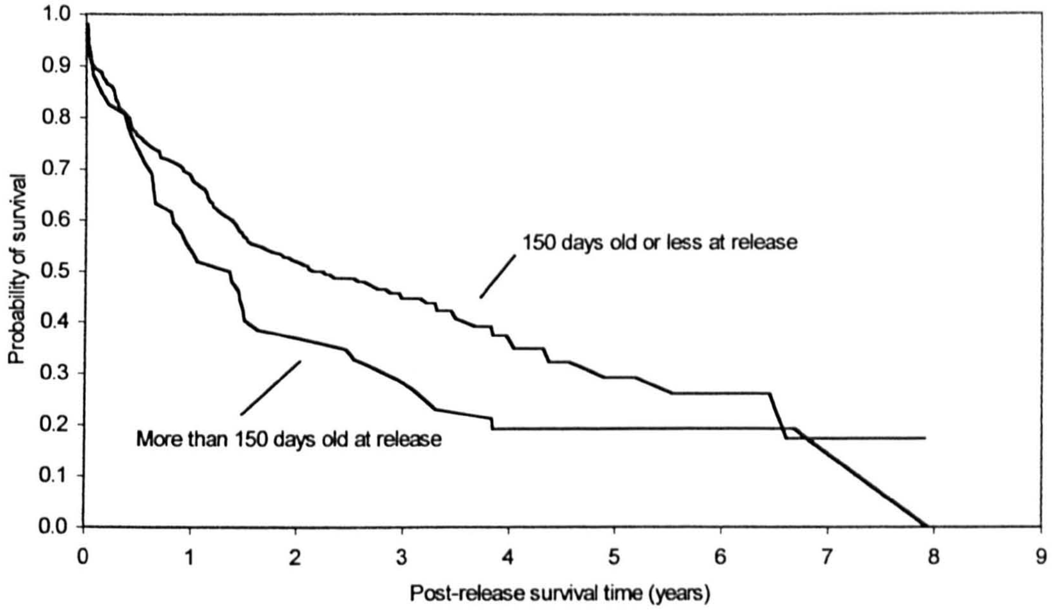

Figure 3.3 Effect of age at release on post-release survival, all sites 1987-98. Kaplan-Meier estimates of survivor function are plotted. Sample size: less than 150 days old at release 196 birds, more than 150 days old 52 birds (36% censored). Post-release survival of older birds was almost significantly poorer than younger birds (P ≅ 0.05).

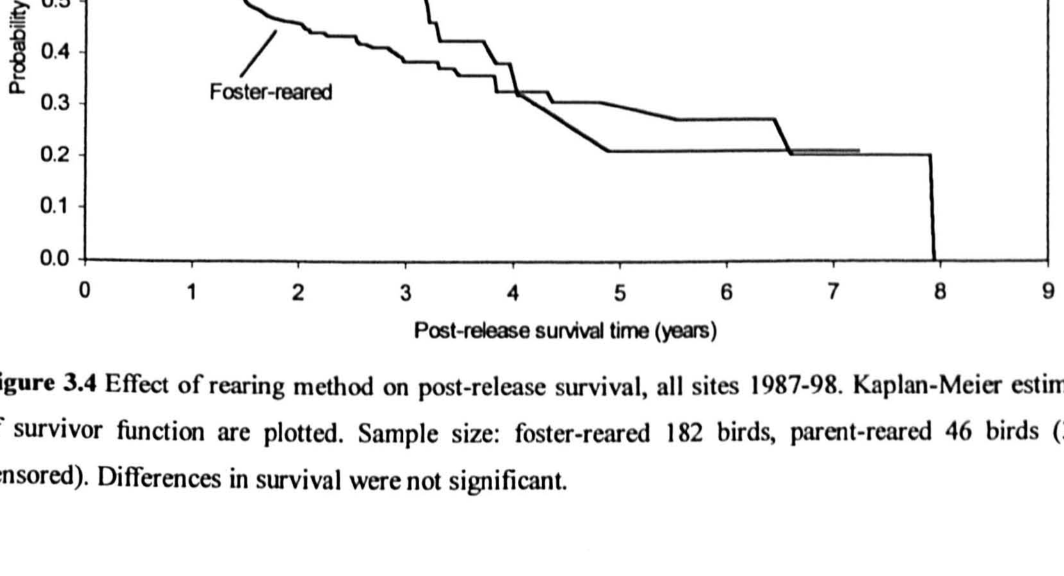

Figure 3.4 Effect of rearing method on post-release survival, all sites 1987-98. Kaplan-Meier estimates of survivor function are plotted. Sample size: foster-reared 182 birds, parent-reared 46 birds (37% censored). Differences in survival were not significant.

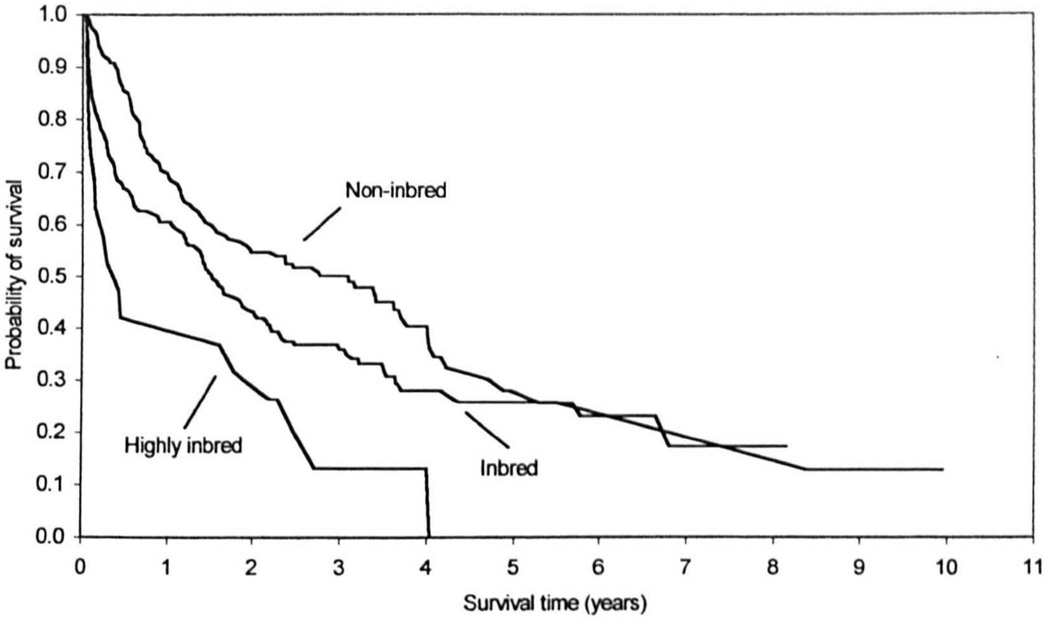

Figure 3.5 Effect of inbreeding on survival, all sites 1987-98. Inbreeding coefficients: non-inbred = 0, inbred > 0 and < 0.25, highly inbred ≥ 0.25. Kaplan-Meier estimates of survivor function are plotted. Sample size: non-inbred 153, inbred 191, highly inbred 19 (64% censored). Effect of inbreeding was highly significant (P < 0.01).

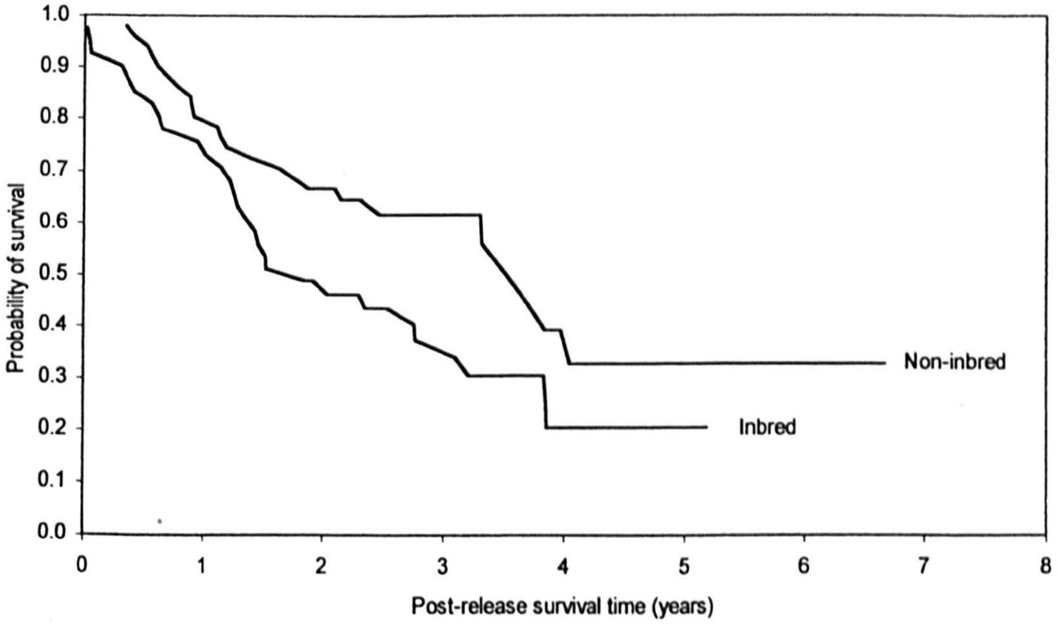

Figure 3.6 Effect of inbreeding on post-release survival of females, all sites 1987-98. Kaplan-Meier estimates of survivor function are plotted. Inbreeding coefficients: non-inbred = 0, inbred > 0. Sample size: non-inbred 51, inbred 41 (42% censored). Survival and post-release survival of inbred females was significantly poorer than non-inbred females (survival P < 0.05, post-release survival P < 0.05).

Age-specific survival and Life History Tables

Actuarial life history data supported general trends in Kaplan-Meier estimates of survival. Survival was poorer for juveniles than for adults (Table 3.3). Mean survival of adults was relatively constant across years. Birds at Ile aux Aigrettes showed overall both poorest juvenile survival (50%) and poorest mean adult survival (77%).

Table 3.3 Life History Tables: percent survival per age group. Survival estimates only where minimum sample size is 10 birds per age group. For sample sizes see Appendix 1. Estimates for males and females in year 0 are biased towards those that survived to one year old.

Age (years)	All birds	Released	Wild	Males	Females	PW	BF	BO	IAA
0	67.5	74.9	63.1	[87.8]	[90.5]	76.3	67.9	78.5	50.4
1	80.1	72.8	86.5	83.5	77.6	90.7	78.2	78.8	74.1
2	85.2	83.3	86.9	85.1	86.4	92.5	80.1	88.6	84.8
3	81.4	81.3	81.5	83.5	78.8	89.3	76.3	79.2	85.0
4	79.9	75.4	83.3	84.6	74.6	84.6	77.8	100	62.9
5	77.2	86.2	72.0	80.5	73.7	68.4	88.6	-	-
6	88.9	86.7	90.5	90.0	87.5	89.5	88.2	-	-
7	90.0	-	-	-	-	-	-	-	-
Mean adult (1-7)	83.2	80.9	83.4	84.5	79.8	85.8	81.5	86.6	76.7
SD (%)	4.9	5.7	6.4	3.1	5.9	0.089	0.054	0.100	0.105

Juvenile survival

Overall, survival of juveniles was not significantly different between mainland sites (P > 0.05, n = 671). However, survival of juveniles was significantly poorer at Ile aux Aigrettes than at mainland sites (P < 0.0001) (Table 3.2). The main reason for poor juvenile survival at Ile aux Aigrettes was the poor survival of wild juveniles, which was significantly poorer than released juveniles at Ile aux Aigrettes (P < 0.0001) and significantly poorer than survival of wild juveniles at mainland sites (P < 0.0001). Survival of released juveniles was significantly better at Ile aux Aigrettes than at Brise Fer (P < 0.05) but post-release survival of juveniles was, overall, not significantly different between release sites (P > 0.05).

Effect of inbreeding on juvenile survival

Inbreeding significantly affected overall juvenile survival (Figure 3.7). Most of this effect was due to the poor survival of highly inbred juveniles which was significantly poorer than non-inbred juveniles (P < 0.05). The survival of inbred juveniles (> 0 and < 0.25) was not significantly different to non-inbred juveniles, despite the observed differences. When data were pooled for inbred and highly inbred juveniles, survival was significantly poorer than for non-inbred juveniles (P < 0.05).

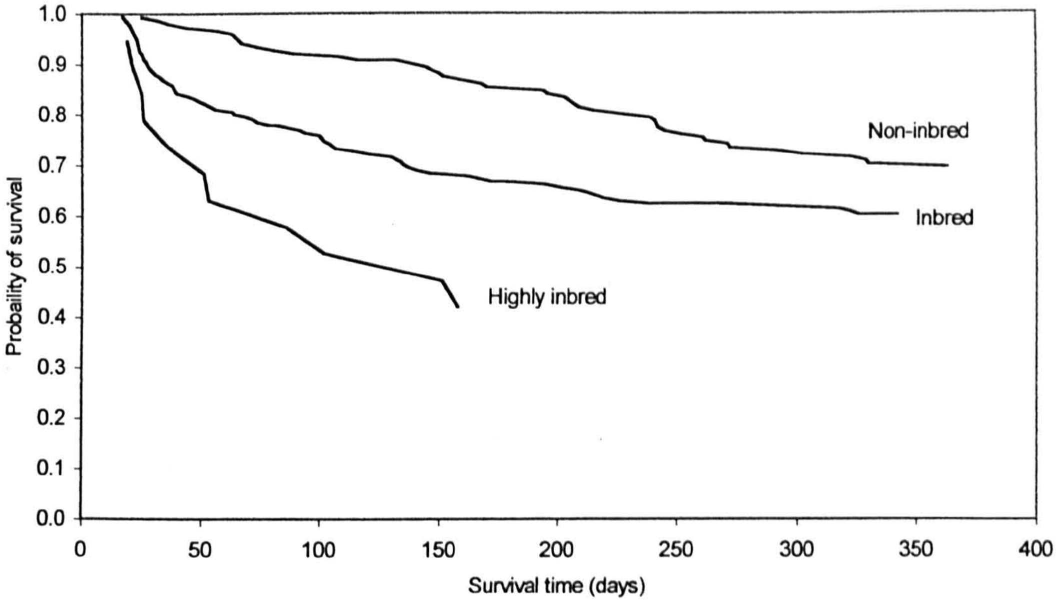

Figure 3.7 Effect of inbreeding on juvenile survival (less than one year old). Inbreeding coefficients: non-inbred = 0, inbred > 0 and < 0.25, highly inbred ≥ 0.25. Kaplan-Meier estimates of survivor function are plotted. Sample size: non-inbred 153, inbred 191, highly inbred 19 (64% censored). Overall differences were significant ($P < 0.05$).

Adult survival

Survival of adults was significantly different between sites ($P < 0.05$) (Table 3.2). This was mostly due to poorer adult survival at Brise Fer ($P < 0.01$) and Ile aux Aigrettes ($P \cong 0.01$). When data for released and wild adults were analysed independently, adult survival and post-release survival of released birds was not significantly different between release sites (survival $P > 0.05$; post-release survival $P > 0.05$, $n = 178$). However, post-release survival of adults at Ile aux Aigrettes was significantly poorer than Bel Ombre ($P < 0.05$) (Table 3.5). Adult survival of wild birds was not significantly different between sites ($P > 0.05$, $n = 232$) but adult survival at Brise Fer was significantly poorer than wild adults at Pigeon Wood ($P < 0.05$). Although survival of wild adults seemed higher than released adults at Bel Ombre and Ile aux Aigrettes (Table 3.4) the sample sizes were too small to analyse independently.

Longevity

The oldest known bird was a male caught in the wild in Pigeon Wood in 1976. He was released on Ile aux Aigrettes at about 20 years old but disappeared seven months after release. The oldest wild-fledged bird was caught as a breeding female at Pigeon Wood in 1989 and was at least 11.5 years old in 1998 when she was still alive. The oldest wild-fledged male was also caught at Pigeon Wood in 1990 as a breeding adult, and who was at least 11.1 years old when he died. The oldest captive-bred bird released as a juvenile was a male released at Brise Fer in 1987 who died at 8.4 years old. The oldest surviving captive-bred female released as a juvenile was released at Brise Fer in 1991, who was 7.2 years old in 1998.

Table 3.4 Life History Tables for released and wild birds: percent survival per age group. Survival estimates only where minimum sample size is 10 birds per age group, sample sizes in Appendix 1.

Age	Brise Fer		Bel Ombre		Ile aux Aigrettes	
(years)	Released	Wild	Released	Wild	Released	Wild
0	66.7	68.9	77.5	80.7	84.0	36.4
1	70.1	85.4	78.3	80.5	66.7	84.1
2	84.9	75.5	86.4	100.0	75.5	100.0
3	83.6	68.4	76.7	-	86.2	-
4	76.5	79.3	100.0	-	60.0	-
5	84.0	-	-	-	-	-
6	86.7	-	-	-	-	-
Mean adult (1-6)	81.0	77.2	85.3	90.2	72.1	92.1
SD (%)	6.3	7.1	10.6	13.8	11.3	11.2

Table 3.5 Life History Tables showing post-release survival: percent survival per age group.

Years post-release	Brise Fer		Bel Ombre		Ile aux Aigrettes	
	No. birds	% survival	No. birds	% survival	No. birds	% survival
0	103	55.9	89	73.0	50	72.0
1	56	76.8	65	79.7	36	63.9
2	43	82.0	50	82.3	23	89.7
3	28	87.0	22	85.2	14	61.5
4	15	80.0	-	-	-	-
5	12	91.3	-	-	-	-
6	10	85.7	-	-	-	-
Mean adult (1-6)	-	83.8	-	82.4	-	71.7
SD (%)	-	5.2	-	2.7	-	15.6

Annual survival

Kaplan-Meier estimates of annual survival varied from 61.2% to 82.2% per year between 1992 and 1998 (Table 3.6). The differences in annual survival were significant (Wald = 14.62, df = 6, $P < 0.01$). Mean annual survival was highest at Pigeon Wood and poorest at Ile aux Aigrettes (Table 3.7). Mean annual survival at mainland sites was 75.6% ± 9.6% per year. At mainland sites, years of unusually poor survival occurred in 1992 at Pigeon Wood, in 1995 at Bel Ombre and in 1996 at Brise Fer.

Table 3.6 Kaplan-Meier estimates of annual survival. Number of birds at the start of the year included dispersers and old birds at release. The mean hazard function indicated the risk of death each year.

Year	No. birds at start of year	No. released	No. fledged	No. died	Percentage surviving	Mean hazard function
1992	28	16	17	17	61.2	0.0501
1993	44	3	35	10	82.2	0.0513
1994	72	42	40	30	72.4	0.1154
1995	124	85	57	59	67.6	0.1970
1996	207	68	110	112	63.5	0.2739
1997	273	5	85	81	75.3	0.1725
1998	282	0	78	63	80.0	0.1399

Table 3.7 Kaplan-Meier estimates of annual survival in different sub-populations. Number of birds at the start of the year excluded dispersers but included old birds at release. Data for Bel Ombre in 1994 excluded the seven birds released in November and December.

	Pigeon Wood		Brise Fer		Bel Ombre		Ile aux Aigrettes	
Year	No. birds at start	% survival	No. birds at start	% survival	No. birds at start	% survival	No. birds at start	% survival
1992	12	49.8	16	70.8	-	-	-	-
1993	17	91.3	26	75.8	-	-	-	-
1994	25	78.0	46	84.2	-	-	0	45.3
1995	27	82.9	56	72.8	7	41.8	33	43.1
1996	34	88.8	84	54.8	44	77.6	36	42.3
1997	51	77.8	84	79.0	76	76.7	51	66.1
1998	62	87.0	89	84.5	72	88.1	52	59.4
Mean	-	79.4	-	74.6	-	71.1	-	51.2
SD (%)	-	14.0	-	10.2	-	20.2	-	10.8

Seasonal survival

Survival was significantly poorer from July to December (high breeding activity) than from January to June (low breeding activity) ($F_{1,6} = 25.2$, $P < 0.01$) (Table 3.8). Most of this variation was accounted for by adult survival, which was significantly poorer during July to December ($F_{1,6} = 7.2$, $P < 0.05$). The number of juvenile deaths was higher from June to September (46%) than at other times of the year whereas adult deaths were highest in the dry season, September to December (42%).

Table 3.8 Kaplan-Meier estimates of survival from January to June (low breeding activity) and from July to December (high breeding activity) (shown as a percentage).

Year	Juveniles		Adults		All birds	
	Jan-June	July-Dec	Jan-June	July-Dec	Jan-June	July-Dec
1992	70.9	80.7	83.7	83.3	87.9	79.6
1993	85.3	92.5	100.0	94.3	94.0	91.5
1994	75.1	82.7	100.0	87.6	98.9	85.0
1995	67.1	77.1	91.9	89.0	93.6	83.9
1996	97.8	72.3	86.5	82.6	88.9	77.4
1997	88.0	72.3	95.8	84.9	98.3	81.6
1998	79.4	74.7	93.5	91.3	97.5	88.7
Mean	80.5	78.9	93.1	87.6	94.2	84.0
SD (%)	10.7	7.2	6.3	4.3	4.4	5.0

Population trends

Overall population trends

During the first four years of the programme (from 1987 to 1990), the population declined from 20 to 16 birds, despite 21 birds released and four fledged in the wild (Fig. 3.8a). The population started to grow in 1991 as an increasing number of birds were released (see Appendix 2 for details of population trends). Between 1994 and 1996, 195 birds were released which was 76% of all birds released over the 12 years since 1987. Releases were stopped in January 1997 owing to a greater number of birds fledging in the wild. Between 1995 and 1998, 329 birds fledged which was 77% of all birds fledged in the wild since the start of the programme. The total number of birds fledged excludes the remnant adult population at Pigeon Wood (12 birds) but includes one wild bird that fledged in 1988. End of year recruitment (the number of birds entering the population, including released birds, after accounting for deaths) was highest between 1994 and 1996 averaging 67 ± 15 birds per year. Between 1996 and 1998, population growth slowed and increased by only 24 birds to achieve a peak population of 297 birds at end 1998.

Population trends at Brise Fer

Between 1987 and 1990, the population declined from eight to six birds, despite 21 birds released. The population grew rapidly between 1991 and 1995 but subsequent growth was poor (Fig. 3.8b). There were two periods of intensive releases between 1991and 1992 and between 1995 and 1996 when 83 birds (77% of all birds) were released. Two periods when peak numbers of birds fledged in the wild occurred between 1993 and 1994 and between 1996 and 1997 when 114 birds (90% of all birds) fledged. Recruitment was highest between 1991 and 1995 averaging 16 ± 8.7 birds per year. This corresponded to peak numbers of birds released in 1991, 1992 and 1995 and peak numbers of birds fledged in 1993 and 1994. In 1997 the population reached a maximum size of 91 birds, but had declined to 79 birds at the end of 1998.

Population trends at Pigeon Wood

The remnant wild population at Pigeon Wood in 1989 consisted of 13 birds, seven females and six males and declined further to its lowest number of 10 birds in 1990 (but see discussion). Since 1988, 122 birds were known to have fledged in the wild, 56% of which fledged between 1996 and 1998. Recruitment was highest between 1995 and 1998 averaging 12.5 ± 3.1 birds per year. The population achieved its maximum size of 77 birds at the end of 1998 (Figure 3.8c).

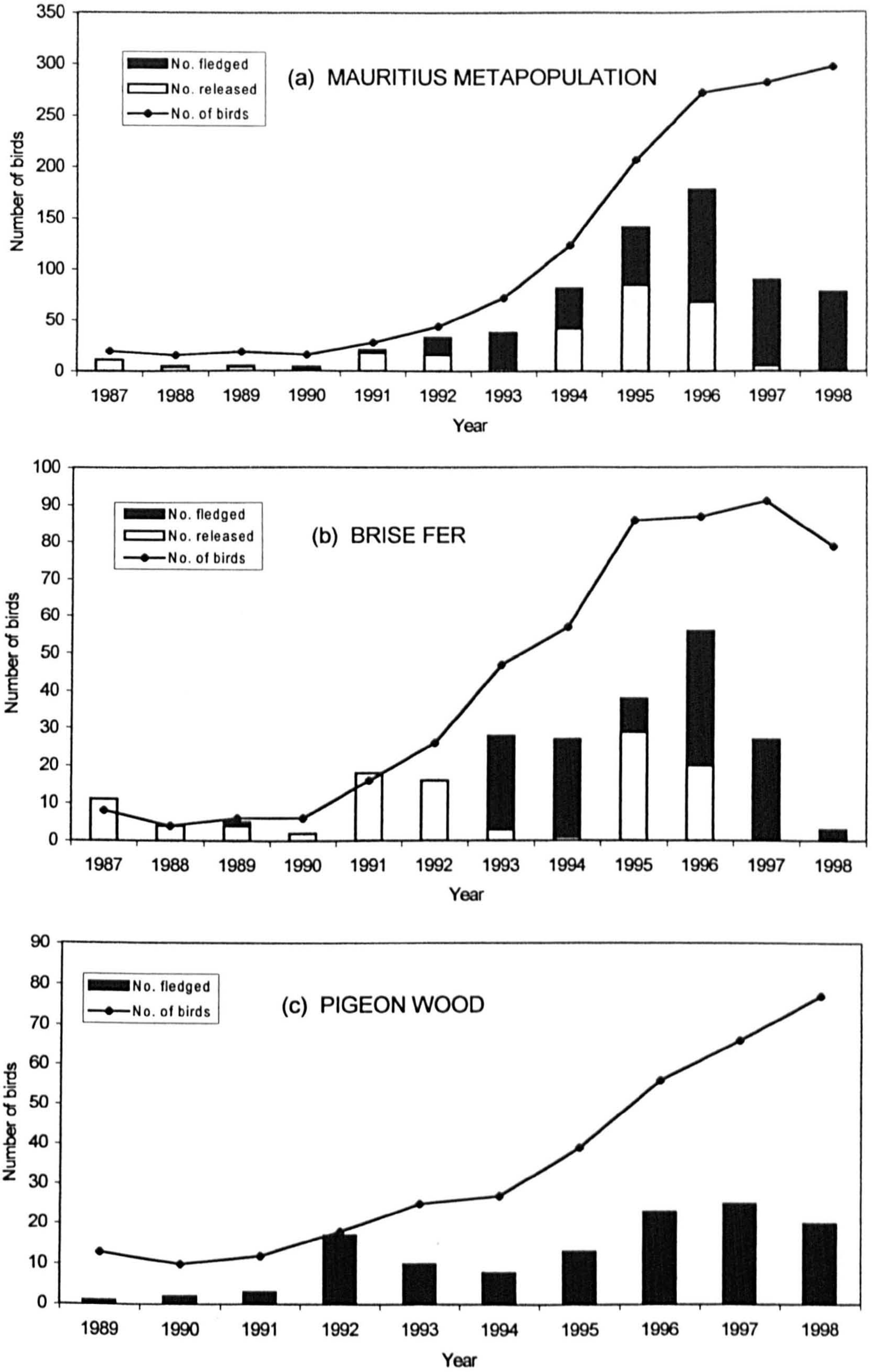

Figure 3.8 Population trends for the pink pigeon on Mauritius, 1987-98: (a) for the pink pigeon metapopulation (all sites) 1987-98, (b) at Brise Fer 1987-98, (c) at Pigeon Wood 1989-98.

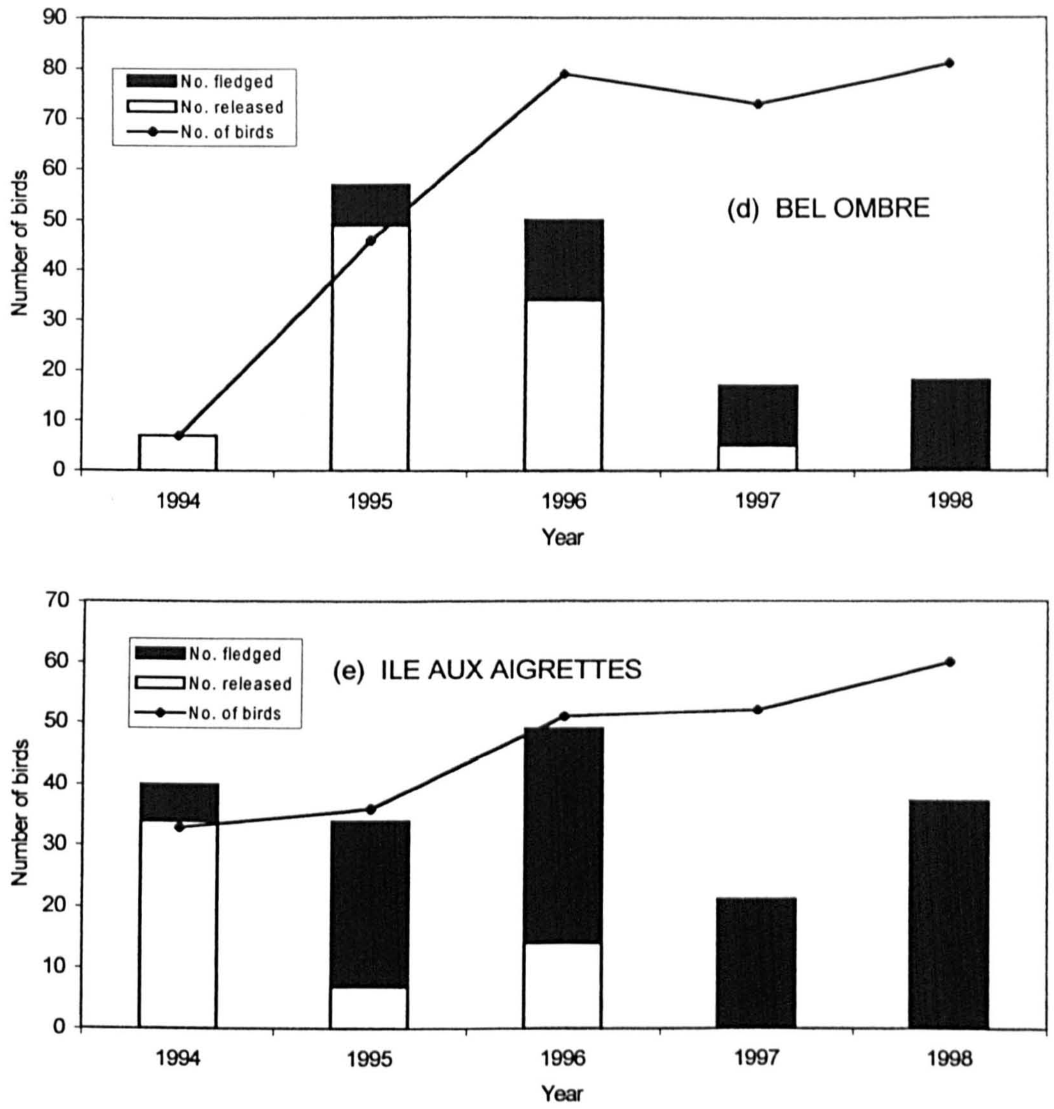

Figure 3.8 Population trends for the pink pigeon on Mauritius, 1987-98: (d) at Bel Ombre 1994-98, (e) at Ile aux Aigrettes 1994-98.

Population trends at Bel Ombre

Releases were carried out at Bel Ombre between November 1994 and January 1997 when 95 birds were released. Initial population growth was rapid and 79 birds were established by the end of 1996 (Figure 3.8d). From 1996 to 1998 population growth slowed and the population reached 81 birds at the end of 1998. The number of wild birds fledged was relatively constant between 1995 and 1998 averaging 13.5 ± 4.4 young per year. Recruitment was highest during 1995 and 1996 when 72 birds entered the population (mean 36 ± 4.2 per year).

Population trends at Ile aux Aigrettes

Releases were carried out between 1994 and 1997 when 55 birds were released, 34 (62%) of which were released in 1994. Two periods of rapid growth occurred in 1996 and in 1998 when the population reached a maximum size of 60 birds (Figure 3.8e). The number of birds fledged in the wild was relatively constant averaging 30 ± 7.4 birds per year from 1995. Between 1995 and 1998, recruitment was generally poor averaging 6.7 ± 6.2 birds per year owing to high mortality of squabs and fledglings.

DISCUSSION

Kaplan-Meier survival analysis

Estimates of survival in birds are usually based on information gained from ring recoveries and live recaptures. These methods may introduce biases including underestimation of survival rates owing to emigration, poor determination of individual ages, variation in reporting rates, compensatory mortality when dealing with individuals reported dead from shooting and survival rates may not be representative of the whole population (review in Clobert & Lebreton 1991). In this study the ability to monitor the whole population closely provided individual survival times, many of which were accurate to a day.

There are various ways to calculate survival rates including finite or instantaneous rates, from age composition data, radio-tagging data and life tables (Krebs 1989). Present methods for analysing data assume that each survival event is independent and has a constant probability over all individuals and all time periods. In natural populations, survival rates are rarely constant, for example between years or between sexes. A range of analysis software is available, some of which may partly deal with these problems (e.g. SURVIV: White 1983, JOLLY: Brownie *et al.* 1986).

The Kaplan-Meier procedure, widely used in medicine and engineering, has been developed for the survival analysis of radio-tagged animals (Pollock *et al.* 1989*a*, 1989*b*) and many examples of its use are found (e.g. Clout *et al.* 1995, Schulz *et al.* 1996, Burger *et al.* 1996). The Kaplan-Meier method does not assume a constant survival time, allows the addition of new individuals during the study period and accounts for individuals that are removed from the study or are still alive at the end. The Kaplan-Meier method does not seem to have been applied to survival data of birds other than for radio-tagged individuals. In this study, the flexibility of the Kaplan-Meier method allowed analysis of individual survival times of only a few days between birds. In addition, censored individuals provided a larger sample size. Many endangered species exist in small isolated populations and any research programme often involves the intensive study of marked individuals. It is suggested that the Kaplan-Meier method could be particularly useful for these situations, for example for the Seychelles magpie robin *Copsychus sechellarum*.

Cox's proportional hazards model provides a powerful test for ecological hypotheses regarding the influence of covariates on survival when standard methods (e.g. log rank test) are not applicable (Pollock *et al.* 1989*a*, 1989*b*). Modelling the hazard function obtains an estimate of the hazard function itself for an individual, from which an estimate of the survivor function can be found. This will in turn lead to an estimate of quantities such as the median survival time which will be a function of the variables in the model (Collet 1994). The median survival time could then be estimated for current or future birds with particular values of these variables. The resulting estimate could be particularly useful in anticipating the survival of future individuals under a set of variables (for example a foster-reared bird released at less than 150 days old at Brise Fer) and devising management strategies to improve survival.

Summary of survival at different sites

Birds at Pigeon Wood and Bel Ombre showed similar survival probabilities, which were highest of the four sites. The two sub-populations are both on the southern scarp of Mauritius where the last population was found in the 1970s. The sites share a similar climate and vegetation type, although Bel Ombre is a released population (at end 1998 64% released birds) and Pigeon Wood is a wild population. Of the mainland sites, survival of birds at Brise Fer was poorest, both for released and wild birds. However, for released birds, survival was poorest mainly during the first year post-release. Poorer survival at Brise Fer was surprising considering that this population occupies some of the best remaining native forest on Mauritius. Poor survival of released birds early on in the programme was due to the development of release techniques.

The population at Ile aux Aigrettes was characterised by high mortality of wild-fledged juveniles, which was the main reason for poor survival at this site. However, survival of adults was also poorer than mainland sites, despite the absence of predators, which was partly due to poorer survival of released adults. There was some suggestion that survival of wild adults was higher than all other sites but a longer period and bigger sample size are needed to confirm this. Disease is probably the main factor influencing survival at this site (see Chapter 7).

Survival estimates of wild-fledged juvenile birds may be slightly overestimated, particularly at mainland sites, owing to undetected post-fledging mortality before birds were ringed. Survival estimates of captive-reared birds prior to release included only those birds released. There will be some mortality of captive-bred birds before selection for release and there was also some mortality while in the release aviary. Both these errors were considered minimal and are unlikely to have affected the overall trends.

Causes of mortality

Several causes of mortality in wild juvenile and adult pink pigeons have been suggested including predation by feral cats *Felis catus* and mongooses *Herpestes auropunctatus*, seasonal food shortages and cyclones (Jones 1987, Jones & Owadally 1988, Jones *et al.* 1989). Competition from exotic doves was also suggested as a factor, which may limit the population (Jones 1987). McKelvey (1976) suggested the mongoose and feral cat as only incidental predators, but Temple (1978) regarded the mongoose as a serious threat. Subsequent work in Mauritius identified the mongoose and feral cat as the main predators of fledgling kestrels (Jones 1987, Jones & Owadally 1988, Jones *et al.* 1991, 1994) and responsible for the deaths of released and wild pink pigeons (Jones *et al.* 1992). Human persecution has never been regarded as a serious threat due to the assumed inedibility of pink pigeon flesh. However during trial releases at Pamplemousses Botanical Gardens, at least 15 out of 22 birds may have been killed or injured by poachers (Todd 1984, Jones *et al.* 1988, 1989). Cyclones have been reported as causing direct mortality of pink pigeons and have been linked to severe population declines (McKelvey 1977, Jones 1987). During cyclone Hollanda in February 1994, wind speeds of up to 216 km/h were recorded, but no mortality of pink pigeons was known which was a direct cause of the cyclone. One bird was seen shortly after the cyclone, which was not seen again and three birds were last seen up to five days before the cyclone. However even if the death of these four birds were due to the cyclone, mortality from this cause was extremely low. Similarly there was no known mortality of echo parakeets *Psittacula eques* or Mauritius kestrels *Falco punctatus* that were being monitored at the time. During this study, known causes of adult and juvenile mortality included predation by mongooses, feral cats and crab-eating macaques *Macaca fascicularis*, disease, injury and accidental death.

Predation

Predation by macaques has not before been identified as a major cause of adult and juvenile mortality, although McKelvey (1976) noted macaques removing most of a pigeon's tail feathers during nest predation. During this study, many pigeons were observed without tail feathers which was regarded as a sure sign of nest predation by macaques or attempted predation on adult and juvenile birds. A number of birds were killed by macaques while sitting on the nest, particularly at Bel Ombre. Macaques also preyed upon birds while they were on the ground. The high mortality at Brise Fer in 1996 was partly due to macaque predation while birds fed on the ground below feeding stations.

At the same time, macaques killed many Madagascar turtle doves *Streptopelia picturata* and barred ground doves *Geopelia striata*. Signs of macaque predation were highly visible as feathers and often pieces of a carcass were strewn around the site.

Remains of pigeons killed by cats included chewed feathers and characteristically eaten carcasses stashed under bushes or logs (Veitch 1985). The remains of seven pink pigeons have been found in cat stomachs and two pink pigeons in mongoose stomachs. Pink pigeon feathers were also found in a mongoose scat (Roy 2001).

It was thought that variation in survival could be partly explained by different predator densities at each site. However, the relationship between pink pigeon mortality and predator densities is highly complex (Roy 2001). Mongooses are opportunistic predators and densities within and between sites are highly variable. Cats however are very territorial, and annual, seasonal and site densities remain relatively constant. Both cat and mongoose densities were probably influenced by densities of prey, which included rats *Rattus rattus* and tenrecs *Tenrec ecaudatus* (Roy 2001). From this study and Roy (2001), cats were considered the main threat to pink pigeon survival. Cats learned to prey upon pink pigeons and exotic doves at sites where high densities were found. In 1992 11 pink pigeons were killed at Pigeon Wood when the maximum population size for that year only reached 19 birds. This included seven juveniles and four adult breeding birds, of which three were females. At Brise Fer, 53 pink pigeons were killed or disappeared between May and December 1996. Other episodes of mortality included eight pigeons that disappeared at Bel Ombre in July 1997 and five birds in November 1997. Episodic mortality is likely a major threat to the population's recovery. Clout *et al.* (1995) identified a similar feature in New Zealand pigeons *Hemiphaga novaeseelandiae* and attributed stoat *Mustela erminia* predation as the cause.

Disease, injury and accidental death

Three main diseases were identified in fledged birds: trichomoniasis, avian pox and leucocytozoonosis, and birds died from one or a combination of these diseases, often associated with inanition (details are provided in Chapter 7). Disease was the main cause of mortality on Ile aux Aigrettes but was not obvious at mainland sites. Birds found with life-threatening injuries were removed to captivity and were re-released if they recovered. Injuries included several birds with a broken tarsus, broken wings and soft-tissue injuries. On the mainland, most injuries were probably caused by macaques. Accidental mortality included several birds flying into field station windows or walls and one bird that got stuck down a coral hole on Ile aux Aigrettes (probably looking for water). One bird probably died as a result of its radio-tag being caught on a branch. Accidents may account for more deaths than known, birds were observed temporarily disorientated after flying into the side of a supplemental feed station or falling off branches.

Other factors affecting survival

Inbreeding

Inbreeding depression is the reduction of viability and fecundity in progeny of matings between close genetic relatives (Lande & Barrowclough 1987). Inbreeding depression results from two effects: the expression of deleterious recessive alleles due to increased homozygosity and the reduction in the frequency of heterozygous loci which results in reduced fitness. In both cases the loss of genetic variation due to inbreeding has detrimental effects on population survival. There is evidence for inbreeding depression in many captive, domestic and wild animals (Soulé 1980, Ballou & Ralls 1982, Ralls & Ballou 1983, Ralls *et al.* 1986, Wildt *et al.* 1987, Thornhill *et al.* 1993) but responses to inbreeding varies with species and in different populations.

Jones (1995) found that high levels of inbreeding affected the survival of captive pink pigeons more than 30 days old. In this study, the similar survival rates in non-inbred and inbred pink pigeons suggest that either a nominal amount of inbreeding is not detrimental or that non-inbred birds have undetected inbreeding in their genealogies, the latter being also suggested by Jones (1995). Inbreeding was determined by pedigree analysis but the relationship of the original captive founder population is unknown. The calculation of inbreeding coefficients assumed that the founders were unrelated but in DNA studies of four founders, two birds were classed as second-degree relatives (Bruford *et al.* 1991, Wayne *et al.* 1994). This finding was supported by Groombridge (2000) and the two unrelated founders shared a haplotype with six other founders. In addition, inbreeding coefficients were analysed in this study in cohorts but are calculated on a continuous scale, for example inbred birds included all those with inbreeding coefficients between 0.0087 and 0.195.

Jones (1995) suggested that the higher mortality of captive females and especially inbred females was due to sex-linked lethal genes as females are the heterogametic sex. This study supported his evidence that inbreeding selectively affected females and further research on survival of juvenile females may provide more evidence. The effect of inbreeding on survival of captive birds may be tempered by management, which improves overall survival. In the wild environmental pressures are likely to increase the effects of inbreeding. The sample size of wild birds with known inbreeding coefficients was too small to analyse independently and this requires further study.

Seasonal mortality and food shortages

The role of food-supply in limiting individuals and populations is unquestionable (Newton 1998). However, exposure of individuals to food shortages may be masked by other causes of mortality such as predation and disease. Food shortages have been suggested as a major cause of population limitation in Mauritian birds (Jones 1987, Jones & Owadally 1988, Jones *et al.* 1992) but there has been little direct evidence to support this. In Mauritius, food shortages are caused by habitat degradation and competition from exotic species, and periodic shortages are caused by cyclones. Food shortage is probably more acute during the dry season (September to December) than at other times of the year. The higher mortality of adults during the breeding season may be partly explained by increased predation rates as birds forage and collect nest material from the ground, when they may be less vigilant and more easily surprised by predators. This effect is exacerbated during the dry season when food supplies become restricted and food-stressed predators may turn to alternative prey. For example at Brise Fer between May and December 1996, macaques heavily preyed upon doves and pigeons and raided supplemental feeding stations and the campsite for food.

The effect of supplemental feeding and predator control on survival

Food supplementation experiments in birds have resulted in improved survival rates, increased density and increased rate of population growth (review in Boutin 1989 and Newton 1998). Survival rates of pink pigeons were not measured prior to supplemental feeding but a comparison of survival rates with a range of other pigeon species indicated much higher survival in juvenile and adult pink pigeons. The mean annual survival rate of pink pigeons was 72% between 1992 and 1998. Depending on the site, mean adult survival ranged from 76.7% to 86.6% and for juveniles from 50.4% to 78.5%. Mean juvenile survival for other pigeon species varied between 31% and 60% and could be as low as 18%. Mean annual adult survival varied between 42% and 66% and could be as low as 32% (Murton 1965, 1966, Rowan 1983, Tomlinson & Dunks 1993, Reeves *et al.* 1993, Martin & Sauer 1993, Johnston & Janiga 1995). However many of these species were shot or harvested as agricultural pests or for food. A comparable survival rate of 81% per year was seen in the New Zealand pigeon where harvesting was banned (Clout *et al.* 1995) but this is also a long-lived species with a low reproductive rate. Pink pigeon survival was comparable to longer-lived species, for example Bewick's swan *Cygnus columbianus bewickii* (60% first-year, 80% as adult), kittiwake gulls *Rissa tridactyla* (79% first-year, 81-86% as adult), snow geese *Anser caerulescens caerulescens* (15-63% first-year, 72-100% as adult) (Scott 1988, Thomas & Coulson 1988, Cooch & Cooke 1991). Pink pigeons can be long-lived and in pristine Mauritius probably had better survival rates than observed in this study. In 1992, prior to predator control, annual survival at Pigeon Wood was only 49.8%. An intensive trapping and poisoning regime resulted in only two birds that were killed the following year, and mean annual survival with predator control was 84.3%. It is likely that the supplemental feeding and predator control regime has contributed to the generally high survival rates observed in released and wild pink pigeons.

Survival of captive-reared and wild-fledged birds

Re-introduced captive-reared animals have poorer survival skills than their wild-bred counterparts and offspring. This has been shown in a number of re-introduction projects including the golden lion tamarin *Leontopithecus rosalia*, Siberian polecat *Mustela eversmanni*, mallard *Anas platyrynchos*, and in raptor and ungulate translocations (Sheperdson 1994, Cade 2000). However, in some cases captive-rearing can be beneficial to survival. Survival of re-introduced captive-reared takahe *Porphyrio hochstetteri* (formerly *mantelli*) was as good as wild-reared birds (Maxwell & Jamieson 1997).

One of the main problems when comparing the survival of released and wild birds was the pre-release period when captive-reared birds were in captivity, but for most birds this was less than three months. For example, survival of released juveniles (from 30 days) was better at Ile aux Aigrettes than at Brise Fer, but post-release survival appeared to be the same at both sites. Some of this might be explained by the older ages of birds released at Ile aux Aigrettes (median age at Brise Fer 85 days, at Ile aux Aigrettes 154 days) so that more birds at Ile aux Aigrettes were still in captivity when birds were already released at Brise Fer. The survival of released and wild birds from the median age at release indicated that survival of released birds was poorer than wild birds, which was most marked at Brise Fer.

Wild-fledged birds may be at high-risk during the first few months post-fledging. The pre-release period in captivity may confer an advantage to released birds, particularly juveniles, by increasing body-weight and reducing the risk of post-fledging mortality. Prior to release, captive juveniles were socialised in groups and kept in planted aviaries which encouraged some development of natural foraging behaviours. Although efforts were made to release captive-reared birds as young as possible, a trade-off exists between the advantages of captivity providing stronger birds for release and the disadvantages of decreasing survival skills the longer they remain in captivity.

In a release programme some deficiencies associated with releasing captive animals must be accepted. In this study, survival of captive-reared birds was good enough to re-establish the population in the wild. In 1999, 14 surplus wild-fledged juveniles were translocated from existing sub-populations to establish a new sub-population within the National Park. Survival of translocated individuals seemed better than the release of captive-bred birds and this may be the method used for future population management.

Release procedures and management techniques

The slow population growth during the first few years of the programme was due in part to experimental release and management techniques being developed. Subsequent population growth occurred when these techniques were refined and improved. In the early years release candidates included birds which had been in captivity for many years and were unsuitable for re-introduction. Mature birds were problematic to release as they were chased out of the area by aggressive and territorial free-living birds. The initial establishment of a released population was the most difficult, but further releases into that population were easier. Poor survival in 1995 at Bel Ombre was because this was the first year when the population was being established and management techniques were being developed for this site.

Other factors of the release programme which may have affected post-release survival included the size of the release group, the effect of bad weather during the release process, the physical environment of the site, the release aviary design and the continuity and skills of the people carrying out releases. There was an optimal size of release group of about four to six birds. Smaller than this and the group did not stay together and when larger it was difficult to keep track of all the birds. Bad weather prolonged releases and early releases at Brise Fer were more difficult owing to its proximity to a steep gorge, in which many birds got lost. Releases were more successful as the releaser gained experience and continuity between releases was considered important.

Population growth

In 1990, the wild population at Pigeon Wood reached its lowest point of 10 birds. This included a male of unknown origin which first appeared in 1989 as a sub-adult at Brise Fer with a released female. The male was subsequently seen briefly in Pigeon Wood in June 1989 but reappeared in November 1990 and became a breeding resident. As there was no known successful breeding at Brise Fer when this bird first appeared, it was assumed that he was the progeny of remnant wild birds and had fledged in 1988. However, as he had appeared at Brise Fer together with a mature released female, it is possible that he was the progeny of released birds, or at least of the released female. Thus the remaining truly wild population may have been only nine birds in 1990.

Without management, the remaining wild population at Pigeon Wood would have undoubtedly become extinct probably within only a few years. It was in fact surprising that the species managed to hold on in the wild for as long as it did. The re-introduction programme enabled the population to increase at a rate that would not have been possible by the wild population alone. This reduced the likelihood of extinction due to demographic variation and stochastic events and reduced the potential risks created by a small gene pool. Once the crisis was over, it was intended that management practices would be developed to ensure the long-term sustainability of the species. This is now the next goal.

Conclusions

Three sub-populations of pink pigeons were established using captive-bred and released birds, and a fourth sub-population comprising the remaining wild population was also monitored. Survival of birds was significantly different between sub-populations, being highest in the truly wild population at Pigeon Wood and poorest on the coralline islet of Ile aux Aigrettes, where disease was the main cause of mortality. Survival of released birds was poorer than wild birds and survival was affected by inbreeding, which mostly affected juveniles and females. Survival averaged 67% for juveniles and 83% per year for adults. The relatively high survival rates were maintained due to management, and contributed to the successful re-establishment of the population, which increased from 20 birds in 1987 to 297 birds at the end of 1998. Successful breeding first occurred in 1989 when the first wild fledgling was produced from a pair of captive-bred released birds, and which is investigated in the next three chapters.

Chapter 4

Reproductive ecology and nest site selection

INTRODUCTION

At the start of this study, little was known about the reproductive biology of the pink pigeon in the wild. Early studies by McKelvey (1976, 1977) and others (Durrell 1977, Hartley 1977, Jones 1987) were limited to a small population that bred in an exotic cedar *Cryptomeria japonica* plantation. Studies of captive birds have provided details of courtship, incubation and brooding behaviour which helped interpret the behaviour of wild birds (Jones & Hartley 1983, Bell & Hartley 1987, Jones 1995). This study had two main aims. The first was to investigate the reproductive biology of the wild pink pigeon with a view to determining reproductive success. The species' ecology today may not wholly reflect that found on pristine Mauritius because habitats are now modified but I hoped these studies would provide data on the basic features, including nest site selection, pair bonds, egg laying, breeding seasonality and annual variation in breeding. The second aim was to investigate the reproductive ecology of captive-bred released birds to see how successfully they re-adapted to life in the wild.

METHODS

Studies on the reproductive biology of pink pigeons were carried out at the four sub-populations up to 1998, starting at Brise Fer in 1988, Pigeon Wood in 1989, Ile aux Aigrettes in 1994 and Bel Ombre in 1995. For some variables (e.g. fertility and clutch size) data from Ile aux Aigrettes were more complete because most nests were accessible. Rainfall data were obtained from 1987 to 1998 from the Meteorological Services of Mauritius.

Nest Site Studies

Locating territories and nests

Territories were located by observing male territorial behaviour such as prominent perching and males performing wing-clapping display flights. Territorial males were also located during aggressive encounters with birds in adjacent territories when they were easily heard. Observations were made in known territories for nest sites, and new nests of a pair were often found by surveys close to previous nests. Typically, nests were located by observing the male collecting twigs and returning to the nest or when the pair changed over on the nest during incubation or brooding. The nest was located by listening for a bird's vocalisations and wing-flaps as it left and returned to the nest. During brooding nests were also located by the squabs 'whistling' vocalisations, which were loudest during feeding. During nest building, birds were most active from dawn to about 11:00 hrs and from 15:00 hrs to dusk, so nest searches were concentrated during these periods.

Nest site studies

Once a nest tree was located, the following details were recorded: tree species, tree height and diameter at breast height of the trunk, nest height within the tree and aspect of the nest. A description of the nest site was made which included nest location within the tree (next to the trunk or on an outer limb), nest location within the canopy (lower, middle or upper), nest cover (exposed or sheltered) and a brief description of the main supports of the nest. It was also noted if the nest was visible from the ground. Nest measurements were obtained after the attempt had finished. A shape index for the nest was calculated as nest length/nest width. Nest site criteria were obtained for nests with and without eggs.

At Brise Fer data for the abundance of different tree species were obtained from Strahm (1993) and used to investigate the relationship between tree abundance and choice of nest tree. An importance value was used for each tree species, which was the sum of the relative density, frequency and cover based on stem area (Barbour *et al.* 1987 *in* Strahm 1993). On Ile aux Aigrettes nest trees were plotted on a map. Each nest tree location was later assigned a vegetation type which was obtained from Seymore (2000) (see Chapter 2 for description of vegetation types). Data from Hosany (1998) was used to investigate the relationship between choice of nest tree and its relative abundance as a canopy species. The relative abundance was calculated as the total number of each species within a vegetation community averaged over all sites with the same vegetation community. The two sources of data were qualitatively similar (Seymore 2000) and the vegetation types of Hosany (1998) were grouped into the comparable vegetation types of Seymore (2000) so that the relative abundance of tree species within the different vegetation types of Seymore (2000) was obtained.

Monitoring nests

Attempts were made to locate every nest and, when found, were usually monitored daily. Weather conditions, the availability of staff and the number of active nests being monitored affected the number of times a nest was checked.

Once incubation had started, most observations were made during the changeover of birds on the nest to ensure that the nest was still active. During brooding, and in particular when the squab was not brooded during the day, the nest was also checked at dusk since the female brooded the squab for the night. Some nests were very concealed and their status could only be determined by the behaviour of the adult birds. These behavioural signs included a bird seen leaving and arriving at the nest site, the appearance of males at feeding stations early morning and late evening before and after changeover, adults with brown stains on their breast feathers from the nest and around their gape which was a result of feeding squabs, vocalisations of adults and squabs from the nest and the pair never being seen together during incubation and the early stages of brooding.

If a nest was suspected to have failed, field signs were searched for in the nest tree and on the ground close to the nest tree. These included egg remains and remains of squabs and/or parents, an abnormal amount of feathers (indicating predation), monkey and/or rat droppings in the nest or nest tree and whether the nest was pulled apart or intact. The pair were searched for to detect if either bird had been attacked (missing feathers) or had disappeared, or if there was possible disruption of the nest by other pink pigeons.

Accessing nests

Most nests in mainland populations were not accessed due to the risk of damaging the nest or eggs while climbing the tree. On Ile aux Aigrettes, where nest trees were usually shorter and more robust, virtually all nests were accessed. Nests were accessed at the morning changeover or before the female sat in the afternoon. Nests were accessed to determine if there were any eggs or squabs, to weigh, ring and check the health of squabs and to determine a possible cause of nest failure. Disturbance to the nest was minimised when squabs were less than five days old and older than 15 days.

The study of pairings

Potential breeding pairs were identified by observing pair-bonding behaviour but a breeding pair was not confirmed until nesting behaviour by both birds was observed. A breeding pair was assigned a pairing number once the first nesting attempt was found (with or without eggs). If the same birds re-paired a new pairing number was assigned. Pairing lengths were calculated from the earliest date a nesting attempt was recorded. This was either when the nest was first found or calculated as 10 days before the first egg was laid, if this date was earlier (in captive birds, median time from pair formation to egg laying was 10 days, Jones 1995). A reason for termination of the pairing was assigned as death or divorce. Where death was the outcome, pair length was calculated as the number of days between the start and death. Where one mate was found in a new pairing, a divorce date for its previous pairing was calculated as halfway between the end of the last nest attempt and the start of the new pairing and pair length was the number of days between start and divorce.

Birds older than 150 days (approximate mean age of maturity, Jones 1995) at release were excluded from calculations of age at first pairing. Also excluded were the original wild adult population, who had most likely bred before monitoring began and a male early on in the release programme when there were no females with which to pair. Eight pairings were excluded from the analysis of pairing lengths and outcome as the pair divorced more than six months after their last known nesting attempt. Two pairings were excluded from the analysis of mean pairing length as the female was removed. When calculating pair lengths two assumptions were made. The pairing started with the first nest attempt found and pairings were assumed to remain together if not found in a new pairing. Life table analysis and Kaplan-Meier estimates of survival (Cox & Oakes 1984) were calculated to investigate the survival probability of pairings (Chapter 3).

Egg studies

For most mainland nests the presence of egg(s) was deduced from incubation behaviour of the pair, the presence of a squab later in the attempt or the remains of smashed eggs found below the nest. On Ile aux Aigrettes the majority of nests were accessed when eggs were present. Clutch size was recorded and the length and width of the egg measured with vernier calipers to the nearest 0.1 mm. A shape index was calculated for the egg as egg length/egg width. Eggs were candled by shining the light from a small torch through the egg to assess fertility at a minimum of three days incubation. For the analyses, fertility of eggs was determined only where nests were found before or during incubation. When calculating the age at which a female laid her first egg and the age of males and females at the first fertile egg, birds older than nine months at release were excluded (median age at first egg lay for captive birds was 9.79 months (Jones 1995)). Also excluded were the original wild females (see above). Seasonal trends and annual variation in egg laying were investigated.

Statistical Analyses

Chi-squared tests were used to test the relationship between the frequency of tree species used as nest trees at different sites, nest orientation and site, pairing length and its outcome, pairing outcome of released and wild birds, pairing outcome and site, clutch size and female age and annual and seasonal trends in fertility. Mann-Whitney U-tests were used to compare median ages at first pairing of males and females, of wild and released birds and median ages of wild and released females when the first egg was laid. Where sample sizes were large, Mann-Whitney U values were converted to a z-score. Regression analysis and ANOVA was used in MINITAB (8.21, 1991) to test the relationship between the age of a male and female when each pair was formed. Cox's proportional hazards model (Chapter 3) was used to investigate the survival of released and wild pairings and pairing survival between sub-populations. A Kruskal-Wallis test was used to compare the median age of females when first eggs were laid between sub-populations. A z-test was used to test the differences in mean egg size in one-egg and two-egg clutches, of the larger and smaller egg in two-egg clutches and between wild and captive birds. A Spearman's rank correlation was used to test the relationship between mean monthly nest success and mean monthly rainfall. All mean values are followed by the standard deviation (± SD).

RESULTS

Nest site selection

Nest tree species

Of 1490 nest attempts 1043 nest trees were identified, 937 (90%) to species and 106 (10%) to genus. Combining data for all sites, nest trees were recorded from 45 genera and 47 species were identified (Table 4.1). Both native and exotic species were used as nest trees but the frequency with which they were used varied between sites (Table 4.2), and at each site some species were used more frequently. The relationship between site and the frequency with which native or exotic species were used as nest trees was significant ($\chi^2_3 = 690.9, P < 0.001$). At Pigeon Wood and Bel Ombre the dominant species were exotic, 96% of nest trees at Pigeon Wood were *Cryptomeria japonica* and at Bel Ombre, 37% comprised *Tabebuia pallida* and 36% were *Pinus elliottii*[1]. At Brise Fer and Ile aux Aigrettes, native species were used more frequently. The dominant trees used at Brise Fer were *Syzigium* species (29%) and *Diospyros* spp. (26%) and at Ile aux Aigrettes, *Diospyros egrettarum* comprised 36% of nest trees and *Tarenna borbonica* comprised 26% of nest trees. Overall, *Diospyros* species were recorded as nest trees at three sites and comprised 19.3% of all nest trees recorded.

Table 4.2 Number of native and exotic trees used as nest trees, 1988-98.

Tree type	Brise Fer		Ile aux Aigrettes		Bel Ombre		Pigeon Wood		Total	
	No. nests	% nests	No. nests	% nests	No. nests	% nests	No. nests	% nests	No. nests	% nests
Native	248	92.0	299	95.0	65	23.3	2	0.9	614	58.9
Exotic	21	8.0	17	5.4	181	76.6	210	99.1	429	41.1
Total	269	100.0	316	100.0	246	100.0	212	100.0	1043	100.0

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[1] *Pinus elliotii* is the only species of *Pinus* recorded in Strahm (1993) and it was assumed that all those used by pink pigeons were this species. However, other species may exist and *Pinus taeda* was identified by foresters at Bel Ombre but it is not known if this was a mis-identification.

Species	Native / Exotic	Brise Fer	Pigeon Wood	Bel Ombre	Ile aux Aigrettes
Adenanthera pavonina	N			1	
Albizia lebbeck	E				1
Aphloia theiformis	N			1	
Araucaria cunninghamii	E			1	
Bamboo	E			1	
Bois balais	N			9	
Bois sagaie	N			1	
Calophyllum tacamahaca	N	1			
Calophyllum sp.	N		1		
Canarium paniculatum	N	2			
Cryptomeria japonica	E		204		
Cyathea sp.	N / E		1		
Diospyros egrettarum	N				115
Diospyros tesselaria	N	26		15	
Diospyros sp.	N	45		1	
Dracaena concinna	N				9
Ehretia petiolaris	N				10
Elaeodendron orientale	N	4			
Erythrospermum monticolum	N	2			
Eugenia lucida	N				41
Eugenia sp.	N	4			
Fernelia buxifolia	N	1			
Ficus reflexa	N				6
Ficus rubra	N				4
Ficus sp.	N				4
Flacourtia indica	E				12
Gaertnera psychotrioides	N			1	
Gastonia mauritiana	N				17
Grangeria borbonica	N	7		10	
Homalium sp.	N	1	1		
Hugonia serrata	N	1			
Labourdonnaisia glauca	N	21		11	
Labourdonnaisia revoluta	N	6			
Labourdonnaisia sp.	N	1		2	
Lautembergia neraudiana	N	2			
Ligustrum robustum	E	12		2	
Ludia mauritiana	N	1			
Mangifera indica	E			3	
Margariteria anomala	N				1
Maytenus pyria	N				4
Mimusops maxima	N	6			
Mimusops sp.	N	11		1	
Nuxia verticillata	N	4			
Pandanus eydouxi	N			8	
Pinus elliotii	E	1	4	86	
Pleurostylia leucocarpa	N	1			
Pongamia pinnata	E				1
Premna corymbosa	N				3
Protium obtusifolium	N	11		1	
Psidium cattleianum	E	8	1		
Securinega durissima	N	5			
Sideroxylon cinereum	N			1	
Sideroxylon sp.	N	5		1	
Syzigium coriaceum	N	1			
Syzigium glomeratum	N	60			
Syzigium sp.	N	16			
Tabebuia pallida	E			88	3
Tarenna borbonica	N				85
Warneckia trinerve	N	3		1	
TOTAL		269	212	246	316

Table 4.1 Species used as nest trees by pink pigeons 1988-98, (number of times used).

N = native, E = exotic (introduced). Bois sagaie = *Doratoxylon apetalum* or *Molinia laevis*. Bois balais = *Grangeria borbonica* or *Erythroxylum hypericifolium*

Relationship between nest tree species used and species abundance

Brise Fer

A correlation existed between the importance values of native tree species and their use as nest trees (Figure 4.1). The two main nest trees used, *Diospyros tessellaria* and *Syzigium* species are main canopy trees with *D. tessellaria* as the major canopy tree in this forest. However, some abundant native species were not used frequently as nest trees e.g. *Erythrospermum monticolum, Elaeodendron orientale.*

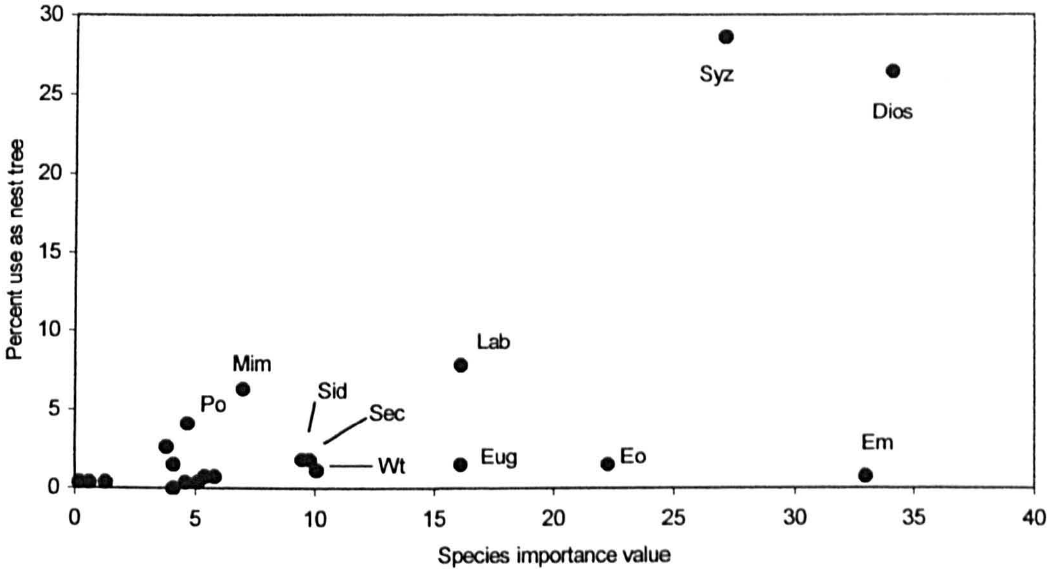

Figure 4.1 Relationship between the percentage of native species of nest tree used by pink pigeons and their abundance at Brise Fer, 1988-98. Syz = *Syzigium* spp., Dios = *Diospyros* spp., Em = *Erythrospermum monticolum*, Eo = *Elaeodendron orientale*, Eug = *Eugenia* spp., Lab = *Labourdonnaisia* spp., Sid = *Sideroxylon* spp., Sec = *Securinega durissima*, Wt = *Warneckia trinerve*, Mim = *Mimusops* spp., Po = *Protium obtusifolium*. The relationship was significant (Spearman's rank test, $r_s = 0.63$, $n = 22$, $P \cong 0.001$).

Ile aux Aigrettes

On Ile aux Aigrettes pigeons were selective in locating nest sites as nest trees were not located in different vegetation types in proportion to the vegetation cover of the island ($\chi^2_8 = 156.8$, $P < 0.001$). For example more than 20% of nests were located in canopy forest and 64% of all nests were located in canopy and Transition 3 type forest which covered only 33% of the island (Table 4.3).

On Ile aux Aigrettes pigeons chose nest trees which were also disproportionate to their relative abundance (Table 4.4). *D. egrettarum* and *T. borbonica* were used in canopy and Transition 3 type forest more frequently than expected ($\chi^2_{11} = 123.4$, $P < 0.001$) and also in other vegetation types where they were at much lower incidence ($\chi^2_{11} = 124.9$, $P < 0.001$).

In contrast, *Ehretia petiolaris* was rarely used in any vegetation type despite a relative incidence of about 25% canopy cover on the island.

Table 4.3 Frequency of nest location in vegetation communities on Ile aux Aigrettes, 1994-98.

Vegetation community	Frequency of nest location	% of nest attempts	Vegetation type as % of island area
Canopy – continuous canopy forest	47	20.6	6.4
Transition 3 - canopy forest with large gaps	98	43.0	26.6
Transition 2 - weeded and replanted, small trees	62	27.2	25.7
Transition 1 – scrubby coastal, occasional mature trees	12	5.3	16.3
Leucaena – monotypic stands of exotic false acacia	3	1.3	9.0
Coastal – thickets of scrubby coastal plants, 2-2.5 m	2	0.9	11.9
Pemphis – monotypic stands, <1 m	0	0.0	2.0
Buildings	4	1.7	1.4
Cleared areas	0	0.0	0.7
Total	228	100	100

Table 4.4 Number of nest trees and their relative abundance in different vegetation types on Ile aux Aigrettes, 1994-98.

Species	Canopy / T3 forest			Other vegetation types		
	Relative abundance	No. nest trees	% nest trees	Relative abundance	No. nest trees	% nest trees
Diospyros egrettarum	15.9	60	43.8	5.2	18	24.7
Tarenna borbonica	20.0	33	24.1	8.1	18	24.7
Eugenia lucida	10.6	18	13.1	3.1	5	6.8
Dracaena concinna	0.0	4	2.9	0.8	2	2.7
Flacourtia indica	1.7	4	2.9	24.0	8	10.9
Ehretia petiolaris	25.3	1	0.7	23.1	3	4.1
Maytenus pyria	13.0	1	0.7	8.3	1	1.4
Premna corymbosa	2.3	1	0.7	0.0	1	1.4
Scaevola taccada	1.9	0	0.0	1.8	0	0.0
Leucaena leucocephala	0.0	0	0.0	10.3	0	0.0
Morinda citrifolia	0.0	0	0.0	0.5	0	0.0
Scutia myrtina	0.0	0	0.0	3.0	0	0.0
Other	9.1	15	10.9	11.8	17	23.3
Total	100	137	100	100	73	100

Nest tree characteristics

The distribution of nest tree height, nest height and nest tree trunk diameter at breast height (dbh) are shown with mean values for mainland sites in Figure 4.2 and for Ile aux Aigrettes in Figure 4.3. Nest trees were on average much shorter at Ile aux Aigrettes than at mainland sites and consequently the average nest height was much lower.

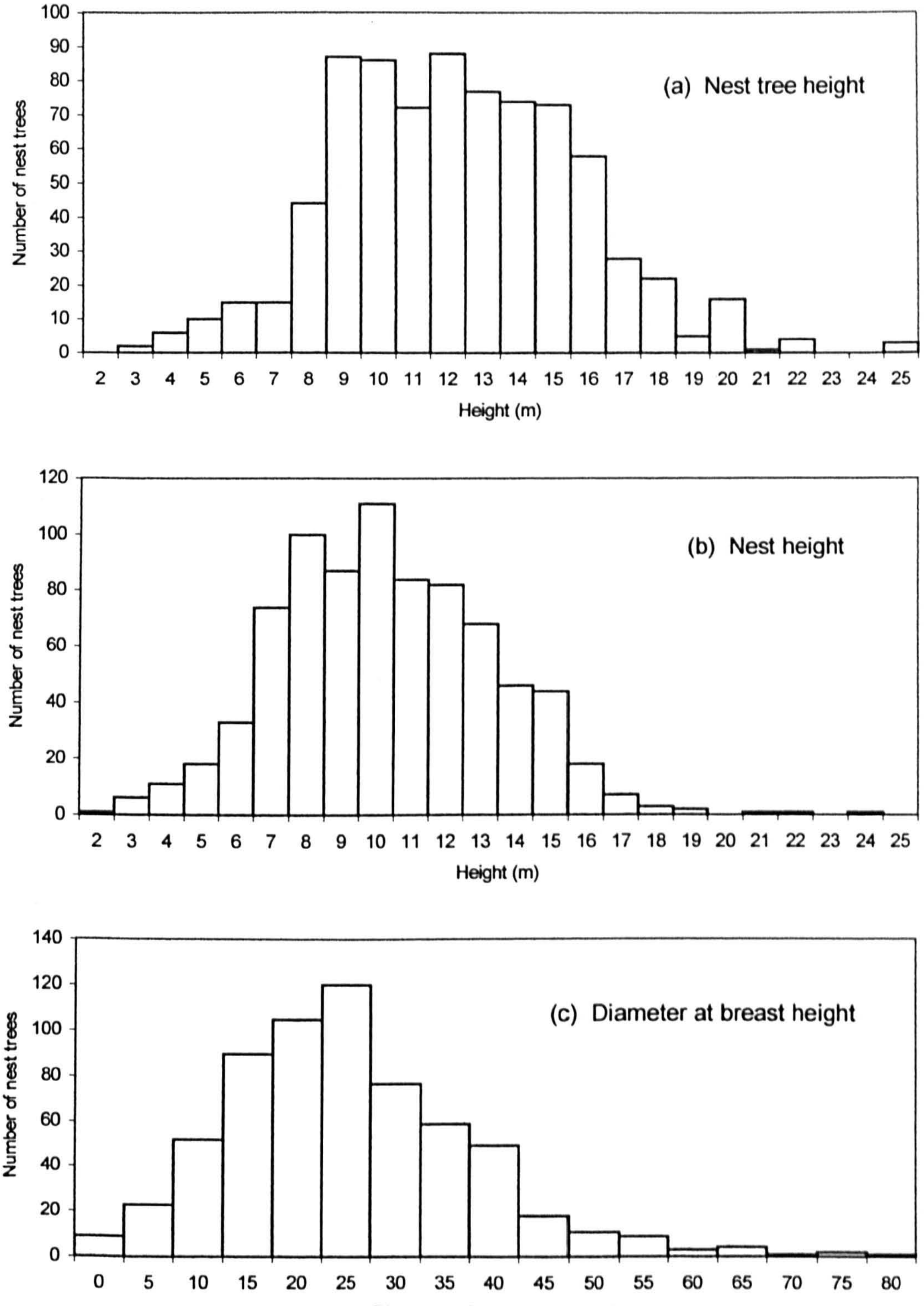

Figure 4.2 Nest site characteristics at mainland sub-populations, 1988-98. (a) Distribution of nest tree height, mean 12.4 ± 3.5 m (n = 786) (b) distribution of nest height within the tree, mean 10.5 ± 3.0 m (n = 798) (c) distribution of diameter at breast height of nest tree, mean 28.0 ± 13.5 cm (n = 634). Mean distance of nest from tree top 1.9 ± 1.5 m (n = 773).

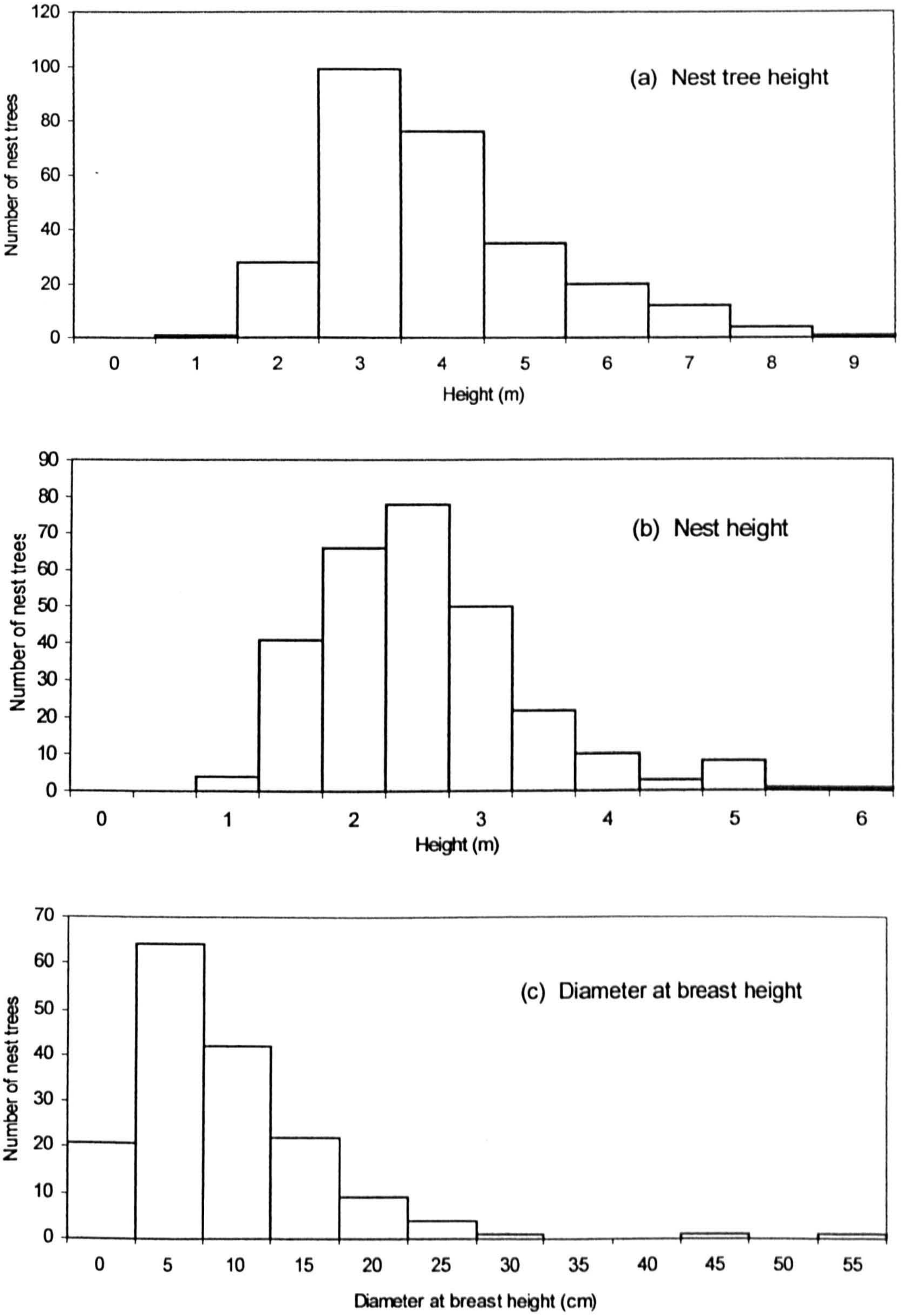

Figure 4.3 Nest site characteristics at Ile aux Aigrettes, 1994-98. (a) Distribution of nest tree height, mean 4.2 ± 1.3 m (n = 276) (b) distribution of nest height within the tree, mean 2.7 ± 0.8 m (n = 284) (c) diameter at breast height of the nest tree, mean 11.4 ± 7.5 cm (n = 165). Mean distance of nest from tree top 1.5 ± 1.1 m (n = 276).

Nest site description

Most nests (about 80%) were visible or partially visible from the ground. Nests were usually located in the middle or upper part of the canopy and, with the exception of Pigeon Wood, most nests were usually built on an outer limb of the tree away from the main trunk. At Pigeon Wood, where *Cryptomeria japonica* was the main tree species used, most nests were built next to the main trunk owing to the flimsy outer branches that provided little support. The majority of nests were sheltered by vegetation. At Brise Fer, Bel Ombre and Ile aux Aigrettes, 248 (45%) nests were located facing a North, north-east or north-westerly direction. This orientation was most noticeable on Ile aux Aigrettes where only seven out of 107 nests were found facing in a southerly direction. The effect of aspect was significant at these sites (Figure 4.4). At Pigeon Wood 86 nests (75%) were oriented in a southerly or easterly direction.

Description of nest

Nest measurements are shown in Table 4.5. Nests were on average sub-elliptical in shape (index of 1.3) and not very deep. A shallow cup was usually present although some nests were flat. Nests were made of twigs which were loosely woven together, and some nests were found lined with pine needles (either *Cryptomeria* or *Pinus*), ferns, lichens, tree roots, feathers and dead leaves. Introduced species, such as *Ligustrum* and *Pinus*, were often used as nest material at mainland sites. A large or forked limb together with several smaller branches and twigs usually supported the nest. Lianas also provided support. Pink pigeons sometimes re-used nests of their own or of other pairs, and would add fresh material to them. Pigeons also used disused nests of the Madagascar turtle-dove *Streptopelia picturata*.

Table 4.5 Nest measurements, all sites. Shape index = length/width.

	Length (cm)		Width (cm)		Depth (cm)		Shape index
	Nest	Cup	Nest	Cup	Nest	Cup	Nest
Mean	26.2	10.8	20.2	8.9	7.9	3.3	1.3
SD	8.2	3.3	7.0	2.9	4.6	2.0	0.2
N	382	227	378	202	350	207	269

The study of pairings

Where eggs were laid, 245 pairings were recorded involving 154 males and 156 females. An additional 31 pairings were recorded where eggs were not known. Of 180 pairings where parents of both mates were known, 19 sibling pairings were recorded, i.e. both mates shared the same parents. Three of these were re-pairings and three did not produce eggs. Four sibling pairings were between wild-fledged birds.

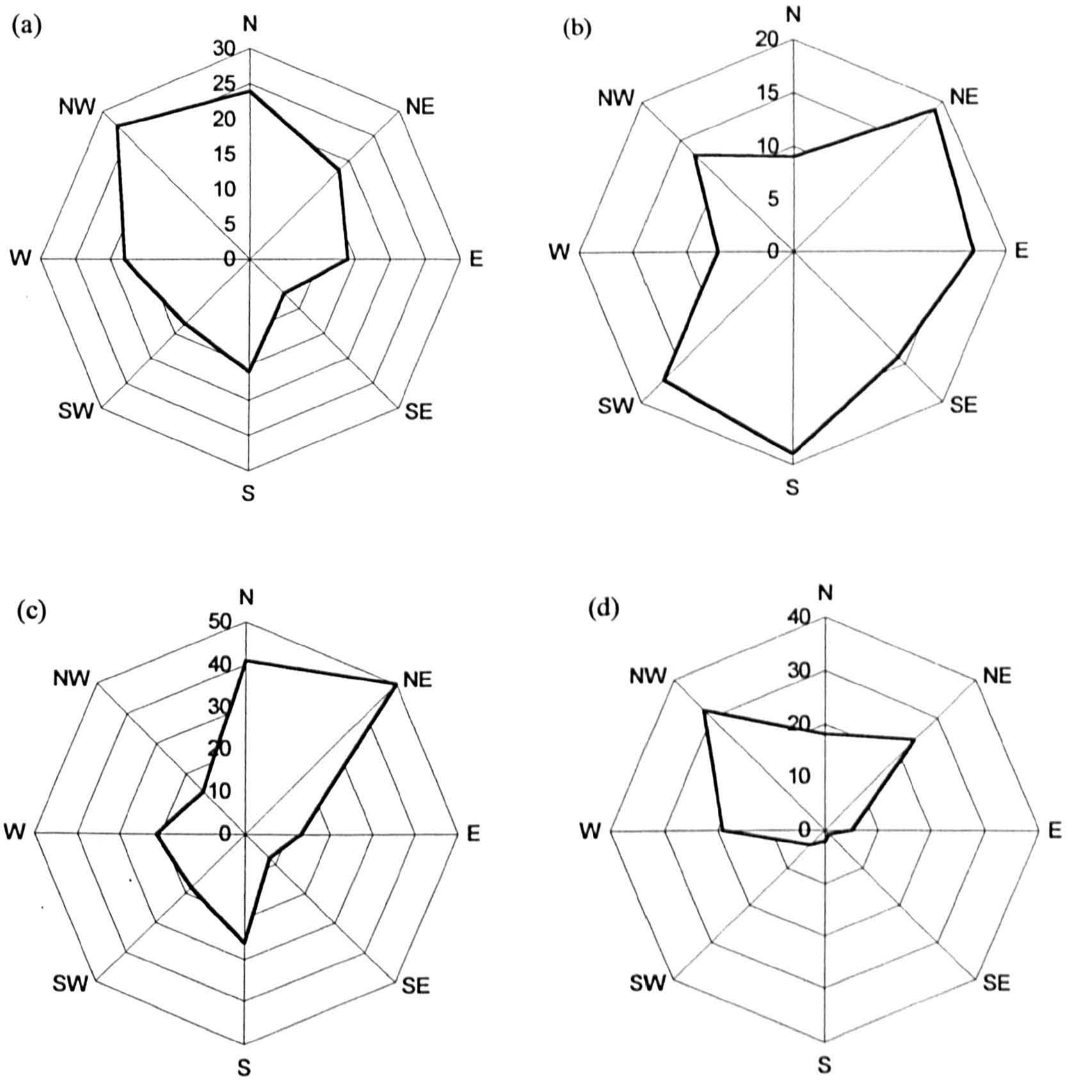

Figure 4.4 Aspect of nests within nest tree (a) Brise Fer (b) Pigeon Wood (c) Bel Ombre (d) Ile aux Aigrettes. The relationship between location of the nest and aspect was significant at Brise Fer ($\chi^2_7 = 16.2$, $P < 0.05$, $n = 137$) and highly significant at Bel Ombre ($\chi^2_7 = 62.4$, $P < 0.001$, $n = 191$) and Ile aux Aigrettes ($\chi^2_7 = 72.6$, $P < 0.001$, $n = 105$). There was no relationship at Pigeon Wood ($\chi^2_7 = 9.9$, $P > 0.05$, $n = 115$).

Age of birds at pairing

The youngest male found with a nest was 118 days old (3.9 calendar months), although a possibly younger male was found at about 94 days old (3.1 months) with a nest, but whose age was less certain. The youngest female with a nest was found at 120 days old (3.9 months). Median ages for males and females were significantly different (Figure 4.5). On Ile aux Aigrettes, median age at first pairing for males was 307 days old (10.1 months) ($n = 20$) and for females was 215 days old (7.0 months) ($n = 25$). There was no significant difference in the median age at first pairing between released and wild females (Mann-Whitney U-test, $z = 0.952$, $P > 0.05$, $n = 63$ released, 74 wild) or between released and wild males (Mann-Whitney U-test, $z = 0.196$, $P > 0.05$, $n = 53$ released, 76 wild). The relationship between the ages of the male and the female when each pair formed was highly significant (Figure 4.6). Young females usually paired with young males and old females with old males.

Duration of Pairings

The stability and duration of pairs varied and 41% were known for more than one year (Table 4.6). The longest pairing was 6.2 calendar years and the pair was still together at the end of the study. Kaplan-Meier estimates of pairing survival comprising both released mates, both wild mates and one released and one wild mate was not significantly different (Wald = 4.42, df = 2, $P > 0.05$, $n = 237$).

Table 4.6 Actuarial estimates of pairing survival comprised of released and wild birds, all sites 1988-98. No. pairs = number of pairs known at the beginning of each year. Cum. survival = Cumulative proportion surviving at end of year, i.e. percent of all pairs known at the beginning of year 0 surviving to the end of each year. % survival = percent of pairs known at the beginning of each year surviving to the end of each year. Actuarial estimates accounted for censored data (i.e. pairs still together within each year interval) by assuming that the censored survival times occurred uniformly throughout the interval and the number of individuals at risk was adjusted to include half the number of censored pairs (see Collett 1994). Released pairs = both mates released, wild pairs = both mates wild, released/wild pairs = one mate wild and one mate released.

Pair length (years)	All pairs			Released pairs		Wild pairs		Released/Wild pairs	
	No. pairs	Cum. survival	% survival	No. Pairs	% survival	No. pairs	% survival	No. pairs	% survival
0-1	237	47.6	47.6	101	39.4	78	57.8	58	48.6
1-2	98	29.4	61.8	37	53.6	38	52.9	23	94.4
2-3	42	19.9	67.6	16	83.3	14	66.7	12	50.0
3-4	15	13.3	66.7	6	45.5	6	100.0	3	50.0
4-5	5	13.3	100.0	2	100.0	3	100.0	-	-
5-6	2	13.3	100.0	1	100.0	1	100.0	-	-
6-7	1	13.3	100.0	1	100.0	-	-	-	-

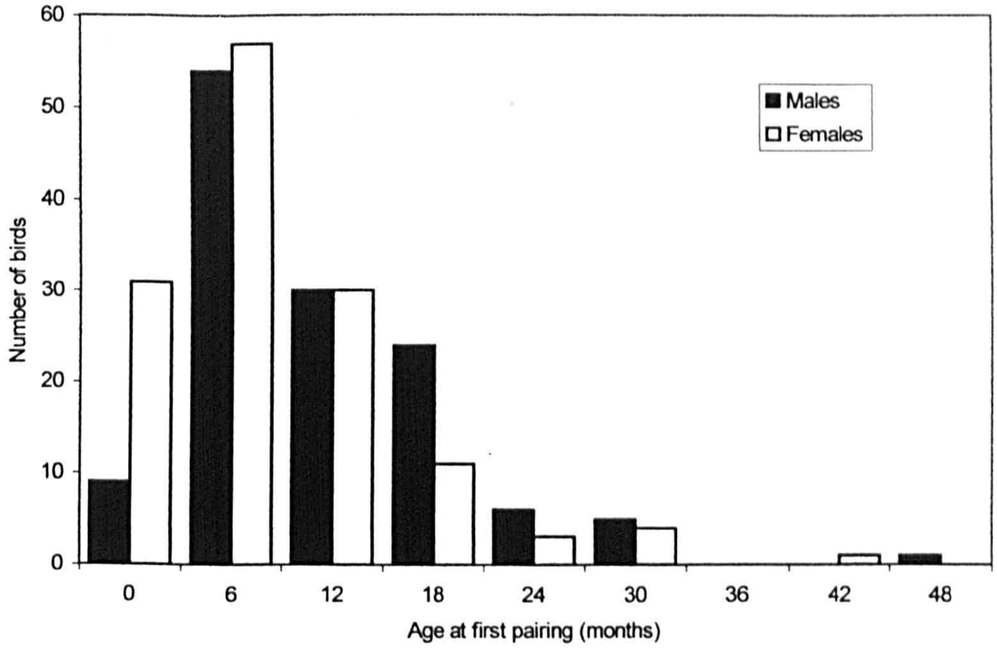

Figure 4.5 Age of males and females when first paired, 1988-98. Data for all sites pooled. Median age of females (297 days old, 9.7 months) ($n = 137$) was significantly different to the median age of males (370 days old, 1.01 years) ($n = 129$) (Mann-Whitney U-test, $z = 3.54$, $P < 0.05$).

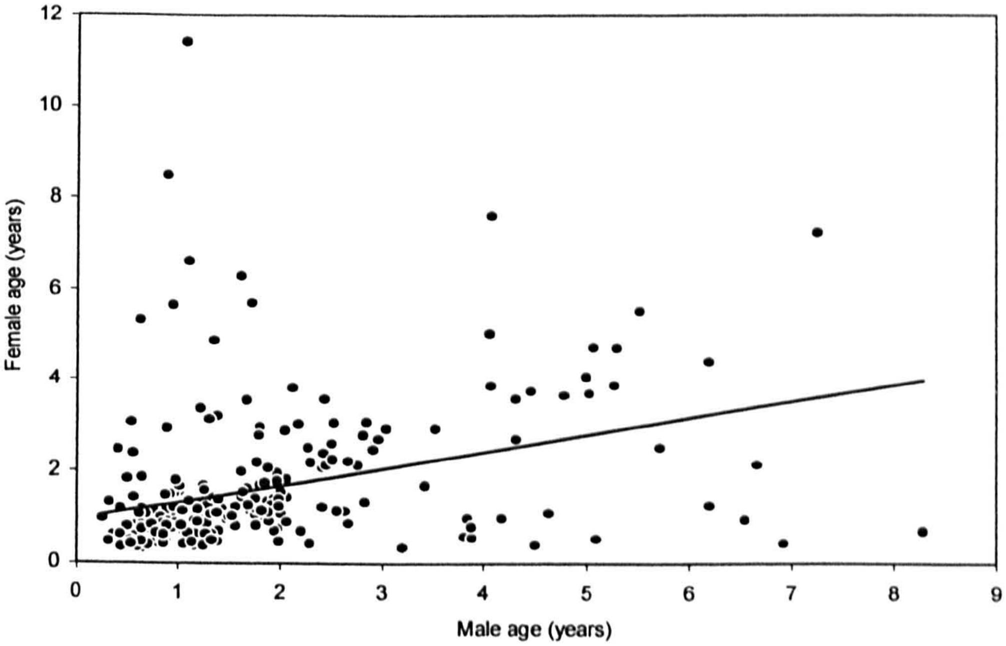

Figure 4.6 Relationship between the age of the male and female when each pair formed, 1988-98. Data for all sites pooled. The relationship between male age (x) and female age (y) was highly significant ($F_{1,243} = 33.81$, $P < 0.001$, $n = 245$): $y = 0.3699_x + 0.9543$.

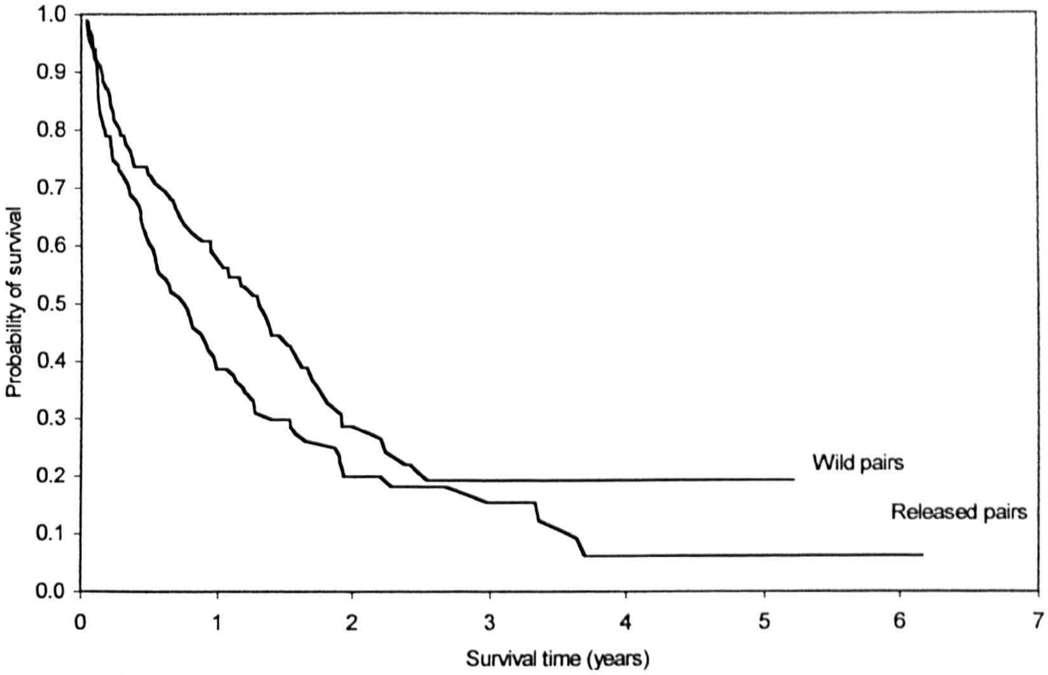

Figure 4.7 Survival of pairings comprised of released and wild birds, all sites 1988-98. Kaplan-Meier estimates of survivor function are plotted. Differences in survival were marginally significant (Wald = 3.72, df = 1, $P \cong 0.05$). Sample size: 101 released pairs, 78 wild pairs (26% censored).

When data for released and wild birds were analysed independently, the differences were marginally significant (Figure 4.7). Survival of pairings was significantly different between sub-populations (Wald = 9.215, df = 3, $P < 0.05$, n = 237, 29% censored). In particular survival of pairings at Ile aux Aigrettes was poorer than other sites, particularly within the first year after pair formation (Table 4.7).

Table 4.7 Actuarial estimates of pairing survival at different sub-populations, 1988-98.

Pair length (years)	Brise Fer		Pigeon Wood		Bel Ombre		Ile aux Aigrettes	
	No. pairs	% survival	No. pairs	% survival	No. pairs	% survival	No. Pairs	% survival
0-1	84	57.5	38	51.3	53	42.6	62	36.1
1-2	42	63.2	18	52.9	19	56.2	19	74.2
2-3	20	67.7	8	71.4	6	75.0	8	60.0
3-4	6	60.0	4	100.0	1	100.0	4	33.3
4-5	2	100.0	3	100.0	-	-	-	-
5-6	1	100.0	1	100.0	-	-	-	-
6-7	1	100.0	-	-	-	-	-	-
Mean 0-4	42	62.1	18	68.9	19	68.4	19	50.9
SD (%)	-	4.4	-	22.6	-	24.9	-	19.6

Outcome of pairings

Death of one of the mates accounted for the termination of 59% of pairings and divorce accounted for the termination of 41% of pairings. Where all pairings were considered including those ongoing at the end of the study period, 42% of pairings ended in death and

29% ended in divorce (Table 4.8). The sex that re-paired the quickest was assumed to have initiated the split. Using this criterion, divorce by the female was more frequently recorded (68%) than divorce by the male (22%). In nine pairings, both male and female re-paired within 10 days of each other and the sex that initiated the split could not be determined. In 68 pairs which divorced, mean time to the first nesting attempt of the new pair was 35 ± 47 days (n = 76 birds). In 19 pairs which divorced, one or both mates were found in new pairings before, or on the same day of, the end of their last nesting attempt. Seventeen pairings which divorced re-paired after nesting with a different mate, one of which re-paired twice. In four pairings divorce was caused by the female when she dispersed to another sub-population. In one pairing at Pigeon Wood, divorce was caused by the male when he left the Wood for nearly eight months.

Table 4.8 Outcome of pink pigeon pairings, all sites 1988-98.

Outcome of pairing	No. of pairings
Female death	50
Male death	49
Divorce – Female re-paired first	44
Divorce – Male re-paired first	15
Divorce – Female & Male re-paired at same time	9
Female removed from site	2
Ongoing	68
Total	237

The number of pairings which ended in death during the first year after pair formation was significantly greater (64%) than in subsequent years (36%) ($\chi^2_1 = 18.9$, $P < 0.001$) (Table 4.9). The number of pairings which ended in divorce was also significantly greater in the first year after pair formation (82%) than in subsequent years (18%) ($\chi^2_1 = 38.6$, $P < 0.001$). The mean length of pairings which ended in death of a mate (11.4 ± 10 months) was significantly different to the mean length of pairings which ended in divorce (7.5 ± 8.3 months) ($z = 2.77$, $P < 0.01$). The mean length of pairings still together at the end of the study was 1.7 ± 1.3 years.

Table 4.9 Pairing length and frequency of pairing outcome in pink pigeons, all sites 1988-98.

Pairing length	Number of pairings		
(years)	Death	Divorce	Ongoing
0-1	63	56	20
1-2	26	7	23
2-3	7	4	14
3-4	3	1	6
4-5	0	0	3
5-6	0	0	1
6-7	0	0	1
Total	99	68	68

Effect of rearing origin on outcome of pairings

There was some suggestion that divorce arose more frequently in pairings where both mates were released (33%) than in pairings where both mates were wild (26%) (Table 4.10). This finding was not significant when divorced pairings were compared to ongoing pairings (i.e. pairings that had not divorced), when only released and wild pairings were considered and when all three categories were considered in the analyses. Death of a mate appeared to occur more frequently in pairings of released birds (47%) than in pairings of wild birds (40%). When pairings that ended in death were compared to ongoing pairings (i.e. pairings that had not ended in death), the relationship between the number of pairings with different rearing origins that ended in death was significant ($\chi^2_2 = 6.53$, $P < 0.05$). However, when only released and wild pairings were considered in the analysis, the relationship was not significant ($\chi^2_1 = 3.5$, $P > 0.05$).

These comparisons were confounded because ongoing pairings were of variable length (Table 4.11) and pairings were therefore not exposed to the same risk of death or divorce. For this reason, pairings for less than one year were analysed independently, as all pairings were then exposed to approximately the same risk. In pairings of less than one year, the differences in the number of pairings which ended in divorce between birds of different origin (compared to ongoing pairs) were significant ($\chi^2_2 = 6.21$, $P < 0.05$). Pairings which ended in death were not significantly different between birds with different rearing origins when all categories were considered, ($\chi^2_2 = 5.31$, $P > 0.05$), but when only released and wild birds were considered, the findings were significant ($\chi^2_1 = 4.22$, $P < 0.05$). Similar comparisons in pairings of more than one year were not significant.

Table 4.10 Frequency of pairing outcome of wild and released birds. Ongoing = pairs together at the end of the study period, Released = both mates released, Wild = both mates wild, Rel/Wild = one mate released and one mate wild.

Pairing	Number of pairings				Percent of pairings		
outcome	Released	Wild	Rel/Wild	Total	Released	Wild	Rel/Wild
Death	48	31	20	99	47.5	40.2	35.1
Divorce	33	20	15	68	32.7	26.0	26.3
Ongoing	20	26	22	68	19.8	33.8	38.6
Total	101	77	57	235	100	100	100

Table 4.11 Frequency of pairing outcome of wild and released birds in relation to the pairing length. Ongoing = pairs together at the end of the study period, Released = both mates released, Wild = both mates wild, Rel/Wild = one mate released and one mate wild.

Pairing length (years)	Number and outcome of pairings								
	Death			Divorce			Ongoing		
	Released	Wild	Rel/Wild	Released	Wild	Rel/Wild	Released	Wild	Rel/Wild
0-1	31	16	16	29	15	12	4	8	8
1-2	14	11	1	2	5	0	5	9	9
2-3	0	4	3	2	0	2	8	3	3
3-4	3	0	0	0	0	1	1	3	2
4-5	0	0	0	0	0	0	1	2	0
5-6	0	0	0	0	0	0	0	1	0
6-7	0	0	0	0	0	0	1	0	0
Total	48	31	20	33	20	15	20	26	22

Outcome of pairings in different sub-populations

The number of pairings that ended in death or divorce was significantly different between sites ($\chi^2_3 = 11.02$, P ≅ 0.01). At Brise Fer more pairings ended in death and fewer in divorce than at other sites, and at Bel Ombre fewer pairings ended in death and more in divorce than at other sites (Table 4.12). A comparison of pairings that ended in death or divorce with ongoing pairs (i.e. not died or divorced) were not significant (death: $\chi^2_3 = 1.99$, $P > 0.05$, divorce: $\chi^2_3 = 6.12$, $P > 0.05$) but the results may have been confounded as explained above.

Table 4.12 Frequency of pairing outcome in different sub-populations.

Pairing outcome	Number of pairings					Percent of pairings			
	Brise Fer	Pigeon Wood	Bel Ombre	Ile aux Aigrettes	Total	Brise Fer	Pigeon Wood	Bel Ombre	Ile aux Aigrettes
Death	41	17	15	26	99	50.0	44.7	28.3	41.9
Divorce	14	11	22	21	68	17.1	28.9	41.5	33.9
Ongoing	27	10	16	15	68	32.9	26.3	30.2	24.2
Total	82	38	53	62	235	100	100	100	100

Unisexual pairings

Eight unisexual male pairings were observed where each male later formed a heterosexual pairing, confirming the male status. Further possible unisexual male pairings were recorded but the sex of one of the pair was not positively confirmed. No unisexual female pairings were observed.

Eggs and egg-laying

Age of female at first egg-laying

The youngest age when a first egg was laid was a wild female at 4.3 months old (130 days) which was also the earliest known age a fertile egg was first laid (Figure 4.8). First eggs were known in females at more than three years old, but this probably reflected an inability to find earlier nests. The youngest age at which a released female laid an egg (which was also the youngest age at which a released female laid a fertile egg) was 4.5 months old (137 days). There was no significant difference in median ages at first laying between released females (332 days) and wild females (333 days) (Mann-Whitney U-test, $W = 0.333$, $P > 0.05$).

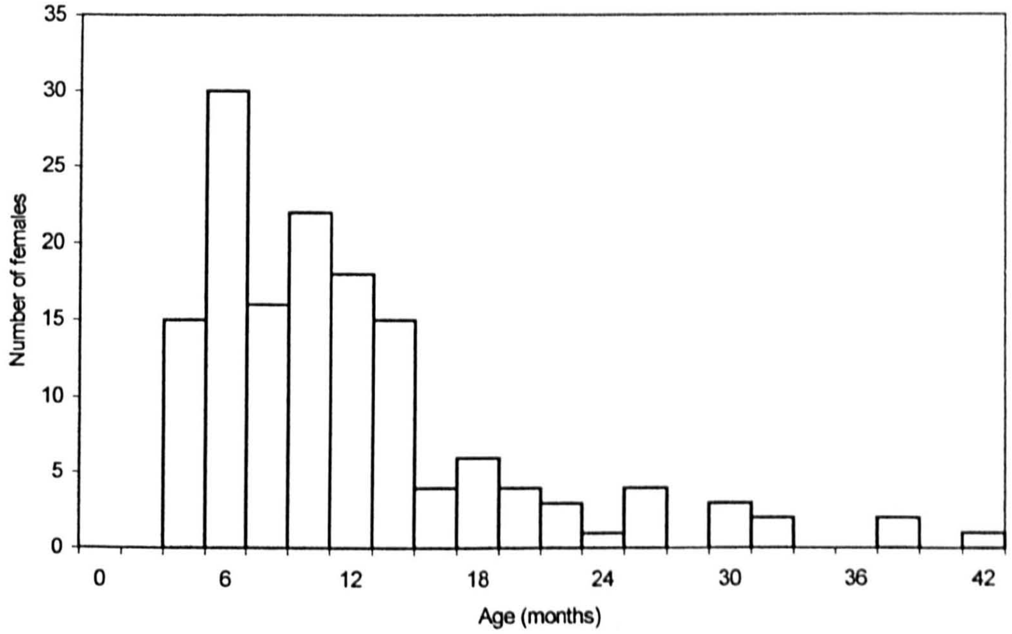

Figure 4.8 Age of female at first egg-laying, all sites 1988-98. Median age for all females 10.9 months ($n = 146$), for females at Brise Fer 10.7 months ($n = 58$), at Pigeon Wood 12.3 months ($n = 22$), at Bel Ombre 11.0 months ($n = 35$) and at Ile aux Aigrettes 8.6 months ($n = 31$). There was no significant difference in the median age at first egg-laying between sub-populations (Kruskal-Wallis test, $H = 7.2$, $df = 3$, $P > 0.05$).

Egg dimensions and shape

Measurements were taken from 319 eggs, 82% of which were from Ile aux Aigrettes. Seven yolkless eggs were excluded from overall mean values. Mean sizes of eggs are shown in Table 4.12. Eggs were sub-elliptical in shape. Sub-elliptical eggs have values of 1.23-1.5 (van Tyne & Berger 1976) and accounted for 97% of all eggs. The size of both eggs in 112 two-egg clutches was known although it was not possible to know which egg was laid first. Using egg length as representative of egg size, the mean size of larger eggs (36.4 ± 1.38 mm x 27.1 ± 0.77 mm) was significantly different to the mean size of smaller eggs (35.3 ± 2.01 mm x 26.7 ± 1.37 mm) (z = 4.78, P < 0.01). The mean size of eggs in a one-egg clutch (36.0 ± 1.87 x 26.8 ± 1.39, n = 36) was significantly smaller than mean size of larger eggs in a two-egg clutch (z = 11.8, P < 0.01) but there was no significant difference in mean size of smaller eggs (z = 1.92, P > 0.05). Mean size of yolkless eggs was 27.5 ± 1.72 mm x 21.1 ± 1.27 mm, (n = 7) four of which were laid by one female.

Using length as representative of egg size, there was no significant difference between wild and captive-laid eggs (z = 1.146, P > 0.01) (Table 4.13).

Table 4.13 Dimensions of pink pigeon eggs, all sites 1989-98. Captive data taken from Jones (1995). Shape index = length/width.

	Wild eggs			Captive eggs		
	Length (mm)	Width (mm)	Shape index	Length (mm)	Width (mm)	Shape index
Mean	36.0	27.0	1.33	35.89	26.8	1.34
SD	1.44	0.89	0.056	1.76	0.92	0.061
Max	42.1	29.2	1.58	41.7	30.4	1.62
Min	31.9	23.5	1.21	30.7	22.4	1.12
Range	10.2	5.7	0.37	11	8.0	0.50
No. eggs	304	311	303	1285	1285	1285
No. females	41	48	41	43	43	43

Clutch size at Ile aux Aigrettes

Two-egg clutches were more frequently laid than one-egg clutches (Table 4.14). Between 1994 and 1996 when clutch size was more accurately recorded, the proportion of one-egg (30.1%) to two-egg clutches (69.7%) was similar to that for all years (n = 229). Mean clutch size was 1.66 ± 0.47. There was evidence that the proportion of two-egg clutches declined as the female became older. Mean clutch size in females up to three years old was 1.68 ± 0.47 (n = 306) and in females more than three years old was 1.47 ± 0.51 (n = 32). The relationship between clutch size and female age was significant ($\chi^2_1 = 5.74$, $P < 0.05$).

Table 4.14 Number of one-egg and two-egg clutches in female pink pigeons, Ile aux Aigrettes 1994-98.

Age (years)	No. one-egg clutches	No. two-egg clutches	Total no. clutches	% two-egg clutches
0	27	49	76	64.5
1	48	102	150	68.0
2	23	57	80	71.2
3	11	12	23	52.2
4	6	3	9	33.3
Total	115	223	338	66.0

Most females laid both one-egg and two-egg clutches but some females consistently laid more two-egg clutches. Of 15 females which laid more than 10 clutches each (mean 17.3 ± 7.14, n = 260), 12 laid more two-egg clutches and two laid more one-egg clutches. One female laid 26 clutches, half of which were one-egg and half were two-egg. Of 24 females, five were known to lay only two-egg clutches and six were known to lay only one-egg clutches, one of which laid six clutches all of one egg.

Seasonal trends in egg-laying

In the pink pigeon metapopulation a strong negative correlation existed between egg-laying and mean monthly rainfall (Figure 4.9). Some egg-laying occurred in every month of the year. A period of low egg-laying activity was seen in the hot, wet months (February to April), when there is a high risk of cyclonic weather and only 10.9% of nests with eggs were found (mean 3.6 ± 1.03% per month). Most egg-laying occurred in the 'dry' season (May to November) and extended early into the wet season (December to April). The period from May to January is subsequently referred to as the breeding season. In the breeding season, egg-laying activity was relatively constant although decreased slightly in August and September. Peak egg-laying occurred in July (11.3%) and October (11%).

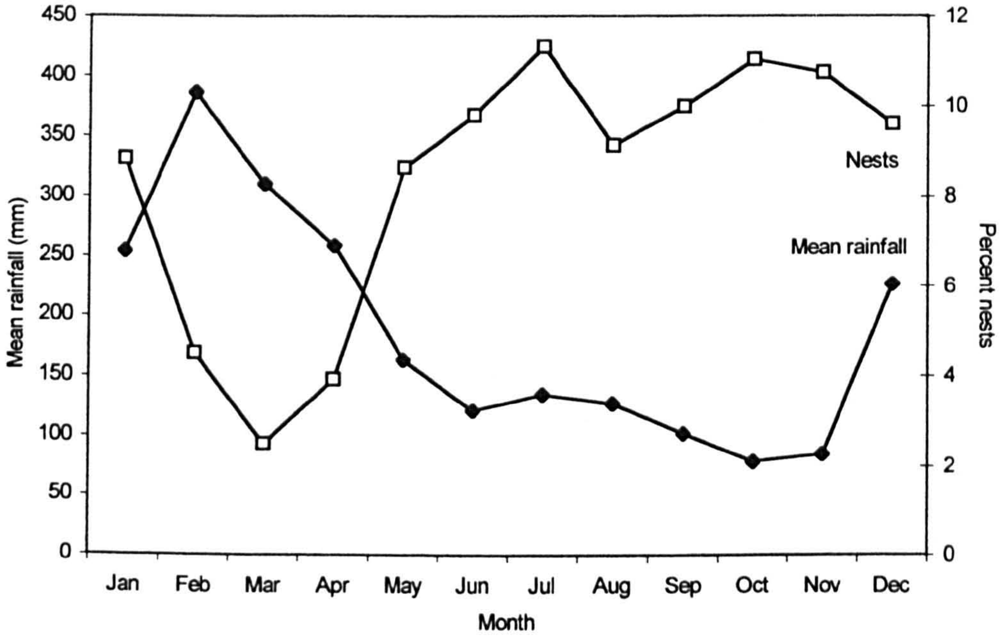

Figure 4.9 Monthly percentage of nesting attempts where eggs were laid and mean monthly rainfall in Mauritius, 1988-98. Data for all sites pooled. Sample size 1042 nests. The negative correlation was significant (Spearman's rank test, $r_s = -0.83$, $P < 0.001$, $n = 12$).

All sub-populations showed a marked period of low egg-laying activity. Differences were seen between sites in the onset and length of the breeding season and pattern of activity over the breeding season (May to January) (Figure 4.10). At Pigeon Wood and Bel Ombre, the onset of the breeding season occurred in May and lasted for nine months through to January. At Brise Fer and Ile aux Aigrettes, onset occurred in June and July and the season lasted for seven months. At Brise Fer breeding was more marked early in the season (May

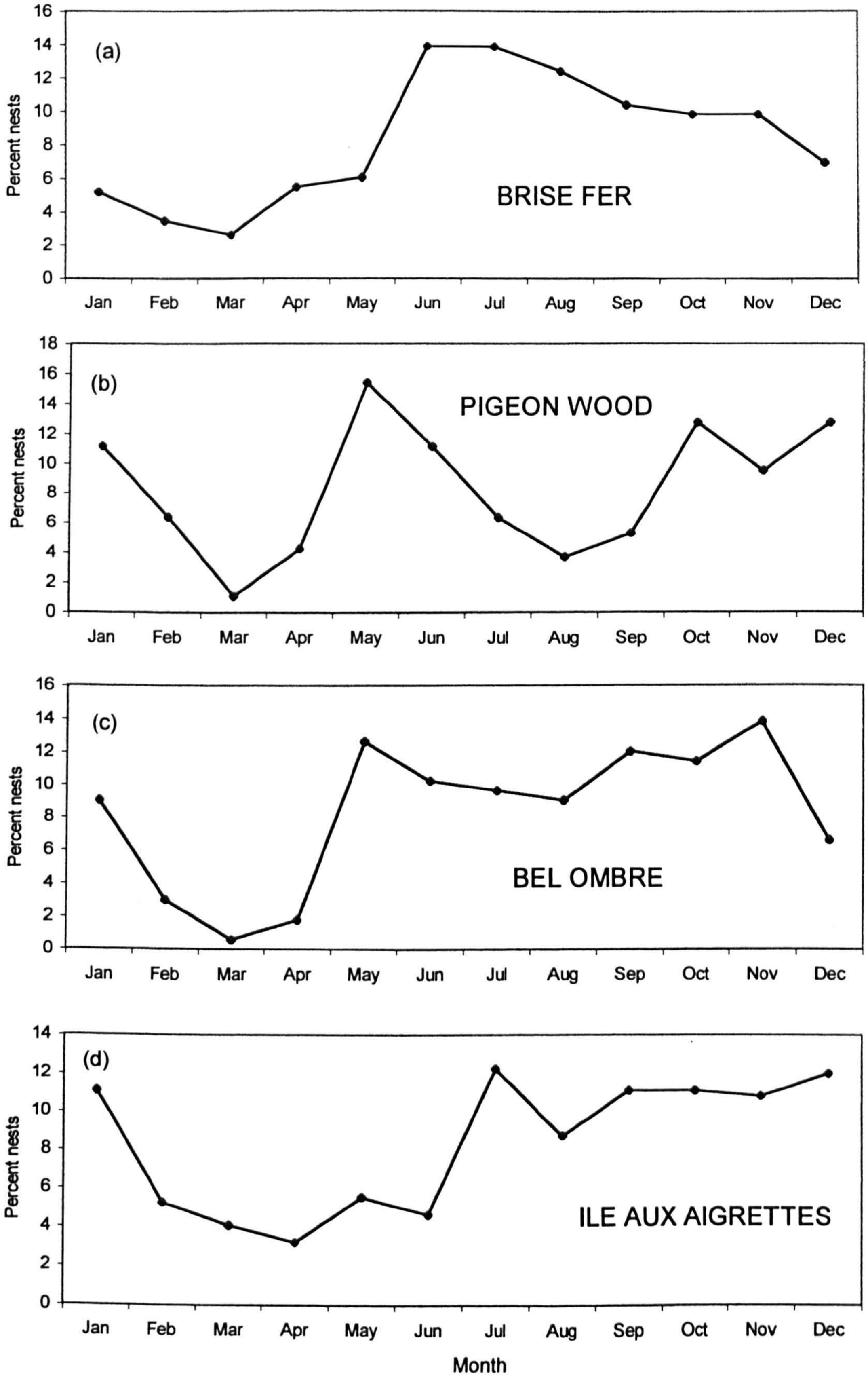

Figure 4.10 Monthly nesting attempts in different sub-populations. (a) Brise Fer, 1988-98 (b) Pigeon Wood 1989-98 (c) Bel Ombre 1995-98 (d) Ile aux Aigrettes 1994-98. Nests where eggs were laid are plotted per month as a percentage of all nests where eggs were laid. Sample size: Brise Fer 346, Pigeon Wood 188, Bel Ombre 166, Ile aux Aigrettes 342.

to August) and at Ile aux Aigrettes, breeding was more prevalent later in the season (September to December). Pigeon Wood showed a winter lull (July to September) in activity which was more marked than at other sites.

Annual variation in egg-laying

Egg-laying showed similar seasonal trends across years (Figure 4.11). However, peak egg-laying occurred earlier (May to August) or later (September to December) in the breeding season in different years. This seasonal shift in the breeding season between years was not always synchronous between sites. In some years there was a marked concentration of breeding effort over a few months. At Brise Fer in 1995 and 1996, 74% and 62% of nests were recorded between May and August and nearly all breeding stopped outside of these months with virtually no breeding from September 1996 to April 1997.

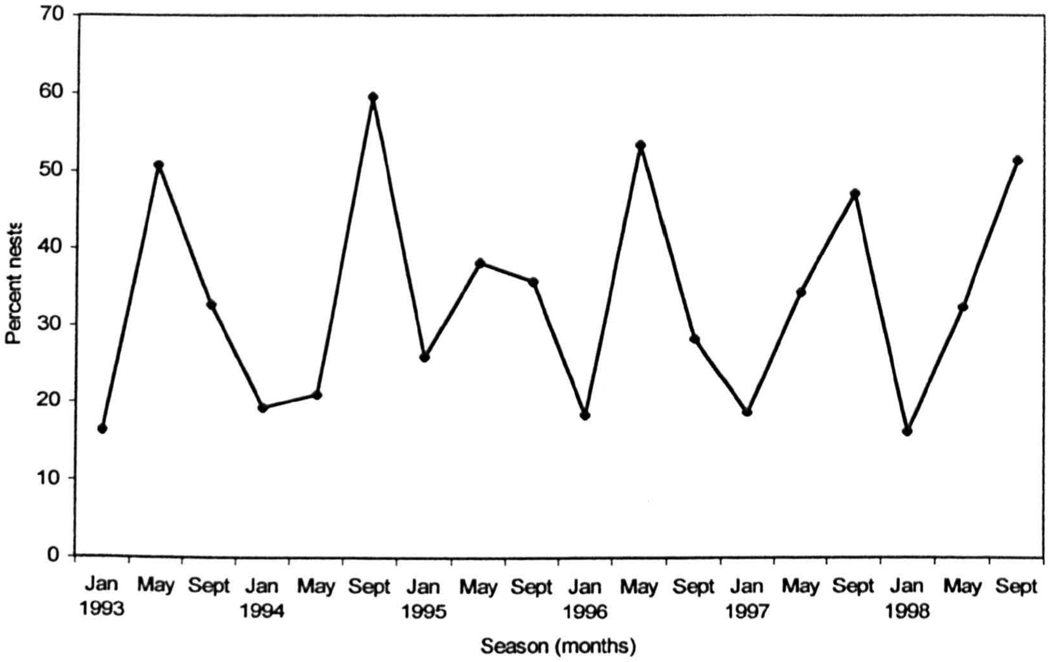

Figure 4.11 Annual and seasonal trends in egg-laying by females, all sites 1993-98. Percent nests where eggs were laid are plotted for each season per year. Seasons = Jan (January to April, hot wet), May (May to August, cool winter), Sept (September to December, hot dry). Sample size: 980 nests where eggs laid.

Fertility of eggs at Ile aux Aigrettes

The median age of females on Ile aux Aigrettes at first laying a fertile egg was 9.0 months old (n = 30). The earliest a male sired a fertile egg was 128 days old (4.2 months) and the median age for males was 8.1 months old (n = 28). Overall fertility was 58.6% (n = 485) (Appendix 3). Fertility in one-egg clutches was 45.6% (n = 68). Where fertility was known for both eggs in two-egg clutches, fertility was 59.9% (n = 402). In 201 nests with two-egg clutches, both eggs were fertile in 50.2% nests, in 19.4% of nests one egg was fertile and the second was infertile and in 30.3% of nests both eggs were infertile.

Monthly and annual trends in fertility on Ile aux Aigrettes

March had the lowest percentage of fertile eggs (25%) which was also the month when fewest eggs were laid and a peak in fertility was seen in April (Appendix 3). Fertility remained relatively high from July-December. The reasons for the high fertility in April were not clear. Monthly trends in fertility were not significant ($\chi^2_{11} = 17.3$, $P > 0.05$) but there was significant annual variation in fertility ($\chi^2_4 = 34.8$, $P < 0.001$) which ranged from 39% in 1996 to 75% in 1998.

DISCUSSION

Nest site selection

Historically, most pink pigeon nests studied have been in *Cryptomeria japonica* at Pigeon Wood as this was the last known breeding site for the species (McKelvey 1976). *Cryptomeria* was first planted within the pink pigeon's range in 1918 to 1920 (Edgerley 1962) and has been widely used for nesting since at least the 1940s or 1950s (Jones 1987). In a study of the Mauritius fody *Foudia rubra* nest success was more than seven times greater in *Cryptomeria* than in other tree species (Safford 1997*c*). The choice of *Cryptomeria* as a nest tree and the concentration of the remaining wild breeding population of pink pigeons in Pigeon Wood may be partly explained by increased nest success, which is further discussed in Chapter 5. A few pink pigeon nests have also been found at this site in the exotic *Eucalyptus robusta* and single nests found in native species *Diospyros* spp., *Labourdonnaisia* spp. and *Sideroxylon bojerianum* (McKelvey 1976, Hartley 1977, Temple 1978, Jones 1987).

Jones (1987) provides an account of nest building behaviour, the main features of which were also observed in this study. In previous studies, nest-building in wild birds was completed in one or two days (McKelvey 1976, 1977, Hartley 1977) and in captive birds over several days (Jones 1987). During this study nest-building was usually more protracted but the time to completion may depend on whether eggs are laid. In some nests the period from nest site selection by the male to egg-laying could take more than two weeks and nest-building may be carried out over a period of at least one week. Material was often added to the nest by the male once incubation had begun.

Selection of nest trees was not limited to native species and probably depended on the tree morphology and the presence of a contiguous canopy. The main native species used were tall with a dense sheltered canopy and plenty of support for the nest. These criteria were also met by the exotic *Cryptomeria*. The fact that pink pigeons chose exotic trees in which to nest was encouraging. At Bel Ombre, pigeons chose exotics over native species despite good numbers of native trees available, including *Diospyros* and *Syzigium* their favoured species at other sites. The exotics chosen, *Pinus* spp. and *Tabebuia pallida*, have rather flimsy and open structures but grew in small monocultures which provided a closed canopy. On Ile aux Aigrettes nest tree availability may be limiting but more nest sites will become available as planted native trees mature and more of the island's forest is restored. At Ile aux Aigrettes two pairs built nests on a window ledge inside a derelict building. One pair used the same building three times and fledged one young.

At Brise Fer, Bel Ombre and Ile aux Aigrettes southerly facing nests were less frequent, a trend which was most marked at Ile aux Aigrettes. This is due to the strong south-east Trade winds (Padya 1989) and Ile aux Aigrettes is particularly exposed to them. The southerly orientation of nests at Pigeon Wood was probably due to the steep southerly slopes that restricted the approach to nests on the northern side of the trees.

Mating systems and pair bonds

Although social monogamy is thought to be the mating system of 90% of bird species (Lack 1968), longer-term partnerships may only be achieved in about 21% of 159 bird families (Black 1996). Pigeons exhibit the whole range of social behaviour from solitude to being gregarious. When not breeding, ruddy quail doves *Geotrygon montana* from Central and South America, and other American quail doves, may live alone. In contrast, the short-billed pigeon *Columba nigrirostris* from Central America may remain with their partners throughout the year. Some columbids typically gather in small or large flocks to roost or forage, particularly in the non-breeding season. Examples include the mourning dove *Zenaida macroura* and band-tailed pigeon *Columba fasciata* in North America, Cape turtle-dove *Streptopelia capicola* in South Africa, wood pigeon *Columba palumbus* in England and the flock pigeon *Phaps histrionica* of Australia (Murton 1965, Goodwin 1977, Frith 1982, Rowan 1983, Skutch 1991). During the breeding season birds may be distinctly territorial, as in the South African rameron pigeon *Columba arquatrix*, or gregarious, as in the South African green pigeon *Treron australis* (Rowan 1983). Pigeons that typically nest in colonies include the white-winged dove *Zenaida asiatica*, the eared dove *Zenaida auriculata* and the flock pigeon (Cottam & Trefethen 1968, Goodwin 1977, Frith 1982). Mourning doves may also nest in densities suggestive of colonial nesting where social hierarchies within assemblages exist (Sayre *et al.* 1993). Monogamy is found in all columbids studied (Blockstein & Westmoreland 1993) and is probably due to the necessity of both parents for incubation and rearing (Birkhead & Møller 1996). Pigeons remain monogamous for the duration of the breeding season, some of which may re-pair in the following season, or mate for life as in feral pigeons *Columba livia* (Johnston & Janiga

1995). Long-term studies of the laughing dove *Streptopelia senegalensis*, Cape turtle-dove, red-eyed dove *Streptopelia semitorquata* and rock pigeon *Columba guinea* also suggest that pairs mate for life (Rowan 1983). In other species, such as the wood pigeon, bonds are known for several seasons (Cramp 1985).

Pink pigeons are socially monogamous and can maintain long stable pair bonds. Observations suggested that pairs remained together when not breeding but that some pairs were less stable than others. Breeding pairs remained together for more than one year in 42% of cases. A one-year period could cover part of two breeding seasons and about 50% of pairs were together for at least part of two breeding seasons.

In feral pigeons, very old and very young individuals are avoided as mates (Burley & Moran 1979). The reproductive performance of very young birds is poor relative to older birds (Johnston & Johnson 1990) and, likewise, very old pigeons (more than seven years) have reduced performance (Levi 1974, Burley & Moran 1979). When a choice is available, feral pigeons choose adults that are not too old (Johnston & Janiga 1995). Many pink pigeons paired with mates of a similar age and 190/245 (77%) of pairings were between birds that were within one year old of each other. This was probably a consequence of a large number of birds released as juveniles that matured at the same time, and the age structure of the population that skewed towards similar aged younger birds (see Figure 6.5, Chapter 6). A small population (particularly early in the programme) may have also affected mate choice, as few birds were available as mates. However, some older birds paired with much younger mates. Fifteen older males (mean age 5.2 ± 1.5 years) were paired with younger females (mean age 0.9 ± 0.6 years), the mean age difference between the mates of each pair being 4.2 ± 1.4 years. Similarly, nine older females (mean age 6.9 ± 2.0 years) were paired with younger males (mean age 1.5 ± 1.0), the mean age difference being 5.4 ± 2.2 years. As the age distribution of the population becomes more stable, the effect of age in mate choice should become clearer.

Divorce in birds occurs due to desertion by a mate (for a better option), usurpation (where one mate in a pair is forced out by new bird) and pre-emption (in migratory species) and there are at least 11 different hypotheses to explain divorce and mate fidelity in birds (review in Black 1996). In the pink pigeon, 41% of pairings were terminated by divorce and 59% by death of one of the mates. Divorce in pink pigeons probably occurred by desertion and usurpation. Reasons for divorce may have included incompatability of a pair, poor reproductive success, better options of mates, errors in original mate choice and poor quality territories. In captive pink pigeons incompatability is one of the main restrictions to successful breeding (Jones *et al.* 1983), which included platonic pairs that did not breed and aggressive pairs in which one bird, usually the female, would chase the other and possibly kill it if it was not removed.

High mortality creates vacancies within pairs and it is logical to suggest that divorce rate may increase with mortality rate, although in recent studies this has not proved conclusive (Birkhead & Møller 1996). In the pink pigeon pair formation and egg laying can occur at only a few months old. High juvenile mortality may disrupt early pair formation, which may have reproductive consequences in later life. Mortality in breeding pairs would have provided a pool of experienced birds but whether this increased divorce in already mated pairs is unknown. During the release programme, newly released juveniles provided a source of potential mates. Birds that paired in the early stages of the programme had a limited choice of mates owing to the small population size. As an increasing number of potential mates became available, divorce rates may have increased. As nesting density increased, frequent territorial fights occurred between males in adjacent territories. High divorce rates and territorial fights were thought to be contributing to poor reproductive success and was one of the reasons that releases were stopped in 1997.

As in many bird species divorce in pink pigeons, and consequently pair formation, appeared to be driven by the female (Ens *et al.* 1996). This is also the case in feral pigeons (Johnston & Janiga 1995). In pink pigeons the period after death or divorce to re-pairing was often very short and some females were found with new males less than one week after a squab from their previous nest had fledged. The incidence of divorce was expected to be higher in released pairings than wild pairings. Captive-reared released birds probably show some behavioural deficiencies owing to rearing methods. Most released birds were reared by foster-parents in small breeding cages and both foster and parent-reared birds were removed from their parents by 30 to 40 days old. Wild-fledged juveniles associate with their parents for up to two to three months after fledging, although supplementary feeding has reduced the reliance of fledged juveniles on their parents for food. In captive pink pigeons there is some evidence that reproductive problems in adulthood may be exacerbated by foster-rearing practices, for example, by denying squabs early interactions with twig nesting material (Perez-Rivera 1987). This study did suggest that, at least in pairings of less than one year duration, divorce may be more frequent in pairs of released birds than wild birds.

Mortality rates of wild and released birds and the different mortality rates of birds between sub-populations were expected to affect the length of pairings. Poor survival of pairings at

Ile aux Aigrettes was probably due to the poor survival of birds at this site. However, poor survival of birds at Brise Fer was not reflected in the survival time of pairings, which was similar to other mainland sites. At Brise Fer individual pairings may persist for longer due to a lower divorce rate. Pairings comprising wild birds seemed to survive for longer than pairings comprising released birds, which was probably due to better survival of wild birds than released birds (Chapter 3), but the evidence was not conclusive. The numbers of released and wild pairings in each sub-population and the effect of different habitat quality between sites confounded the results. There were no released pairs at Pigeon Wood and there were fewer wild pairs at Bel Ombre and Ile aux Aigrettes, whose populations were established more recently.

Pairing outcomes were difficult to interpret owing to the variation in individual pairing lengths and the different ages of birds in pairings. Statistical comparisons were made between ongoing pairs and pairs that terminated because of death or divorce. Not all ongoing pairs had been exposed to the risk of death or divorce for the same length of time. Sample sizes were too small to analyse the pairing outcome within each year paired, particularly for sub-sets of birds (released or wild or at different sub-populations). Pairings that ended in death were probably affected by the individual ages of the birds, and pairings involving at least one mate younger than one year old was more likely to end in death due to the higher juvenile mortality rate. A low mortality rate may result in a higher divorce rate, and mortality may contribute to divorce by providing surplus breeding birds. Without the effects of divorce, all pairings will eventually end in death and the mortality rate will just influence for how long they persist. It is expected that as the population achieves a more stable age distribution, a slower growth rate and as more wild-fledged birds form breeding pairs, divorce may be less common and longer pair bonds may persist with subsequent benefits for reproductive success (Chapter 6).

Extra-pair copulations

Extra-pair copulations were frequently observed but were not studied in detail. Some males mounted submissive birds (either females or juveniles) but this was thought only to be a male dominance behaviour, and coition probably did not occur. Extra-pair copulations and extra-pair paternity are now recognised as occurring routinely in many species of birds but are usually low in species where male parental care is essential (Birkhead & Møller 1996), as in pigeons. Extra-pair copulations were only occasional in feral pigeons and were not thought to contribute to divorce (Johnston & Janiga 1995). A female's choice of mate is often constrained and in pigeons, for example, the importance of male parenting skills may be paramount. Extra-pair copulations enable a female to modify her choice of partner and may result in genetic benefits to her offspring or may be a precursor to mate change. What role extra-pair copulations have in the breeding behaviour of pink pigeons and if they resulted in extra-pair paternity is unknown and deserves careful study.

Unisexual pairings

Male unisexual pairings behaved in some ways as heterosexual pairings, with one bird assuming more of the 'female' role. Unisexual pairings may be due to the inability of an individual to recognise the sex of the other owing to plumage or behavioural deficiencies. However, in some cases, particularly early in the programme, it may also have been caused by a limited availability of females. Mutual preening and copulation was observed between 'pairs'. Unlike heterosexual pairings both birds collected nest material and built the nest. Male unisexual pairs typically sat intermittently on the nest until it was abandoned. Unisexual pairs were known to maintain a bond for up to five months and build several nests. Most males were young (about one year old or less) except one old bird which paired with another male early in the release programme.

Females and eggs

The youngest and median age at which females first laid eggs were comparable to that known for captive birds (Jones 1995), which suggested that first recorded nests of wild pairings were accurate. The earlier first laying date recorded at Ile aux Aigrettes could be due to more accurate monitoring of pairings. Mean clutch size of eggs on Ile aux Aigrettes falls between recorded figures for captive pairs of 1.76, 1.65 (Jones 1987) and 1.58 (Jones 1995). Mean clutch size declined with age, which was also found for captive birds after four years old (Jones 1995). Although the usual clutch size for pink pigeons is two eggs, they lay a high proportion of single egg clutches which is unusual in other pigeon species which normally lay either one or two eggs (Rowan 1983, Jones 1995). Fertility was slightly higher in this study than for captive birds. This may have been because the captive population included more older birds.

Breeding seasonality

The published accounts of the pink pigeon's breeding season (Jones 1987) do not mention the lack of breeding activity in the months of cyclone activity. Jones (1987) suggested that the peak breeding occurred January to June and decreased during the drier winter months. Staub (1976) suggested year round breeding with seasonal peaks. At Pigeon Wood, from which the early accounts were described, there was little breeding during the winter months, probably because this is the coldest and wettest site. On pristine Mauritius the breeding season was probably the same as was seen in this study, with a marked non-breeding period in the wettest months (February and March) when the risk of cyclones is greatest. The breeding seasonality seen in pink pigeons was comparable with other species of tropical pigeons (Frith 1982, Rowan 1983).

Conclusions

It has been difficult to compare the reproductive ecology of released birds with truly wild birds, to indicate how well released birds have re-adapted to the wild, because the wild population were not breeding in native forest. The ecology of the remaining wild population will not have represented their ecology in pristine Mauritius, owing to the small population size, habitat loss and habitat degradation. It has only been through studies of birds released into native forest areas, and their progeny, that pink pigeon reproductive ecology has been better understood. These studies have highlighted some current problems for the species, such as low fertility which may limit the population growth, but have also indicated that pigeons can utilise a variety of habitat types in which to nest. This will be very important for the long-term survival of the species.

Chapter 5

Nest success and causes of nesting failure

INTRODUCTION

Nest success in the pink pigeon is very poor and has been implicated in the decline and rarity of this species (McKelvey 1976, Collar & Stuart 1985, Jones 1987, Jones & Owadally 1988). In this chapter nest success and the causes of nesting failure are examined in relation to site, seasonal and annual differences, rearing origin and inbreeding.

METHODS

The methods for monitoring nests and breeding pairs are described in Chapter 4. A breeding attempt was defined as one where an egg or eggs were laid. Data from Ile aux Aigrettes provided information on fertility and hatchability, which was not available at mainland sites.

Proportion of birds breeding

A census of breeding age individuals (more than one year old) was calculated for the 31st December of each year, to obtain an estimate of the number of birds breeding per year as a proportion of the total number of breeding age birds. Released birds were only included in the census if they were at full liberty (more than one month after first released). The number of individuals alive at the end of each year and that bred within each year was calculated as a proportion of the total number of breeding age birds alive at the end of the year. This indicated a general trend but there were some birds that bred within the year, which were dead at the end of year census, which were not accounted for.

Nest success

Nest success was estimated for nests in all four sub-populations up to 1998. At Pigeon Wood and Brise Fer nest success was calculated from 1992, at Ile aux Aigrettes from 1994 and at Bel Ombre from 1996. Prior to 1992, sample sizes at Brise Fer and Pigeon Wood were very small. Where sub-sets of data have been used, the years are referred to in the relevant sections. Excluded from the analyses were 49 nests that were manipulated at the egg or brood stages. Nests where squabs were rescued were included in the analyses and, since the squabs were unlikely to have survived, the day of rescue was treated as the date failed. Nest success was calculated following Mayfield's method (Mayfield 1961, 1975) and only nests where eggs were laid were considered. Nest success was calculated for the incubation period (14 days from egg-lay date, Jones 1995), nestling period (23 days from hatch date) and overall success from the start of incubation to fledging. Confidence limits were calculated following Johnson (1979). The outcome of a nesting attempt was classified as successful, failed or unknown. A successful nest was one that fledged at least one young. The kinship coefficient of a pairing is the inbreeding coefficient of a pair's progeny and was calculated for pairs at Brise Fer, Bel Ombre and Ile aux Aigrettes as described in the methods in Chapter 3. Where a pairing did not produce progeny, the kinship coefficient was obtained from the trial pairing facility of the database. Kinship coefficients of pairings are shown in Appendix 5.

Breeding success was also calculated for Ile aux Aigrettes using absolute numbers of eggs laid, squabs hatched and young fledged and was compared with rates for captive birds. At all sites wild-fledged young were ringed on the nest or after fledging as described in the methods in Chapter 3.

Squab survival on Ile aux Aigrettes

Survival of squabs to fledging on Ile aux Aigrettes between 1994 and 1998 was calculated using Kaplan-Meier estimates of survivor function (Chapter 3). Squabs removed into captivity before fledging were treated as censored data. In broods of two, when it was not known if a squab was first-hatched or second-hatched, the second-hatched squab was taken as the one with the lower mass. When analysing the effects of brood size on squab survival, nests involved in foster attempts (whether donating or receiving a squab) were excluded. A comparison of squab mortality between seasons was made using absolute numbers of squabs that died. Inbreeding coefficients were obtained for squabs using the database described in Chapter 3, and are shown in Appendix 6.

Causes of nest failure and squab mortality

For nests where eggs were laid and which failed, a cause of failure was recorded. Where the cause was unknown, evidence of nest failure was described. Evidence of nest failure included remains of eggs or squabs in the nest or close to the nest tree, destruction of the nest, rat or monkey faeces in or close to the nest, observations of predators at the nest, unhatched eggs in the nest or the disappearance of eggs or squabs. Nests that failed due to rat or monkey predation were only assigned where there was good evidence. At mainland sites, cause or evidence of failure was determined for individual nests. On Ile aux Aigrettes, where nests were easily accessed and regularly inspected, causes of individual squab mortality were also recorded. Some squabs on Ile aux Aigrettes were treated for disease which affected the results. Nest data for Ile aux Aigrettes was compared to mainland sites to highlight causes of failure in the absence of predators.

Statistical analyses

Nest data were analysed for each sub-population and, where relevant, data were pooled for all sub-populations. Analysis of variance (ANOVA) was used in MINITAB (8.21, 1991) to test the differences in nest success between incubation and nestling phases, annual and seasonal nest success at different sites, nest success between pairs with different rearing origins and the effect of inbreeding. Repeated measures of alternate nests were used to increase the sensitivity of the test and were used to investigate interaction effects between some of the variables. Repeated measures were not used when testing for differences in nest success between incubation and nestling phases within sites, nor when testing the effect of inbreeding on nest success because sample sizes were too small. Nest data were arcsine transformed. A Spearman's rank correlation was used to test the relationship between the mean monthly nest success and mean monthly rainfall. Kaplan-Meier estimates of squab survival were compared using Cox's proportional hazards model (Chapter 3) and a Chi-squared test was used to compare seasonal squab survival. All mean values are followed by the standard deviation (± SD).

RESULTS

Accuracy of the data

Not all nests were found. The total number of fledglings caught and ringed provided a measurement against which the completeness of the nest data could be assessed. Of 1490 nests found, 1042 had eggs and 330 young fledged from 287 nests. The number of unringed young caught was 429. Figure 5.1 shows the annual number of young fledged from known nests and the number caught and ringed. The total number of nests with eggs from which 429 young had fledged was calculated as 1355 ((429 + 330) x 1042). Applying this calculation to the annual number of nests, the percentage of nests found each year at each site averaged 77% ± 24% between 1990 and 1998.

Data for 1997 and 1998 from Pigeon Wood were incomplete. In 1997 69% of breeding age females and 58% of breeding age males were known in breeding pairs but only 24% of nests were found. In 1998, 43% of breeding age females and 52% of males were known in breeding pairs but only 20% of nests were found. This was due to young birds moving out of the Pigeon Wood to breed in a nearby pine plantation which was difficult to access and due to inadequate monitoring of known pairs. Data were also inadequate in 1998 at Bel Ombre when 66% of adult birds were known in breeding pairs but only 44% of their nests were monitored.

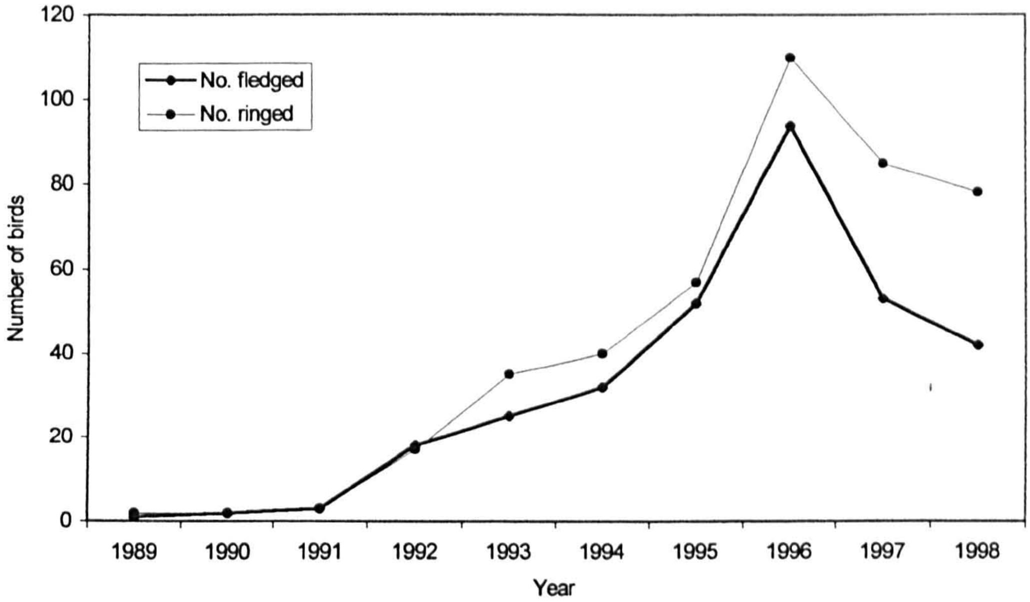

Figure 5.1 Number of young fledged from nests and the number ringed, all sites 1989-98. Number fledged is from observed nests. Fledge date is plotted for both number fledged and number ringed. For birds not ringed on the nest, fledge date was calculated as 23 days from hatch date.

Proportion of non-breeding birds

Not all birds of breeding age bred. Some birds did not form breeding pairs and some pairs built nests but did not produce eggs. Some breeding birds did not breed every year. Thirty-one pairings involving 30 females and 27 males built nests but did not produce eggs. Of these, 16 females did not lay eggs in other pairings and eight males were in other pairings where eggs were not laid. Many of these pairings had few nest attempts before the pairing split but several pairings of more than six months duration resulted in three to seven nest attempts with no eggs produced. Of potential breeders (birds which survived more than one year old), 55 males (28%), 39 females (22%) and 25 birds of unknown sex did not breed (i.e. lay eggs) (mean 119/401, 30%). Figure 5.2 shows the proportion of birds that never bred and those that did breed but were not in a breeding pair for at least one year. From 1994, the non-breeding portion of the adult population (more than one year old) was relatively consistent between years (Figure 5.3). Between 1992 and 1998 a mean of 81% ± 8.9% adult females and 73% ± 9.1% adult males were paired each year. Data for Pigeon Wood_females in 1998 and for Pigeon Wood males in 1997 and 1998 were excluded.

Proportion of nests with eggs

On average 60% of all nesting attempts resulted in one or two eggs laid but the proportion of nests resulting in eggs was much higher at Ile aux Aigrettes than at mainland sites (Table 5.1). Pairings that produced eggs did not produce them at every nesting attempt. At mainland sites, pairings with 10 or more nests on average produced eggs in every 2.0 ± 1.3 nesting attempts (Table 5.2). The proportion of nests that resulted in eggs was similar for

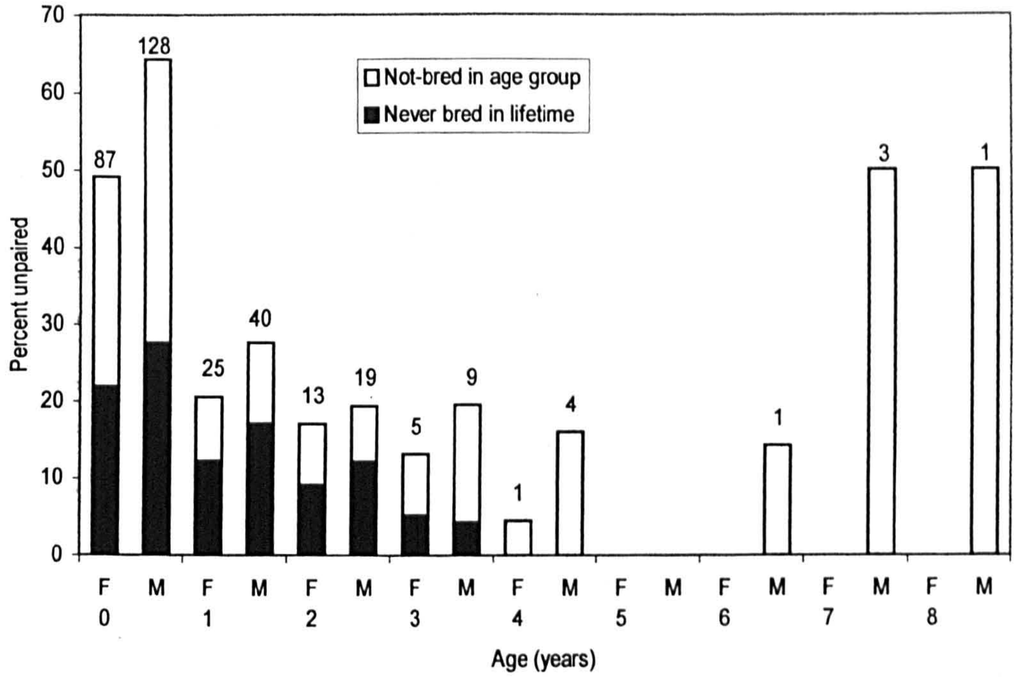

Figure 5.2 Proportion of non-breeding birds per age group, all sites 1987-98. Breeding was defined as egg-laying. Not-bred in age group was birds which did breed but were not recorded breeding in that age group. Never bred in lifetime included birds which built nests but did not lay eggs. M = male, F = female. Figures are total number of birds that did not breed.

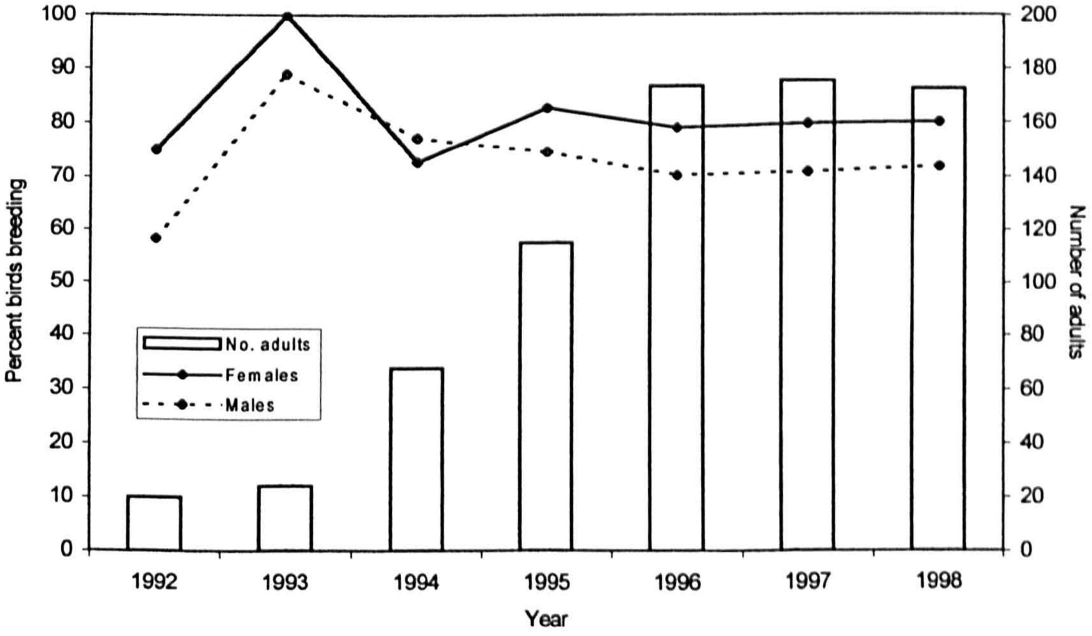

Figure 5.3 The number of pink pigeons breeding per year as a proportion of all birds of breeding age (more than one year old), all sites 1992-98.

these pairs (61% at mainland sites, 97% at Ile aux Aigrettes) as for all pairs. It was not known why the proportion of eggs laid at mainland sites was smaller than at Ile aux Aigrettes but some mainland nests likely failed before eggs were detected.

Table 5.1 Number of nests per pairings where eggs were laid (including pairs not known to produce eggs).

Site	No. of years	No. nests	No. nests with eggs	% nests with eggs
Brise Fer	11	572	346	60
Pigeon Wood	10	272	188	69
Bel Ombre	4	283	166	59
Ile aux Aigrettes	5	363	342	94
Total	11	1490	892	60

Table 5.2 Number of nests per pairing resulting in eggs, in pairings with ten or more nesting attempts.

Site	No. nests	No. pairings	No. nests with eggs	Percentage with eggs	No. nests per pairing resulting in eggs
Brise Fer	261	17	157	60.1	2.1 ± 1.3
Pigeon Wood	120	9	84	70.0	1.8 ± 1.3
Bel Ombre	82	5	42	51.0	2.3 ± 1.4
Ile aux Aigrettes	191	12	185	96.8	1.0 ± 0.1

Number of nests with eggs per year per pair

Pink pigeons re-nested several times during a year. In pairings of more than six months duration ($\geq$ 180 days) between 1992 and 1998, 830 nests where eggs were laid were known from 144 pairings. The mean number of nests per year was 118.6 ± 65.8 and the mean number of pairings where eggs were laid per year was 39.9 ± 23.2. The number of nests ranged from 1-11 per pairing per year. The mean number of nests with eggs per pairing per year ranged from 2.5 ± 1.6 - 3.9 ± 2.4, and was overall 3.0 ± 2.1. Fifteen pairings of less than 180 days duration were recorded with a mean 3.7 ± 0.72 nests with eggs per pairing over a mean pairing length of 134 ± 36 days. One pairing at Brise Fer had four nests with eggs in 50 days.

Nest success

Differences in nest success between incubation and nestling phases

Kaplan-Meier estimates of survivor function were plotted for the incubation and nestling phases (Figure 5.4). A mortality rate of nests (and consequently a survival rate) was calculated for each day as the number of nests that failed as a proportion of the number of nests under observation. The number of nests under observation each day changed, depending on the age at which nests failed (and therefore left the data set) and new nests were found (and entered the data set). The number of nests at risk was therefore adjusted to account for the variable number of nests under observation. Nest success was significantly poorer for the incubation phase than for the nestling phase when data for all sites were pooled (Figure 5.4). This difference was most marked at Pigeon Wood and Brise Fer but was only significant at Brise Fer ($F_{1,12} = 21.01$, $P < 0.001$), where year also had a significant effect ($F_{5,12} = 5.11$, $P = 0.01$). Interaction effects were significant between incubation and brooding and year at Pigeon Wood ($F_{6,14} = 4.11$, $P \cong 0.01$) and Ile aux Aigrettes ($F_{4,10} = 4.97$, $P \cong 0.01$). There was a drop in nest success at day 14 due to unhatched eggs (infertile or embryo death) and death at hatching.

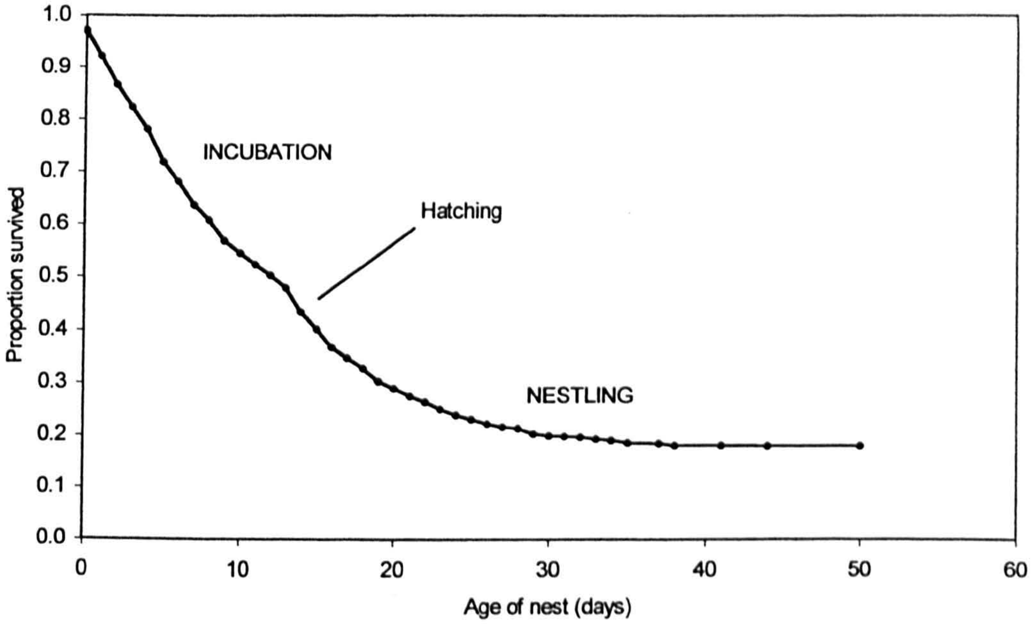

Figure 5.4 Survivorship of nests from incubation to fledging, all sites 1988-98. Kaplan-Meier estimates of survivor function plotted as a proportion of nests observed per day. Sample size was 964 nests (no censored data). Nest success was significantly poorer for the incubation phase than the nestling phase ($F_{1,14} = 4.84$, $P < 0.05$).

Annual nest success in different sub-populations

There was considerable annual variation of nest success within sites and overall mean annual nest success for 929 nests was 18.4% ± 5.1% (Table 5.3) (Figure 5.5). Data from Pigeon Wood, Brise Fer and Ile aux Aigrettes between 1994 and 1998 were used to test for significant differences in nest success between sites and years. The same test for all sites and all years could not be carried out due to years with missing data, which this subset excluded. A two-way ANOVA failed to show any significant differences in overall nest success between sites and between years (Table 5.4). However, during the incubation period, both site and year had a significant effect on nest success and there were significant

Table 5.3 Nest success in different sub-populations (Mayfield estimates).

Site	Years	No. Nests	No. failed	Incubation			Nestling			Incubation – fledging		
				% nest success	95% confidence limits		% nest success	95% confidence limits		% nest success	95% confidence limits	
Pigeon Wood	1992-98	150	96	44.2	36.2	53.6	59.1	48.2	71.0	26.1	17.4	38.1
Brise Fer	1992-98	320	252	28.5	24.0	33.6	52.4	42.0	62.8	14.9	10.4	21.9
Ile aux Aigrettes	1994-98	315	224	45.3	39.6	51.7	44.9	38.2	53.3	20.3	15.1	27.6
Bel Ombre	1996-98	144	119	40.2	31.6	51.0	39.2	27.9	54.6	15.7	8.8	27.8
Total	1992-98	929	691	37.9	34.8	41.4	48.5	43.7	53.8	18.4	15.3	22.1

Table 5.5 Seasonal nest success, mainland sites 1992-98 (Mayfield estimates).

Season	No. Nests	No. failed	Incubation			Nestling			Incubation - fledging		
			% nest success	95% confidence limits		% nest success	95% confidence limits		% nest success	95% confidence limits	
January-April (hot, wet)	116	82	31.8	23.9	41.8	60.0	46.0	78.0	19.1	11.0	32.6
May-August (cool winter)	271	196	36.9	31.3	43.2	57.6	48.3	67.8	21.3	15.1	29.3
September-December (hot, dry)	262	215	31.2	26.0	37.3	43.1	33.8	54.8	13.5	8.8	20.4

Table 5.6 Seasonal nest success at Ile aux Aigrettes, 1994-98 (Mayfield estimates).

Season	No. Nests	No. failed	Incubation			Nestling			Incubation - fledging		
			% nest success	95% confidence limits		% nest success	95% confidence limits		% nest success	95% confidence limits	
January-April (hot, wet)	70	51	34.8	24.5	48.6	50.2	34.6	74.2	17.5	8.5	36.1
May-August (cool winter)	100	75	47.9	38.3	60.2	42.5	31.2	56.6	20.3	11.9	34.1
September-December (hot, dry)	145	98	49.3	40.7	60.1	44.8	35.5	57.3	22.1	14.4	34.4

interaction effects. During the nestling period, only year significantly affected nest success but there were also significant interaction effects.

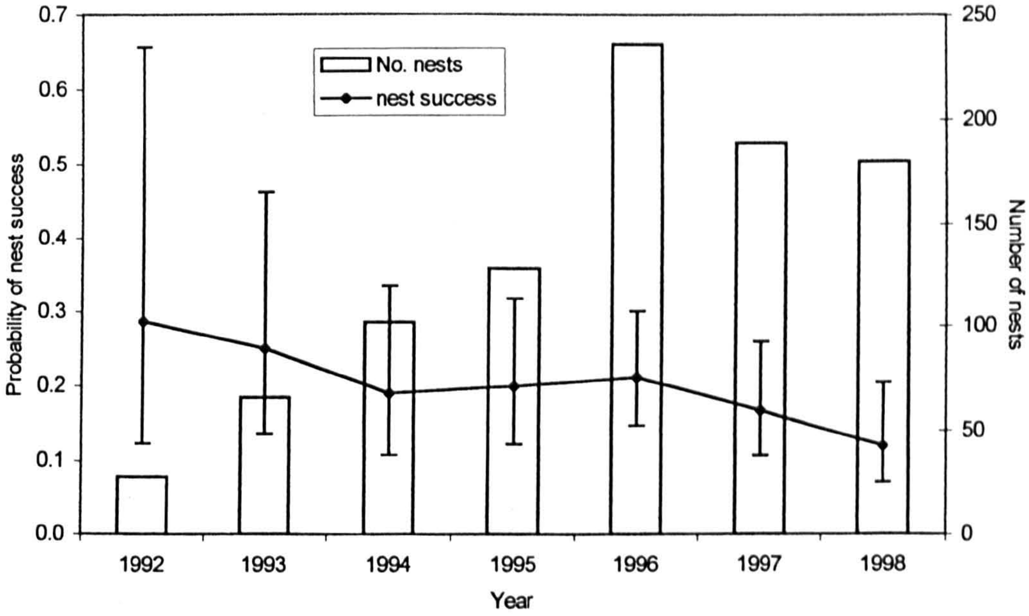

Figure 5.5 Mean annual nest success of pink pigeons, 1992-98. Data from all sites pooled. Error bars are 95% confidence limits.

Table 5.4 Effect of site and year on nest success at Pigeon Wood, Brise Fer and Ile aux Aigrettes 1994-98 (excluded years with missing data). df = degrees of freedom, F = F statistic, P = probability.

Variable	Source	Sum of squares	df	Variance	F	P
Overall nest success (incubation to fledge)	Site	0.12251	2	0.06126	2.77	> 0.05
	Year	0.10223	4	0.02556	1.16	> 0.05
	Site and year	0.31051	8	0.03881	1.76	> 0.05
	Error	0.33113	15	0.02208		
Incubation period	Site	0.33595	2	0.16798	4.37	< 0.05
	Year	0.55902	4	0.13975	3.63	< 0.05
	Site and year	0.89516	8	0.11189	2.91	< 0.05
	Error	0.57677	15	0.03845		
Nestling period	Site	0.45278	4	0.11319	2.38	> 0.05
	Year	0.46476	2	0.23238	4.90	< 0.05
	Site and year	1.60837	8	0.20105	4.24	< 0.01
	Error	0.71198	15	0.04747		

Seasonal nest success

Seasonal trends in overall nest success were influenced by differences in success during incubation and nestling phases. At mainland sites, overall nest success was highest in the winter period (May to August) and poorest in the dry season (September to December) (Table 5.5) but at Ile aux Aigrettes nest success was lower in the wet season (January to April) and higher in the dry season (Table 5.6). Overall nest success was significantly different between sites but not between seasons and there were no significant interaction effects (Table 5.7). During the incubation period, site and season significantly affected nest success and there were significant interaction effects. Significant seasonal and site effects were not seen during the nestling period. Seasonal differences were significant at Brise Fer ($F_{2,3} = 13.3$, $P < 0.05$) where overall nest success was highest in the winter (19.5%) and lowest in the dry season (8.3%). At Brise Fer nest success in the dry season during both the incubation period (19.5%) and the nestling period (42.7%) were poorer than at other times of the year. There was no significant seasonal trend in mean monthly nest success with mean monthly rainfall (Spearman's rank test, $r_s = 0.583$, $P > 0.05$).

Table 5.7 Effect of site and season on nest success in pink pigeons, all sites 1988-98. df = degrees of freedom, F = F statistic, P = probability.

Variable	Source	Sum of squares	df	Variance	F	P
Overall nest success (incubation to fledge)	Site	0.06112	3	0.02038	5.93	= 0.01
	Season	0.01323	2	0.00662	1.92	> 0.05
	Site and season	0.01490	6	0.00248	0.72	> 0.05
	Error	0.04126	12	0.00344		
Incubation period	Site	0.11608	3	0.03869	14.2	< 0.001
	Season	0.03397	2	0.01699	6.26	≅ 0.01
	Site and season	0.05953	6	0.00992	3.65	< 0.05
	Error	0.03258	12	0.00272		
Nestling period	Site	0.22910	3	0.07637	2.16	> 0.05
	Season	0.07576	2	0.03788	1.07	> 0.05
	Site and season	0.05011	6	0.00835	0.24	> 0.05
	Error	0.42392	12	0.03533		

Variation in nest success between pairs with different rearing origins.

Overall nest success was significantly poorer for pairs of released birds than pairs of wild-fledged birds, when data for all sites were pooled (Table 5.8 and Table 5.9). Where a pair comprised one released and one wild bird, there was no significant difference in nest success to pairs of released birds or to pairs of wild birds, although the latter result was marginal. Nest success of released pairs that had been foster-reared was not significantly different to released pairs comprising one foster-reared and one parent-reared bird ($F_{1,12} = 0.78$, $P > 0.05$).

Table 5.8 Nest success in pairs with different origin and rearing methods, 1992-98 (Mayfield estimates).

Rearing method of mates in pair	No. nests	No. failed	% nest success	95% confidence limits	
Released pair	429	342	16.0	11.7	21.5
Wild fledged pair	286	186	23.2	16.8	31.1
One mate released, one mate wild fledged	227	172	17.1	11.4	25.1
Released pair – both foster-reared	239	195	14.5	4.1	22.1
Released pair – both parent-reared	16	12	17.5	-	-
Released pair – one foster-reared, one parent-reared	126	99	17.1	9.9	29.0

Table 5.9 Effect of rearing origin of birds on nest success, all sites 1992-98.

Variable	Source	Sum of squares	df	Variance	F	P
Released pairs vs wild pairs	Rearing origin	0.05015	1	0.05015	14.69	< 0.01
	Year	0.09297	5	0.01859	5.45	< 0.01
	Origin and year	0.11615	5	0.02323	6.81	< 0.01
	Error	0.04096	12	0.00341		
Released/wild pairs vs released Pairs	Rearing origin	0.00065	1	0.00065	0.07	> 0.05
	Year	0.02659	5	0.00532	0.59	> 0.05
	Origin and year	0.01311	5	0.00262	0.29	> 0.05
	Error	0.10826	12	0.00902		
Released/wild pairs vs wild Pairs	Rearing origin	0.04733	1	0.04733	4.21	> 0.05
	Year	0.13250	5	0.02650	2.36	> 0.05
	Origin and year	0.07529	5	0.01506	1.34	> 0.05
	Error	0.13486	12	0.01124		

Nest success and inbreeding in released sub-populations

Nest success was lowest in pairings with high levels of inbreeding (kinship coefficients ≥ 0.25) (Table 5.10). Nest success was significantly affected by inbreeding (Table 5.11). This was mostly seen during the nestling phase where nest success of highly inbred pairings was significantly poorer than non-inbred pairings ($F_{1,5} = 11.11$, $P < 0.05$). A higher nest success during the incubation phase in highly inbred pairings could not be explained.

Table 5.10 Nest success and inbreeding in released sub-populations, 1993-98. Kinship coefficient of pairings: non-inbred = 0, inbred > 0 and < 0.25, highly inbred ≥ 0.25.

Kinship coefficient of pairings	No. Nests	No. failed	Incubation phase % nest success	Incubation phase 95% confidence limits		Nestling phase % nest success	Nestling phase 95% confidence limits		Inc – fledge % nest success
Non-inbred	110	90	37.7	29.8	47.9	43.9	31.0	62.5	16.6
Inbred	402	297	37.8	33.1	43.2	49.8	42.7	57.8	18.9
Highly inbred	70	54	45.5	33.9	60.2	27.9	16.5	46.8	12.7

Table 5.11 Effect of inbreeding on nest success in released sub-populations, 1993-98.

Source	Sum of squares	df	Variance	F	P
Inbreeding	0.021528	2	0.010746	4.26	≅ 0.05
Year	0.014450	5	0.002890	1.14	> 0.05
Error	0.025281	10	0.002528		

Breeding success on Ile aux Aigrettes

Figure 5.6 shows the annual and monthly trends in breeding success on Ile aux Aigrettes, where actual numbers of fertile eggs, number of squabs hatched and fledged from 34 females are plotted. A comparison of breeding success with captive birds indicated that hatchability of eggs was higher on Ile aux Aigrettes than in captivity but that fledging success from hatched eggs was lower (Table 5.12).

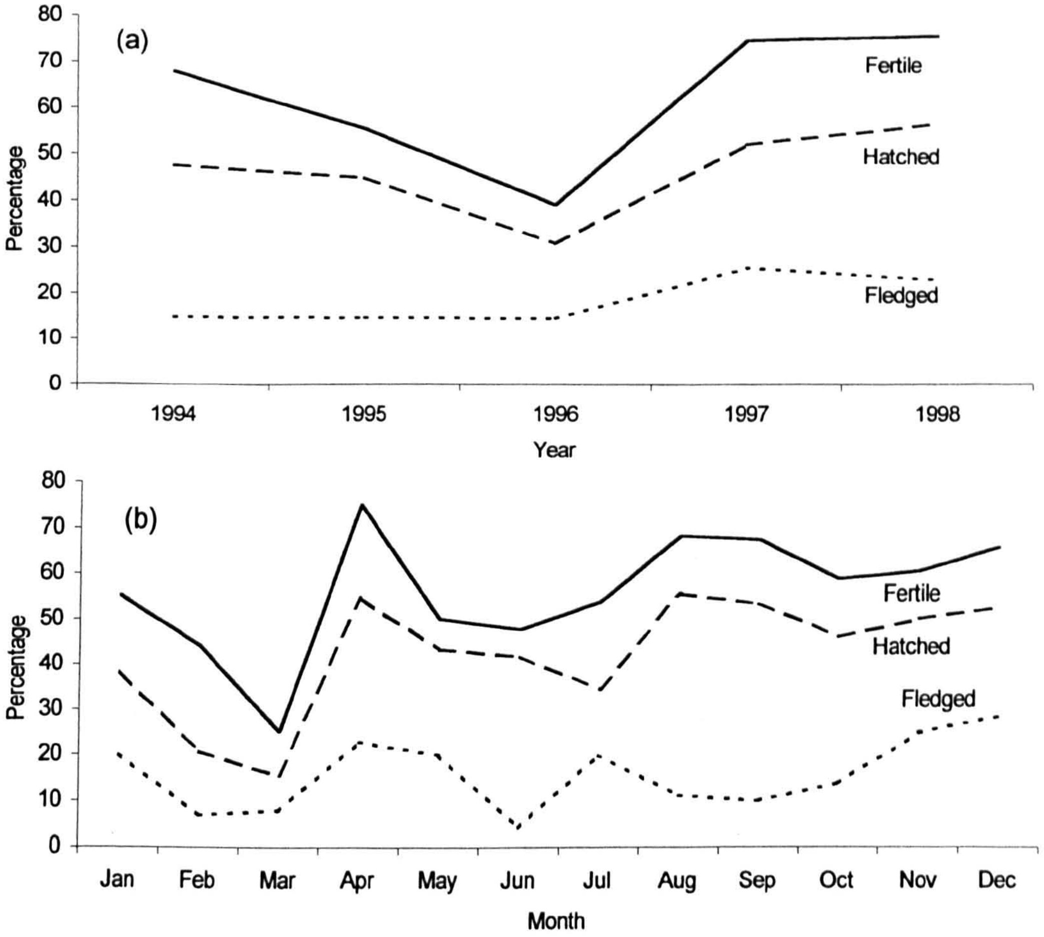

Figure 5.6 Trends in breeding success on Ile aux Aigrettes, 1994-98. (a) Overall rates of annual breeding success, (b) overall rates of monthly breeding success. Percentages of all eggs laid (excluding unknowns for percentage fertile). Sample size: 522 eggs laid, 485 where fertility known, 284 fertile, 233 hatched, 90 fledged.

Table 5.12 Breeding success of wild and captive pink pigeons. Data from Ile aux Aigrettes is from 1994-98 and Black River Aviaries from 1977-93.

Breeding success		Ile aux Aigrettes	Black River Aviaries (captive)
Overall rates	% fertile of known eggs	58.6	53.2
	% hatched of eggs laid	44.6	26.3
	% reared of eggs laid	17.2	16.2
Relative rates	% hatched of fertile eggs	82.0	65.8
	% reared of hatched	38.6	61.8
Number of eggs		522	1676

The effect of inbreeding on breeding success at Ile aux Aigrettes

There was no clear evidence that inbreeding in birds on Ile aux Aigrettes affected fertility or hatchability (Table 5.13). Fledging rates were higher in inbred pairings (> 0 and < 0.25) which could not be explained. The higher fertility and overall hatchability in pairings with high levels of inbreeding could not be explained.

Table 5.13 Breeding success and inbreeding in pairings on Ile aux Aigrettes, 1994-98. Kinship coefficient of pairings: non-inbred = 0, inbred > 0 and < 0.25, highly inbred ≥ 0.25.

Kinship coefficient of pairings	Number					Overall rates of breeding success			Relative rates of breeding success	
	No. laid	No. fertile	No. known	No. hatched	No. fledged	% fertile of known	% hatched of laid	% fledged of laid	% hatched of fertile	% fledged of hatched
Non-inbred	110	60	105	48	12	57.14	43.64	10.91	80.00	25.00
Inbred	348	179	318	147	67	56.29	42.24	19.25	82.12	45.58
Highly inbred	49	36	47	30	7	76.60	61.22	14.29	83.33	23.33

Squab survival on Ile aux Aigrettes

Mean survival of squabs to fledging (up to 30 days) was 43% (n = 270). There were no significant seasonal differences in survival (hot wet: January to April, cool winter: May to August, hot dry: September to December) ($\chi^2_2 = 0.836$, $P > 0.05$). Overall survival was significantly different for squabs in different brood sizes (Figure 5.7). This was mainly due to poorer survival of second-hatched squabs (19%). Survival of first-hatched squabs reared in broods of two (59%) was not significantly different to squabs reared singly (46%) (Wald = 1.29, df = 1, $P > 0.05$). Survival of second-hatched squabs was significantly poorer than survival of first-hatched squabs in broods of two (Wald = 14.4, df = 1, $P < 0.001$) and significantly poorer than squabs reared in single broods (Wald = 9.72, df = 1, $P \cong 0.001$). Survival of squabs reared in single broods from one egg clutches (51%, n = 55) and from two-egg clutches (41%, n = 65) was not significantly different (Wald = 0.883, df = 1, $P > 0.05$). Of 64 two-egg clutches where both squabs hatched, both squabs fledged from 10 (16%) nests.

Squab survival and inbreeding

When data were pooled for all squabs, inbreeding significantly affected survival (Figure 5.8). This was mostly because survival of highly inbred squabs (29%) was significantly poorer than survival of inbred squabs (48%) (Wald = 5.32, df = 1, $P < 0.05$), but was not significantly different to survival of non-inbred squabs (41%). Survival of inbred squabs was not significantly different to non-inbred squabs. When data were pooled for first-hatched squabs in broods of two and squabs reared in single broods, the pattern was similar to that for all squabs and differences in survival were significant (Wald = 2.31, df = 2, $P < 0.01$). This was mainly because survival of highly inbred squabs (29%) was significantly poorer than survival of inbred squabs (57%) (Wald = 12.30, df = 1, $P < 0.001$), but was not significantly different to survival of non-inbred squabs (52%) (Wald = 3.51, df = 1, $P > 0.05$). Survival of inbred squabs and non-inbred squabs was not significantly different (Wald = 2.59, df = 1, $P > 0.05$).

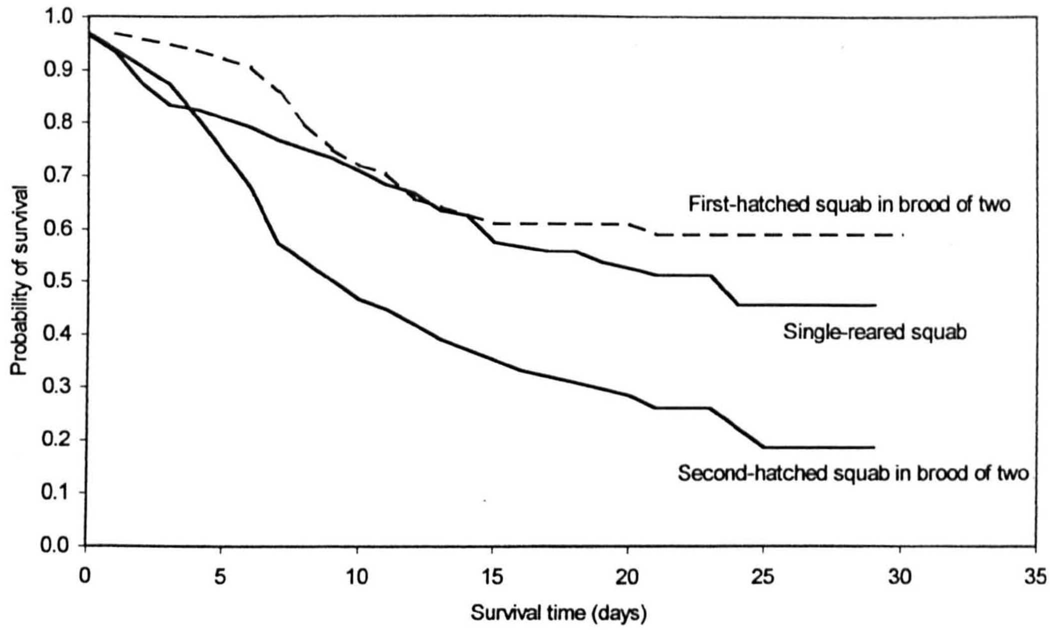

Figure 5.7 Survival of squabs to fledging (up to 30 days, mean 23 days) on Ile aux Aigrettes, 1994-98. Sample size: single broods 120, broods of two 64 (48% censored). Differences in survival were significant (Wald = 16.57, df = 2, $P < 0.01$).

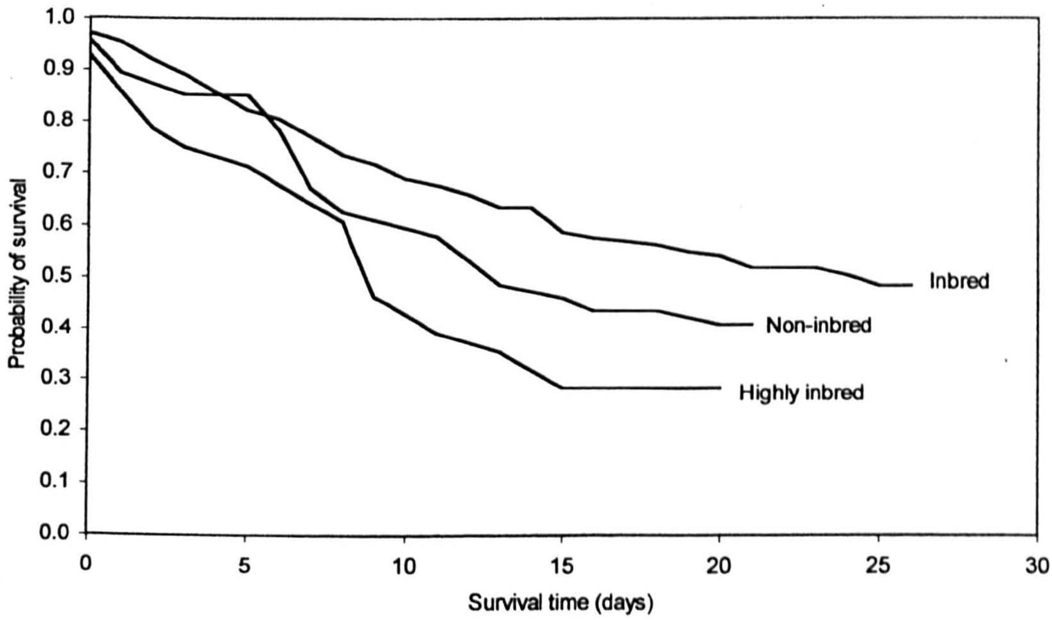

Figure 5.8 Effect of inbreeding on squab survival to fledging (up to 30 days, mean 23 days) on Ile aux Aigrettes, 1994-98. Data included 13 manipulated nests (19 squabs). Inbreeding coefficients: non-inbred = 0, inbred > 0 and < 0.25, highly inbred ≥ 0.25. Sample size: non-inbred 48, inbred 175, highly inbred 38 (49% censored). Differences in survival were significant (Wald = 6.48, df = 2, $P < 0.05$).

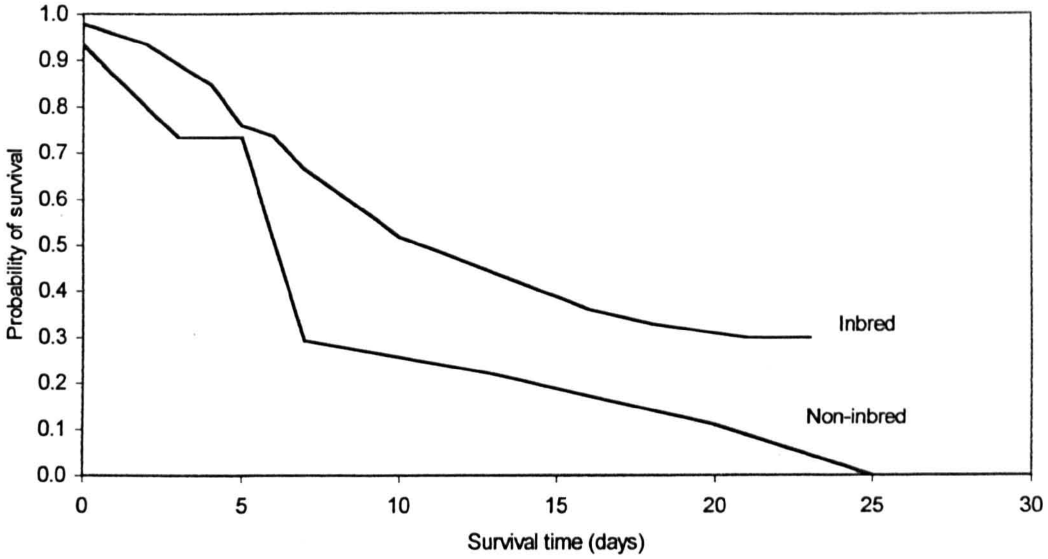

Figure 5.9 Effect of inbreeding on survival of second-hatched squabs to fledging on Ile aux Aigrettes, 1994-98. Inbreeding coefficients: non-inbred = 0, inbred > 0. Sample size: non-inbred 15, inbred 47 (31% censored). Survival of second-hatched non-inbred squabs was significantly poorer than second-hatched inbred squabs (Wald = 3.92, df = 1, $P < 0.05$).

When data for second-hatched squabs were analysed independently, non-inbred squabs showed significantly poorer survival than inbred squabs (25%) (data pooled for inbred and highly inbred squabs) (Figure 5.9). No non-inbred second-hatched squabs survived more than 25 days but sample sizes were small.

Causes of nest failure and squab mortality

Causes of nest failure during the incubation phase

At mainland sites, 25% of nests failed for a reason other than predation (Table 5.14), 8.8% failed due to predation leaving a further 66% that possibly failed due to predation. However, on Ile aux Aigrettes 56% of nests failed due to unhatched eggs, compared to 21% at mainland sites, and 44% on Ile aux Aigrettes failed due to reasons other than predation. At mainland sites evidence of smashed eggs was not sufficient to assume predation. Most smashed eggs found were on the ground and did not show characteristic signs of rat predation (Moors 1978).

Table 5.14 Frequency of nest failure during incubation, all sites 1988-98.

Outcome of nest	BF	PW	BO	IAA	All Sites
Predation (rats or monkeys)	17	10	7	0	34
Cyclonic weather	4	6	2	1	13
Smashed eggs found (predation/weather/behaviour)	106	26	42	14	188
Unhatched eggs (infertile/dead embryo) or failed at hatching	35	22	24	76	157
Poor incubation, desertion, disruption of nest	1	0	1	5	7
Parent dead/sick	0	0	2	1	3
Unknown	51	9	23	39	122
Total no. nests	214	73	101	136	524

Causes of nest failure during the nestling phase at mainland sites

At mainland sites, 46% of nests failed for a reason other than predation (including nests where dead squabs were found, which had not been depredated) (Table 5.15). Only six cases were definitely attributed to predation, leaving a further 48% that could have failed due to predation. Predators probably took many of the squabs that disappeared. In five cases of predation by monkeys evidence included remains of the squab found in and close to the nest, monkey faeces in the nest and in one case a monkey was found sitting in the nest. In one case of rat predation, the five-day old squab had disappeared and a rat was seen in the tree. Other causes of mortality, which also accounted for some of the cases where squabs were found dead, included poor parental care, hypothermia, inanition, bad weather and displacement from the nest. The latter could be caused by poor nest structure, poor parental behaviour, poor condition of the squab, bad weather and displacement by a second squab. In some cases a combination of factors (e.g. poor parental care, inanition and bad weather) led to mortality.

Table 5.15 Frequency of nest failure during the nestling phase at mainland sites, 1988-98. Nests with a brood of two included only those nests where one cause of failure was attributed. In one nest with a brood of two, one squab was found dead in the nest and the second disappeared. In four other nests with a brood of two, one squab was found dead on the ground and one squab disappeared.

Outcome of nest	Number of nests		
	Single squab	Brood of two	Total
Abandoned	2	0	2
Disease/deformity/inanition/injury	2	1	3
Cyclonic or bad weather	11	1	12
Dead in nest (unknown cause)	12	1	13
Dead on ground (unknown cause)	13	1	14
Disappeared (unknown cause)	45	3	48
Predation (rats or monkeys)	4	2	6
Live on ground (removed)	2	0	2
Total	91	9	100

Causes of squab mortality on Ile aux Aigrettes

Table 5.16 shows the causes or evidence of squab mortality on Ile aux Aigrettes and included nests with broods of two where only one squab died. Disease, associated with inanition or injury, was the main known cause of mortality and accounted for 39% of squab deaths. Many cases where squab remains were found, or where squabs disappeared, were probably also due to disease. In broods of two, 34% of second-hatched squabs disappeared and in single broods 31% of squabs disappeared. Squabs that disappeared were usually very young, 26 (55%) disappeared between 0 and three days old and remains were not found. There was one case of predation by a Mauritius kestrel *Falco punctatus* and one suspected case but the squab was also suffering from disease. Squabs removed from the nest suffered disease, injury, inanition and/or abandonment by the parents and were unlikely to survive. In some cases, one squab in a brood of two was removed to improve the survival of the remaining squab.

Table 5.16 Causes and evidence of squab mortality on Ile aux Aigrettes, 1994-98. First-hatched and second-hatched squabs refer to the squabs that died in a brood of two and included nests where only one squab died. In 26 nests, the first-hatched squab survived and the second-hatched squab died or was removed. In four nests, the second-hatched squab survived and the first-hatched died. In 32 nests with broods of two where both squabs died or were removed, 21 nests failed because both squabs died for the same reasons but 12 nests failed because the cause or evidence of death for each squab was different. (1) A second case of predation by a Mauritius kestrel was suspected but the squab was also suffering from trichomoniasis and cause of death was entered as disease.

Cause/evidence of squab mortality	Number of squabs			
	Single Squab	Brood of two		All Squabs
		1st-hatched squab	2nd-hatched squab	
Disease/inanition/injury	26	14	22	62
Cyclone/bad weather	1	2	1	4
Hypothermia	0	1	1	2
Predation (kestrel)	1	0	0	1(1)
Dead on nest (unknown cause)	11	4	3	18
Dead on ground (unknown cause)	0	0	2	2
Disappeared (unknown cause)	20	7	20	47
Removed	4	8	9	21
Unknown	2	0	0	2
Total	65	36	58	159

DISCUSSION

Interpretation of the data

Pink pigeon reproductive success was measured against a background of management practices that provided a constant food supply, improved survival, optimised nest success and improved habitat. Management practices varied between sites, the most intensive at Ile aux Aigrettes, and were improved over time with experience. Nest success was probably influenced by some changes in management over the study period.

Some errors must be considered when assessing nest success, in particular at mainland sites. There was a period of two to three days between full incubation and hatching when it was difficult to accurately determine if an egg had failed due to infertility or embryo death or had hatched and the squab died before detection. This was particularly so when nests were first found with parents already incubating. This meant that a nest recorded as failed due to unhatched eggs may have failed due to early squab death and vice versa. In some cases unhatched eggs were taken by predators after abandonment and where infertility should have been the cause of nest failure, predation may have been recorded.

Nesting success

Patterns of nesting in columbids

The constraints on brood size imposed by crop milk production have limited the reproductive options of columbids. Multiple broods per season and clutch overlap, whereby a pair starts another clutch while continuing to attend the nestling from their previous brood, are two strategies that enable columbids to increase their reproductive potential. In addition, columbids are capable of rapidly re-nesting after the loss of eggs or squabs. Mourning doves *Zenaida macroura* in North America may nest five or six times in warm southern climates but average only two or three attempts in northern states (Sayre & Silvy 1993). Wood pigeons *Columba palumbus* in England rear one or two broods and may rear three in favourable years (Murton 1965). In the tropics and sub-tropics an extended breeding season allows pigeons to re-nest frequently. In East Africa, a pair of red-eyed doves *Streptopelia semitorquata* nested five times in twelve months and ruddy ground doves *Columbina talpacoti* in Trinidad occupied a nest for five consecutive broods (Skutch 1991). One pair of rock pigeons *Columba guinea* in Southern Africa produced nine successive clutches (three abandoned) in one year. In this species, two successive broods were noted seven times, three broods six times, four broods twice and six broods once, with three the average number of broods per season (Rowan 1983). In the Eastern Cape of South Africa under favourable conditions, Cape turtle doves *Streptopelia capensis* may raise nine or 10 broods per season but in the south-west Cape, which is cold and wet, five or six broods per pair may be the maximum (Rowan 1983). Inter-brood interval may be determined by the stage at which the nest fails, or if it succeeds, and losses of adults through predation and other causes may interrupt the breeding cycle of an individual. In Cape turtle doves, failure by destruction of eggs or chicks means re-nesting after a shorter interval (4-15 days) than when a brood fledged (one or two months) (Rowan 1983). After losing a clutch or brood, female mourning doves may lay a new clutch from two to 25 days later, but usually three to six days (Skutch 1991).

Nesting success in pink pigeons

Pink pigeons showed repeated re-nesting where clutches failed to hatch or were lost. One pair at Ile aux Aigrettes had 12 nest attempts (all with eggs) with on average one every 33 days almost continuously for just over one year, but only fledged two young. Another pair at Ile aux Aigrettes had nine attempts in 1996 all with eggs and fledged six young but in

1997, the same pair had 12 attempts with eggs and only fledged two young. One pair on Ile aux Aigrettes had 25 successive nesting attempts in 3.2 years (on average one nest every 47 days) of which 24 had eggs and 12 young fledged. At Ile aux Aigrettes, most nests had eggs but at mainland sites, many attempts to re-nest did not result in eggs being laid. One pair at Brise Fer had 21 nest attempts over nearly two years, with on average one nest every 31 days, but in only nine attempts were eggs laid. After fledging young, pairs did not recycle so quickly and subsequent attempts often failed. Several pairs produced young in two and three successive nests but no birds produced young from every attempt made.

Clutch or brood overlap has been recorded in many species of columbids (Robertson 1985, Clout *et al.* 1988, Sayre & Silvy 1993, Powlesland *et al.* 1994), although it may be more frequent in experienced pairs and in captive pigeons (Skutch 1991). Clutch overlap probably occurs when food supplies are particularly abundant or nutritious. It was often seen in pink pigeons and was probably encouraged by the provision of supplemental food. Males were observed to rear squabs when the female died but this probably only occurs occasionally and if the squab is older. The female of one pair at Brise Fer died with two squabs in the nest at seven and nine days old. The second squab died at 12 days old but the other one fledged, reared only by the male. In one pair at Pigeon Wood, the female was killed with a 13 day-old squab in the nest. The male immediately began to court a new female and the squab died four days later. Male pigeons increasingly care for nestlings as they get older and feed them after fledging. The chances of squab survival was probably better when a female rather than a male died or divorced and post-fledging survival was probably increased by supplemental feeding.

Breeding success in this study was similar to previous records for the pink pigeon in the wild and in captivity. Breeding success of wild birds in the mid-1970s ranged from 19% to 31% between June and December and between 0.10 and 0.21 young produced per nesting attempt (Jones 1987). Breeding success of captive birds was similar to this study, despite many captive young reared by foster-parents. Breeding success in pink pigeons was extremely poor when compared with a range of pigeon species (Table 5.17). Species with similar nesting success rates included those where nest predation was very high, for example the white-crowned pigeon *Columba leucocephala* and mourning dove in Puerto Rico, common ground dove *Columbina passerina* and the New Zealand pigeon *Hemiphaga novaeseelandiae*. Squab survival was poorer than most cases cited, although survival of single and first-hatched squabs was comparable to or higher than some species, e.g. New Zealand pigeon and white-crowned pigeon (Wiley & Wiley 1979, Clout *et al.* 1995).

Species	No. nests/eggs		% nest success	% eggs hatched	% fledged of hatched	% fledged of eggs laid	Mean no. of broods (ranges)	Mean number of young (ranges)		Source
	nests	eggs						pair per year	per nest	
Bolle's Laurel pigeon										
Columba bollii Tenerife	68	68	47	59	80					(1)
White-tailed Laurel pigeon										
Columba junoniae Tenerife	22	22	27							(1)
Feral pigeon										
Columba livia (a)		24-1697		50-95.3		21-80	(3-9)	(1.1-10.6)	0.62-0.93	(2)
Kansas, USA		717		69.7	62	43.2				(2)
Stock dove										
Columba oenas Belgium		360		54	70.5	37.8				(10)
UK		152		66.4	60.4	40.1				(10)
Germany	399						1.78	3.25 (1-8)		(10)
Wood pigeon										
Columba palumbus UK	115			61.4	92.4	56.7	(1-3)	2.9 (2.6-3.1)		(3)
UK		1704		42	73	31		2.1		(3)
Rock pigeon										
Columba guinea South Africa	64	124		61.3	69.7	42.7	3 (2-6)	2.58		(4)
Scaly-naped pigeon										
Columba squamosa Puerto Rico	40		44							(5)
White-crowned pigeon										
Columba leucocephala Puerto Rico	27	54	25.9	38.9	33.3	13	(2-4)		0.3	(15)
Puerto Rico	49	98	59.2	66.3	69.2	45.9			1.4	(15)
Puerto Rico	82	163	53.7	77.3	61.1	47.2			0.9	(15)
Puerto Rico	121	239	67.8	70.7	70.4	49.8			1.0	(15)
Cape turtle dove										
Streptopelia capicola										
South Africa (SW Cape)	380	731		52.8	71.2	37.6	3 (3-6)	2.16		(4)
Red-eyed dove										
Streptopelia semitorquata										
South Africa	33		38.1				3	2.2		(4)
Laughing dove										
Streptopelia senegalensis										
Cape, South Africa	380	548		61.1	75.5	45.9	5 (4-6)	4.6	0.9	(4)
Transvaal, South Africa			36					(1.8-3.82)	0.7	(4)
USSR		84				48.8				(10)
Collared dove										
Streptopelia decaocto										
Czechoslovakia		436				68.6				(10)
Turtle dove										
Streptopelia turtur UK		621				39				(10)
Namaqua dove										
Oena capensis South Africa	35	69		62.3	48.4	30.4				(4)
White-winged dove										
Zenaida asiatica Puerto Rico	20		29							(5)
USA (Citrus)		11464				29.7	2 (1-4)	1.9		(8)
USA (Brush)		6060				35.2				
Zenaida dove										
Zenaida aurita Puerto Rico	86		39							(5)
Puerto Rico	68		51							(16)
Mourning dove										
Zenaida macroura USA	16300		48				2 (2-6)	3.6		(7)
USA	1556			44	55	22				(7)
Puerto Rico	27		21							(5)
Eared dove										
Zenaida auriculata Argentina	1126	2300	47			33				(15)
Galapagos dove										
Zenaida galapagoensis Galapagos	56	110				72				(15)
Ruddy ground dove										
Columbina talpacoti Costa Rica	21		23.8	50	40	20	5		0.38	(13)
Gold-billed ground dove										
Columbina cruziana Ecuador	283		56.5	76.7	81.4	55.2			0.93	(14)
Common ground dove										
Columbina passerina Puerto Rico	51		17							(5)
Ruddy quail dove										
Geotrygon montana Costa Rica	17	33	29			30				(15)
Torres Strait pigeon										
Ducula spilorrhoa Queensland	181	181		91						(9)
New Zealand pigeon										
Hemiphaga novaeseelandiae										
New Zealand	74	74	13	23	59	13	(1-3)	0.24		(6)
H. novaeseelandiae chatamensis	10	10	60			60				(11)
Chatham Islands, NZ	37	37	65			65		1.5		(12)

Table 5.17 Nesting success in columbids.

(a) USA, UK, Finland, Poland, Switzerland, Russia, Bohemia, Slovakia, Croatia, India, New Zealand.
Nest success is defined as percent nests fledging one or more young. For most species, nest success was calculated simply from the number of nests and includes all mortality. For the red-eyed dove and for columbids from Puerto Rico, references (6), (14) and (16), Mayfield estimates of nest success are shown. Mean number of broods is of successful nests per year or breeding season.

Source: (1) Hernandez *et al.* 1999 (2) Johnston & Janiga 1995 (3) Murton 1965 (4) Rowan 1983 (5) Rivera-Milan 1996 (6) Clout *et al.* 1995 (7) Sayre & Silvy 1993 (8) Cottam & Trefethen 1968 (9) Crome 1975 (10) Cramp 1985 (11) Powlesland *et al.* 1992 (12) Powlesland *et al.* 1994 (13) Skutch 1956 *in* Ricklefs 1969 (14) Marchant 1960 *in* Ricklefs 1969 (15) Wiley & Wiley 1979 (16) Rivera-Milan 1999.

Nest success at mainland sites may have been overestimated because nests that were abandoned or depredated soon after egg-laying (where eggs were undetected) were not included in the sample. Investment in the nest during the early stages is poor and abandonment or predation was more likely before full incubation started (the first egg is partially incubated and full incubation starts with the second egg). At mainland sites the proportion of nests with no eggs was higher in the non-breeding season and at the end of the breeding season from December to March (50%) than at the beginning and during the breeding season from April to November (33%).

Variation between sub-populations as an indication of differences in habitat quality

The effect of habitat and territory quality on nest success has been discussed in a number of bird species (reviewed in Clutton-Brock 1988 and Newton 1998). Differences in nest success between sub-populations were expected in the pink pigeon because of the variation in habitat quality between sites. When data were grouped into seasons, there were significant site differences in overall nest success. Site differences were most marked during the incubation period, which may have reflected differences in predator densities. At some sites differences in nest success during incubation and the nestling period offset one another so that overall nest success was similar. Management, in particular supplemental feeding and predator control, may also have reduced the effect of different habitat quality between sites. A longer period of study may provide further evidence of differences in nest success between sub-populations.

Nesting success of wild and released breeding pairs

Nesting success of wild birds was expected to be better than released birds owing to poor behavioural development of captive-reared birds (Chapters 3 and 4) which was true in this study. There was some suggestion that even if only one of the pair was released, it depressed nest success but the evidence was not conclusive. Differences in nest success between released and wild birds were confounded by their distribution between sites, and the better nest success in wild-fledged pairs may have partly been due to habitat. No pairs of released birds bred at Pigeon Wood and 47% of all wild pairs nested in Pigeon Wood, where overall nest success was higher. Sample sizes were too small to compare differences in nest success of wild and released pairs within sites.

Causes of nest failure

In previous studies, causes of nest failure in birds include hatching failure (infertility, death of the embryo or death during hatching), desertion, starvation of the nestling, predation, inclement weather, death of a parent (which may result in desertion or starvation) infestation with parasites and competition for nest sites (Ricklefs 1969). Pink pigeon nests have failed due to all of these reasons. In a review of nesting failure in pigeons the most frequently cited causes were predation, desertion and inclement weather (Table 5.18). In Puerto Rico, nest predation of ten native Columbids accounted for an average 81% of failed nests (Rivera-Milan 1996), higher than suspected for pink pigeons in this study. In previous studies desertion was cited as a cause of nest failure in about 18% of cases. Although reasons for desertion were not specified, they probably included infertile or unhatched eggs due to embryo death. In this study predation and desertion of nests with eggs at mainland sites as a cause of nest failure may have been underestimated because the proportion of nests with eggs was also underestimated.

Infertility and embryo death

On Ile aux Aigrettes, infertility and embryo death were the main causes of poor hatchability and, since fertility of free-living birds (58.6%) was similar to captive birds (Chapter 4), it was assumed that fertility rates were the same at mainland sites. Fertility rates are not often recorded in ornithological studies and infertility is not widely quoted as a major cause of nest failure in birds. Johnston & Janiga (1995) recorded 24% egg mortality in feral pigeons *Columba livia* due to infertility or embryo death but in other cases, rates were generally low (Table 5.17). In six New Zealand birds, infertility was reported in 4% to 62% of eggs accounting for 7% to 89% of unhatched eggs and embryo deaths accounted for 11% to 25% of unhatched eggs. However, in the New Zealand pigeon, infertility and embryo deaths was reported in only 4% of eggs laid (Jamieson & Ryan 2000). The percentage of infertile eggs laid by captive pink pigeons was about three times that found in domestic pigeons (Jones *et al.* 1989). Factors contributing to infertility in captive birds included inexperience, senility, cumulative egg production of the female (fertility decreased with egg production) and failure to copulate successfully. Inbreeding depresses fertility and may cause abnormalities in male spermatozoa (Jones *et al.* 1989, Jones 1995). Pathogens in the egg or in the parent birds may also reduce fertility but this has not been investigated.

Fertility rates in this study and in captive birds may be underestimated due to inaccuracies in detecting fertility. Early embryonic death is difficult to detect by candling and the egg may appear clear as if infertile. Embryo death is common in captive eggs and was also found in wild eggs but the causes of embryo death and its contribution to poor hatchability in wild birds are unknown. In the pink pigeon, infertility may be the main factor limiting reproductive success and further research is needed to investigate its causes and if remedial management is possible.

Species		No. nests/eggs/squabs			% nest failure	Infertility/ embryo dth	Predation		Desertion		Weather		Starvation	Other	Source
		nests	eggs	squabs		eggs	eggs	squabs	eggs	squabs	eggs	squabs	squabs		
Bolle's Laurel pigeon	*Columba bollii* Tenerife	68	68		53		86								(1)
White-tailed Laurel pigeon	*Columba junoniae* Tenerife	22	22		73		100								(1)
Feral pigeon	*Columba livia*														
	Humberside, UK		812	541	52.7	5.3	18.7	8.1	9.2			---- 20.9 ----			(10)
	Manchester, UK		327		22[a]	12	10								(10)
	Eastern Kansas, USA					24.1	17.7	30.5	22	10.2	5	2.9		Mites (4.4%)	(2)
Stock dove	*Columba oenas* Belgium		360		62.2	5.8	19	9.8	21.2				19.7		(10)
	Germany	399						7	38.6		16.8				(10)
Wood pigeon	*Columba palumbus* UK		1112		43.3	11.7[b]	31.3		8						(3)
	UK		1704		57.9[a]	0.4	55.2		1.9		0.13			Human disturbance 0.3%	(3)
Rock pigeon	*Columba guinea* South Africa	64	124	76	57.3	7[c]	12.5	17.1	23			?	?	3 broods to humans, injuries to squab	(4)
Scaly-naped pigeon	*Columba squamosa* Puerto Rico	40			66		89								(5)
Cape turtle dove	*Streptopelia capicola*													20% eggs disappeared.	
	South Africa (SW Cape)	380	731	333	62.4		4	16	11		12	?		Dead in nest or below (13%)	(4)
Laughing dove	*Streptopelia senegalensis*														
	Cape, South Africa	380	548	340	54.1		3	11	8		13	5	8	10% eggs disappeared.	(4)
	USSR		84		51.2		< 28.6	< 17.8							(10)
Collared dove	*Streptopelia decaocto*														
	Czechoslovakia		436		31.4		< 2.8	c.3.7							(10)
Turtle dove	*Streptopelia turtur* UK		621		61		34	< 8							(10)
Namaqua dove	*Oena capensis* South Africa	35	69	43	69.6	6	?	?			5.7	4.3		17% squabs unknown causes	(4)
White-winged dove	*Zenaida asiatica* Puerto Rico	20			71		67								(5)
Zenaida dove	*Zenaida aurita* Puerto Rico	86			61		78								(5)
	Puerto Rico	68			49		88				8.8			1 loss to human	(16)
Mourning dove	*Zenaida macroura* USA						80		27		7			Hunting?	(7)
	Puerto Rico	27			79		68								(5)
Ruddy ground dove	*Columbina talpacoti* Costa Rica		40		71		< 50	< 30							(13)
Gold-billed ground dove	*Columbina cruziana* Ecuador		477		43.5		< 23.3	< 21.5							(14)
Common ground dove	*Columbina passerina* Puerto Rico	51			83		92								(5)
Torres Strait pigeon	*Ducula spilorrhoa* Queensland	181	181									?			(9)
New Zealand pigeon	*Hemiphaga novaeseelandiae*														
	New Zealand	74	74		87	4.7	39.1	9.4	6.25					Fallen egg 5, parent killed 3, 28% eggs unknown	(6)
	H. novaeseelandiae chatamensis														
	Chatham Islands, NZ	37	37		35	15.4[d]	7.7	7.7	7.7		7.7				(12)

Table 5.18 Causes of nesting failure in columbids

Figures are percentages of failed nests, eggs or squabs. Percent nest failure taken from Figure 5.17 or other sources. ? = recorded as a cause of failure but not quantified.
(a) eggs only (b) includes deserted eggs, one actual estimate of 9% infertility (c) eggs which failed to hatch or hatchling died (d) 2 infertile eggs represent 7.1% of 28 nests for which fertility was known.

Source: (1) Hernandez *et al.* 1999 (2) Johnston & Janiga 1995 (3) Murton 1965 (4) Rowan 1983 (5) Rivera-Milan 1996 (6) Clout *et al.* 1995 (7) Sayre & Silvy 1993 (8) Cottam & Trefethen 1968 (9) Crome 1975 (10) Cramp 1985 (11) Powlesland *et al.* 1992 (12) Powlesland *et al.* 1994 (13) Skutch 1956 *in* Ricklefs 1969 (14) Marchant 1960 *in* Ricklefs 1969.

Predation of nests

The adverse effect of mammalian predators on breeding success of native faunas, which have evolved in the absence of such predators, has been well documented (Atkinson 1985, King 1985, Johnson & Stattersfield 1990). Exotic mammalian predators have been implicated in poor nesting success of several endemic birds in Mauritius (Cheke 1987, Jones 1987, Jones *et al.* 1989, Jones & Duffy 1993, Safford 1997*c*). Even in bird species that live with native predators, predation may be a major cause of egg and chick losses often accounting for about half of all nesting attempts and more than 80% of all nest failures (Newton 1998). Predation has been recorded as the main cause of nest failure in pink pigeons (Jones 1987). Crab-eating macaques *Macaca fascicularis* and rats *Rattus rattus* have been identified as major nest predators (McKelvey 1976, 1977, Jones 1987, Jones *et al.* 1989, Jones *et al.* 1992), which was confirmed in this study. In early egg manipulations at Pigeon Wood, plaster dummy eggs that were taken by predators showed teeth marks of rats and macaques. Poor nesting success during incubation at Brise Fer was probably due to high rat densities and at Bel Ombre, nest failure was frequently due to macaques which were more common there. Recent studies have suggested that at Pigeon Wood, Japanese red cedar *Cryptomeria japonica* provides a refuge from mammalian predators owing to its concealing morphology and sticky sap, and the nesting success of the Mauritius fody *Foudia rubra* was much higher there than in native vegetation (Safford 1997*c*). Carter & Bright (2000) showed that rats were at similar densities at this site as elsewhere but that macaques were virtually absent. In this study nesting success during incubation at Pigeon Wood suggested that predation pressure was similar to other mainland sites, but higher squab survival could be partly explained by the absence of macaques. There were no mammalian predators on Ile aux Aigrettes but two possible avian predators may occasionally take eggs and young. These were the common mynah *Acridotheres tristis* (Todd 1984) and the little green heron *Butorides striatus* although they were not known to cause any nest failures.

Predation was probably highest during incubation when eggs were taken by both rats and macaques, and decreased with the age of the nestling. Older nestlings adopt an aggressive display towards intruders and ship rats were less likely to take larger nestlings. During this study, nest failure due to predation by rats may be reduced by rat control carried out at mainland sites (Chapter 2) and without rat control, nest predation may be higher. However, data from Ile aux Aigrettes suggests that, even in the absence of predators, nest success is generally poor.

Predation at mainland sites may have masked the effect of poor hatchability due to infertility and embryo death and many depredated eggs probably would not have hatched. The data from Ile aux Aigrettes suggest that predation may have also masked other reasons why nests failed. At mainland sites smashed eggs found below the nest was usually interpreted as evidence of predation. However on Ile aux Aigrettes where mammalian nest predators were absent, smashed eggs were found at 10% of failed nests, and which were attributed to poor nesting behaviour or inclement weather. Indisputable evidence of predation as being the cause of nest failure was difficult to obtain and mis-interpretation of the causes of failure was common. High losses due to nest predation may have less effect on the annual productivity because pink pigeons make several nesting attempts per season. Considering all the above factors, the real effect of predation, particularly at the egg stage, may be lower than it appears.

Other factors affecting nesting success

Food availability

The effects of food shortages on breeding success can be manifest through non-egg laying, reduced clutch size, egg-desertion, poor chick growth and survival, reduced number of nesting attempts per season and reduced survival of adults (review in Newton 1998). Food shortages, associated with habitat degradation and introduced species, are suspected to limit nest success and productivity in Mauritian birds (Jones 1987, Jones & Owadally 1988) and variation in nest success could be partly explained by annual, seasonal and site differences in food availability and climate. This study provided some evidence that food resources were limiting by indicating seasonal differences in nesting success. At mainland sites, squab survival was poorest in the dry season and at all sites more young successfully fledged in the wet season. The most extreme seasonality was seen at Brise Fer (the driest of mainland sites) when only 8% of nests fledged young in the dry season. The provision of supplemental food may have reduced the effects of food shortages but do not seem to have eliminated them. Supplemental food (maize and wheat) provides additional nutrition but was not a complete diet. Heavy rainfall associated with cyclones and tropical depressions may improve nest success in subsequent years by increasing food availability. In 1996, 110 pink pigeons fledged which was the highest number recorded in one year and almost twice that of the previous year. In addition, nesting success was highest for all sites since 1994 and at Brise Fer the highest recorded. This success may have been related to five tropical depressions and cyclones that brought higher than average rainfall in 1995 and 1996. The effect of food availability in relation to breeding success requires further research.

The effect of cyclones

Cyclones have been cited as a cause of decline in the pink pigeon (Jones 1987). Severe cyclones may cause direct mortality, destroy nests and birds may be weakened by post-cyclone food shortages. In December 1994 tropical cyclone Hollanda passed 20 km from Mauritius with wind speeds of up to 216 km/hour. The cyclone caused no known mortality of adult or juvenile pink pigeons, echo parakeets *Psittacula eques* or Mauritius kestrels *Falco punctatus* (Chapter 3). Pink pigeon nests were destroyed by the cyclone but several large squabs were found alive on the ground having been blown out of the nest, and were rescued (*pers. obs.*) Pigeons were quick to re-nest and no deleterious effect was made to the population, although supplemental feeding may have reduced mortality due to any post-cyclone food shortages. Historical declines were likely caused by severe cyclones together with habitat destruction acting on very small localised populations.

Density dependence

Density dependent factors have probably acted on some or all of the sub-populations, particularly at Ile aux Aigrettes and Pigeon Wood where birds were restricted to a defined area of habitat. At all sites territories were clustered around supplemental feeding stations and within predator controlled areas which may encourage higher than normal densities. Density dependent factors are known to affect nesting success in pigeons, which may show compensatory mortality where a population is enabled to remain stable through selective desertion of eggs (Johnston & Janiga 1995). In wood pigeons, breeding success in nests close together averaged 24% compared to 32% in more dispersed nests (Murton 1965). Johnston & Janiga (1995) recorded 66% breeding success of feral pigeons in a high density breeding site compared to 71% and 78% success in a lower density site. Cottam & Trefethen (1968) observed a nesting success of 35% and 38% in colony nesting white-winged doves *Zenaida asiatica* compared to 50% in dispersed nesters. A high density of nests and territories increases the risk of predation, as well as disease and territorial disputes, which can disrupt breeding and also increase predation (Murton 1965, Cottam & Trefethen 1968, Rivera-Milan 1999).

Since 1996, breeding success has declined as the population has increased (Figure 5.5) and there has been some evidence that density may be limiting. Between 1997 and 1998, some juveniles left the Pigeon Wood and established territories in a pine plantation nearby. It was assumed that the Pigeon Wood was saturated with territories and young birds were forced to leave. On Ile aux Aigrettes some sub-adults were thought to have left the island. Young birds were observed flying to the mainland and there were unconfirmed reports of adult birds feeding in gardens along the coast. One sub-adult was found dead in the sea on the mainland coast. Flying to the mainland was possible but birds probably did not survive very long. An emaciated female (which had previously been at liberty at Brise Fer for more than five years) was re-trapped on the mainland six days after release and later died. Ile aux Aigrettes may not be able to support more than 30 to 40 breeding pairs (with the current availability of native habitat), the maximum known was 34 pairs in 1995.

Squab survival and causes of squab mortality

Brood size and squab survival

Pigeons which lay clutches of two eggs show facultative brood reduction as part of their reproductive behaviour (reviewed in Johnston & Janiga 1995). When food is abundant, both squabs fledge and when food is scarce, brood reduction may occur. A differential fledging success of siblings was recorded in feral pigeons where 70% of first squabs fledged and 57% of second squabs. Differential survival is caused by asynchronous hatching and sexual size dimorphism, the larger males arising from first eggs and females from second eggs (Johnston & Janiga 1995). This study supported the theory of brood reduction, although food shortage as the cause was not tested. Supplemental feeding did not appear to improve food availability sufficiently to allow second-hatched squabs to survive.

In feral pigeons single squabs show increased survival over siblings of a pair (Johnston & Janiga 1995) but in this study single squabs showed similar survival to first-hatched siblings of a pair. The survival of each squab in a brood of two was probably influenced by the survival time of the second squab. A squab whose sibling died at only a few days old was more likely to survive than a squab whose sibling survived for longer owing to competition for resources. Many of the squabs in broods of two were reared singly for most of the nestling period, which is not clear from the data.

Pink pigeons lay either one or two eggs, but individual females show consistent clutch size (Jones 1995 and this study, Chapter 4). About half of the single-reared squabs hatched from clutches of one egg. How the brood reduction model operates in a species with variable clutch size was not clear.

Disease

Disease was not cited as a major cause of squab mortality in other pigeon species (Table 5.18). The effect of disease on squab survival on Ile aux Aigrettes was comparable to the effects of predation on the mainland so that overall, squab survival was similar. Disease in captive squabs only accounted for 7% of deaths (Jones *et al.* 1989). The effect of disease on squab survival is discussed in Chapter 7.

The effect of inbreeding on nest success and squab survival

Jones *et al.* (1989) suggested that inbreeding depression was probably the ultimate cause of poor breeding in captive pink pigeons and that unrecorded inbreeding reduced the viability of captive birds. Inbreeding affected fertility and squab survival, but there were no effects on hatchability (Jones 1995). Captive pink pigeons showed similar depressed breeding to a highly inbred population of captive Hawaiian geese *Nesochen sandvicensis* (Kear & Berger 1980). In great tits *Parus major* van Noordwijk (1988) found that at least half of all eggs failing to hatch may be attributed to inbreeding depression.

This study supported the evidence that inbreeding in pink pigeons affected nestling survival and that squab mortality was highest in highly inbred birds. However, this study also suggested that nominal inbreeding (kinship coefficients < 0.25) did not significantly reduce squab survival. There was some similar evidence in Jones (1995) that survival of squabs was mainly affected when inbreeding coefficients reached 0.125 and more.

Other factors limiting squab survival

On the mainland, the disappearance of a squab from the nest was often interpreted as evidence of predation. However, on Ile aux Aigrettes the number of squabs that disappeared was also high and which could not be attributed to mammalian predation. Mortality of squabs due to reasons other than predation is probably underestimated at mainland sites. In captive squabs up to 12% died from poor parenting skills, which included inanition, (not fed by the parents and/or squabs do not beg), falling from the nest, feather plucking, chilling, and squabs were crushed or attacked by a parent. Developmental problems contributed about 17% of deaths (Jones *et al.* 1989, Stewart 1999). Captive squabs were most at risk up to three days old when 60% of deaths occurred (Jones *et al.* 1989, Jones 1995, Stewart 1999). This was similar for wild squabs and, on Ile aux Aigrettes, 55% of squabs that disappeared were between 0-3 days old. Mortality in the wild during this period is probably underestimated due to inaccuracies in recorded hatch dates.

Conclusions

Nest success was poorer than for other pigeon species during both incubation and nestling phases. The ultimate reason for poor breeding success during incubation is probably infertility and embryo death, but this is masked by other causes of nest failure such as predation. Predation undoubtedly reduces nest success and may have a greater impact without predator control, but the real effect is difficult to assess owing to interaction with other factors, such as food shortages. Inbreeding effects may be greater than observed because there is probably unrecorded inbreeding. Density dependent factors may have begun to limit nest success and management may be needed to reduce this effect. Between 1988 and 1992 breeding success was poor owing to a small number of breeding birds, some of which were old. Since 1993 breeding success improved once a larger breeding population was established and management techniques were refined. It is anticipated that as the proportion of wild-fledged breeding pairs increases, breeding success will continue to improve.

Chapter 6

Individual productivity and lifetime reproductive success

INTRODUCTION

Long-term studies of marked individuals have enabled the measurement of lifetime reproductive success, that is the total number of young raised by individuals during their life-span. Lifetime reproductive success provides a key measure of individual performance, reveals the full extent of individual variation and is the best estimate available of biological fitness, that is of the contributions that particular individuals make to future gene pools (Newton 1989*a*). This chapter examines productivity of individuals, lifetime reproductive success and looks at factors causing individual variation in productivity.

METHODS

The methods for monitoring nests and breeding pairs are described in Chapter 4. Productivity was defined as the number of fledged young produced by an individual and was monitored up to 1998. At Brise Fer productivity was monitored from 1988, at Pigeon Wood from 1990, at Ile aux Aigrettes from 1994 and at Bel Ombre from 1995. Productivity was calculated in two ways. Known pairs were monitored at nests and the number of young fledged was counted, which gave an absolute figure of productivity from nests of known pairs. This is referred to as 'known productivity'. However, some young fledged from undetected nests because the number of fledged young that were caught and ringed was more than the number fledged from known nests (Chapter 5). It was assumed that the young that fledged from undetected nests had fledged from parents in the same proportion as those that fledged from known pairs of known age. This gave an estimate of total productivity for different age classes and for each year, and is referred to as 'total productivity'. It was also assumed that all breeding pairs were known. Where young that fledged from known nests were not ringed while in the nest, it was assumed that there was no mortality between fledging and subsequent ringing.

Productivity estimates were obtained for birds during their life-span within the study period and from those that were still alive at the end. Productivity was investigated in relation to sex, age, pairing length, total time paired, annual trends, sub-population and rearing origin. Only pairings where eggs were laid were considered. Total productivity estimates were used when investigating male and female productivity in different age classes, annual productivity and productivity at different sites. Known productivity (number fledged from known nests) values were used when investigating productivity of individuals, productivity in relation to pairing length, survival time, lifetime productivity and productivity of released and wild birds.

Lifetime reproductive success

Lifetime reproductive success was calculated only for birds which died within the study period and for which nesting data was relatively complete. Productivity was calculated for females only if paired in their first year and males only if paired in their first or second year. This meant that birds were monitored from the start of their reproductive life-span. If released, only birds released at less than one year old were considered.

Statistical analyses

Regression analysis and ANOVA (SPSS 9.0 1998) was used to test the relationship between productivity and total time paired, survival time and length of individual pairings. ANOVA (MINITAB 8.21, 1991) was also used to test differences in productivity between wild and released birds. All mean values are followed by the standard deviation (± SD).

RESULTS

Productivity of individuals

Productivity was higher for some birds than others and at each site a small proportion of birds contributed a large percentage of young. Of 156 egg-laying females monitored between 1988-98, 14 (9%) produced 141 (43%) young, six (4%) produced 76 (23%) young and 58 (37%) produced no young. However, 50 (32%) breeding females did produce one or two young each. This pattern was similar in males. Of 155 males, 18 (12%) produced 149 (45%) young, 53 (34%) produced no young, and 79 (51%) produced one or two young each (Figure 6.1).

Productivity of pairings showed a similar pattern to that of males and females. Of 248 pairings, 112 (45%) produced no young, 11 (4%) produced 89 (27%) young and 89 pairings (36%) produced one or two young each.

Productivity, pairing length and survival time

The relationship between the total time for which individuals were paired and the number of young fledged was significant (Figure 6.2). However, some birds paired for several years and produced few if any young while others produced a larger number of young in only a few years. One pairing on Ile aux Aigrettes produced 12 young in less than two years.

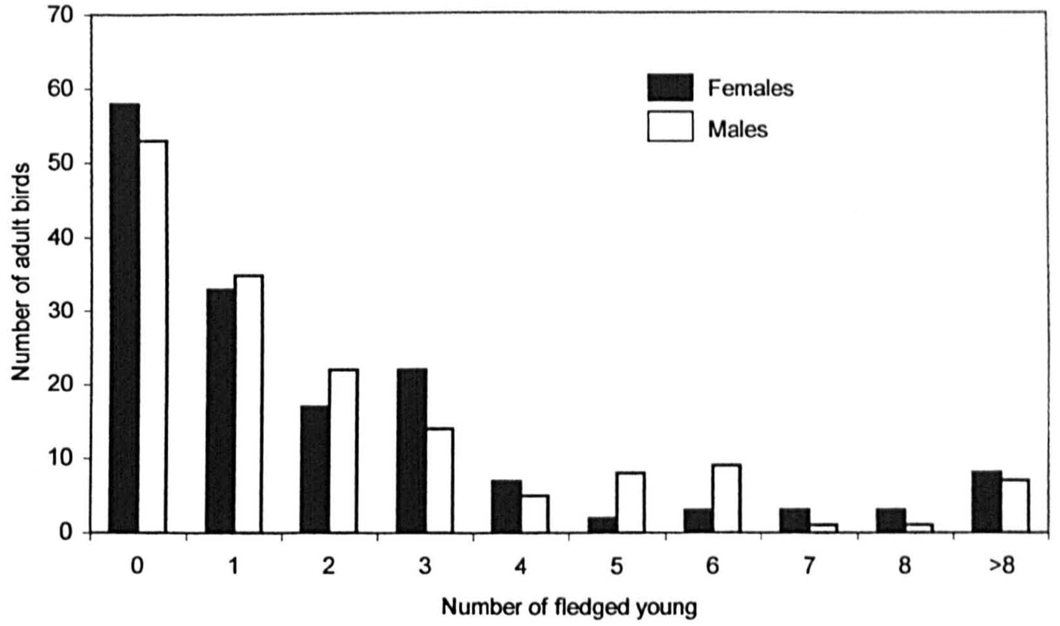

Figure 6.1 Productivity of male and female pink pigeons, 1988-98. Data for all sites pooled and included birds alive at the end of the study. Sample size: 156 females and 155 males. This pattern of productivity for all birds was similar to patterns of productivity for birds for which lifetime production was known.

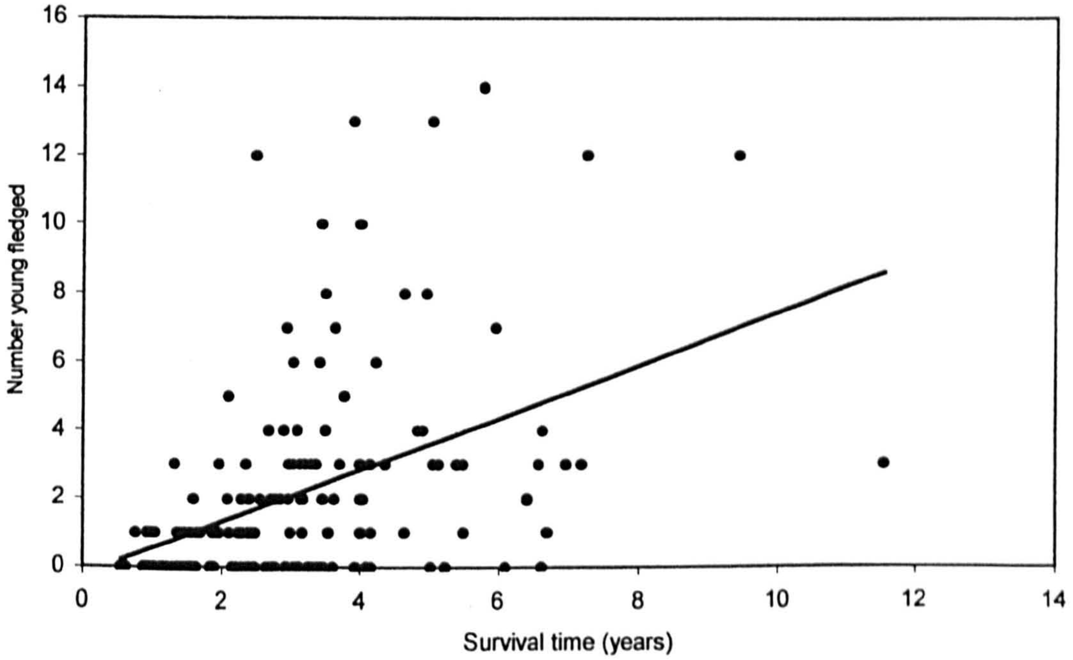

Figure 6.2 Female productivity in relation to survival time, 1988-98. Each spot represents the number of fledglings produced by an individual female. Data for all sites pooled, sample size 155 females. Relationship between productivity (y) and survival time (x) was significant for females ($F_{1,153} = 38.8$, $P < 0.001$): $y = 0.753_x - 0.158$, and for males ($F_{1,152} = 40.1$, $P < 0.001$): $y = 0.705_x - 0.241$. Relationship between productivity (y) and total time paired (x) was significant for females ($F_{1,148} = 43.5$, $P < 0.001$): $y = 1.010_x + 0.324$, and for males ($F_{1,151} = 39.2$, $P < 0.001$): $y = 0.875_x + 0.575$. Relationship between productivity (y) and individual pairing length (x) was significant ($F_{1,235} = 44.1$, $P < 0.001$): $y = 0.717_x + 0.520$.

Productivity in relation to survival time of individuals was also significant although some long-surviving individuals produced few young while some short-lived individuals produced many young. One female on Ile aux Aigrettes (different to above) produced 12 young when less than two years old. Birds that produced eight or more young tended to be longer-lived, although females were on average younger than males (male mean 6.1 ± 1.6 years, n = 8, female mean 4.95 ± 2.0 years, n = 11).

The relationship between individual pairing length and productivity of a pair was significant. However, as individuals had on average 1.13 ± 0.11 pairings during the study period, most productivity was likely to have occurred within a single pairing and corresponded closely to the total time paired for an individual. The mean pairing length for the top 11 productive pairs (six or more young fledged per pair) was 2.2 ± 0.9 years.

Female productivity and age

Table 6.1 shows age-specific productivity in female pink pigeons. Productivity was generally poor ranging from 0.85 to 1.15 young reared per female per age cohort over the first six years of reproductive life. Peak productivity occurred in year one (one to two years old) and remained relatively stable up to year five, after which productivity declined dramatically. After year five only females at Pigeon Wood were known to fledge any young and the high productivity in year eight was due to two females.

Table 6.1 Female productivity and age (total number reared), 1988-98. Total number fledged is to the nearest whole number.

Age (years)	No. females paired	No. pairings	Mean no. pairings per female	Total time paired (years)	Mean time paired (years)	Total no. fledged	Mean no. fledged per paired female	Mean no fledged per year paired
0	100	112	1.12	31.01	0.53	84	0.85	1.59
1	129	155	1.19	87.25	0.68	148	1.15	1.70
2	98	111	1.13	65.49	0.67	91	0.93	1.39
3	60	69	1.15	40.36	0.67	49	0.82	1.22
4	33	36	1.09	21.72	0.66	26	0.80	1.21
5	19	21	1.11	11.70	0.62	19	1.02	1.66
6	12	13	1.08	7.53	0.63	4	0.33	0.52
7	5	6	1.20	2.37	0.47	1	0.26	0.55
8	2	3	1.50	1.58	0.79	5	2.60	3.30
9	2	2	1.00	1.44	0.72	0	0.00	0.00
10	1	1	0.00	0.18	0.00	0	0.00	0.00
11	1	1	1.00	0.10	0.10	0	0.00	0.00

Male productivity and age

Male productivity followed a similar pattern to that of females with peak productivity occurring in year one (Table 6.2). Males continued to produce young up to year six after which productivity declined. In year eight only one male was known to produce young which was paired to a female in her first year. Two other eight year old males were paired but failed to produce any young.

Table 6.2 Male productivity and age (total number reared), 1988-98. Total number fledged is to the nearest whole number.

Age (years)	No. males paired	No. pairings	Mean no. pairings per male	Total time paired (years)	Mean time paired (years)	Total no. fledged	Mean no. fledged per paired male	Mean no. fledged year paired
0	75	86	1.15	36.73	0.49	56	0.75	1.53
1	129	156	1.21	77.87	0.60	160	1.24	2.05
2	112	125	1.12	79.37	0.71	101	0.91	1.28
3	73	79	1.08	43.56	0.60	43	0.58	0.98
4	33	39	1.18	23.68	0.72	28	0.84	1.17
5	21	23	1.10	12.89	0.61	25	1.17	1.91
6	12	15	1.25	7.48	0.62	13	1.08	1.74
7	4	5	1.25	2.57	0.64	1	0.33	0.51
8	3	3	1.00	0.92	0.31	3	0.87	2.83
9	1	1	1.00	0.96	0.96	0	0.00	0.00
10	0	0	0.00	0.00	0.00	0	0.00	0.00
11	0	0	0.00	0.00	0.00	0	0.00	0.00

Lifetime reproductive success

Mean lifetime productivity was 1.9 ± 3.0 young per female (n = 46) and 1.6 ± 2.2 young per male (n = 48). The pattern of age-specific lifetime productivity of males and females was similar to that described above for individual productivity of all birds although mean values per age group were lower (Tables 6.3 and 6.4). Seventeen females (37%) produced no young at all, five females (11%) produced 46 young (52%) and 17 females (37%) produced one or two young each. Nineteen males (40%) produced no young at all, six males (12%) produced 38 young (49%) and 23 males (48%) produced one or two young each. Although some of these birds may have had incomplete breeding histories, it was believed that these results were close estimates of lifetime productivity.

Table 6.3 Age-specific productivity of females for which lifetime production was known (number reared by known females), 1988-1998.

Age (years)	No. females	No. pairings	Mean no. pairings	Total time paired (years)	Mean time paired (years)	No. fledged	Mean no. fledged per female	Mean no fledged per year paired
0	46	50	1.1	13.35	0.50	27	0.59	1.18
1	40	52	1.3	23.51	0.59	39	0.98	1.66
2	18	21	1.2	11.16	0.62	17	0.94	1.52
3	11	14	1.3	6.68	0.61	8	0.73	1.20
4	6	7	1.2	2.95	0.49	5	0.83	1.69
5	1	1	1.0	0.48	0.48	0	0.00	0.00

Table 6.4 Age-specific productivity of males for which lifetime production was known (number reared by known males), 1988-98.

Age (years)	No. males	No. pairings	Mean no. pairings	Total time paired (years)	Mean time paired (years)	No. fledged	Mean no. fledged per male	Mean no fledged per paired year
0	29	33	1.1	7.74	0.46	18	0.62	1.36
1	43	52	1.2	23.59	0.55	30	0.70	1.27
2	22	24	1.1	14.78	0.67	17	0.77	1.15
3	11	12	1.1	5.33	0.48	4	0.36	0.75
4	3	4	1.3	1.86	0.62	0	0.00	0.00
5	2	3	1.5	0.89	0.45	5	2.50	5.62
6	1	2	2.0	0.56	0.56	3	3.00	5.34

Annual productivity

Figure 6.3 shows mean annual productivity per paired female from 1992. Mean annual productivity per paired male showed a similar pattern. From 1994, mean annual productivity remained relatively constant (0.98 ± 0.16 young per female). The high productivity of females in 1992 and 1993 was due both to the release of 34 young birds in 1991 and 1992 and the start of intensive predator control and nest protection efforts. Since the productivity of males and females were similar, further comparisons have focussed on female productivity.

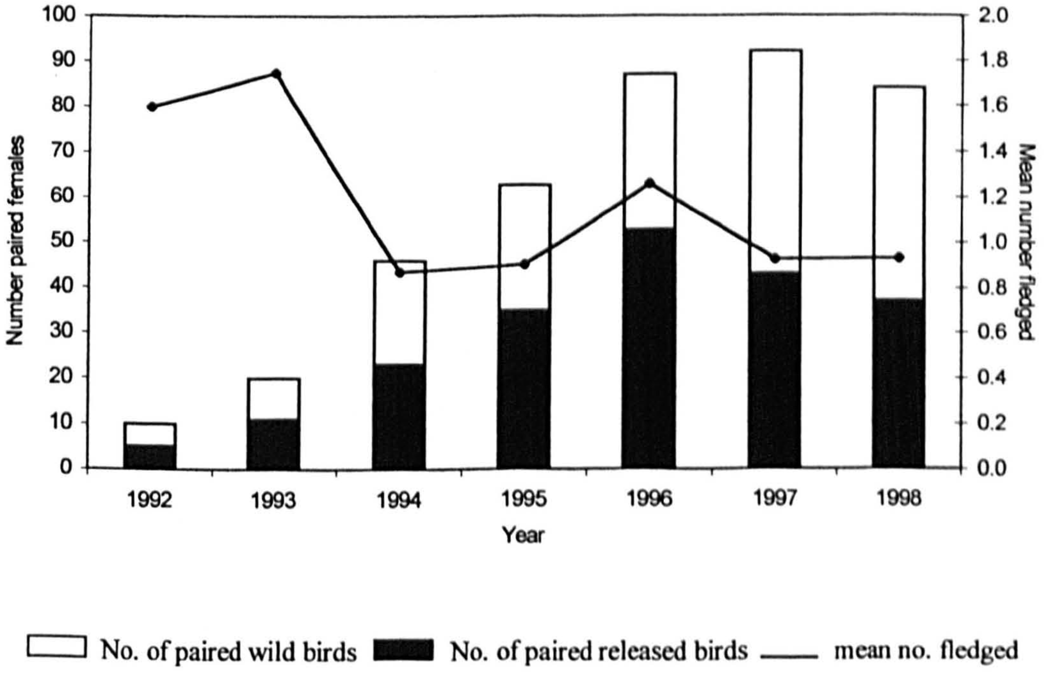

Figure 6.3 Mean annual productivity of female pink pigeons, 1992-98. Mean annual productivity 1.18 ± 0.37. Sample size 78 released females, 78 wild females. Bars represent number of breeding females paired per year. Mean number fledged is per paired female per year. Between 1992 and 1998 mean annual productivity for males was 1.14 ± 0.34.

Female productivity in different sub-populations

The pattern of productivity of females was similar between sites but at some sites, females were more productive than at others (Table 6.5). Within the first three years, productivity per year was highest at Ile aux Aigrettes and was on average twice that at Brise Fer and Bel Ombre. At Pigeon Wood productivity per year was slightly less than at Ile aux Aigrettes during the first three years but females were productive for longer. After three years old, Pigeon Wood females were about twice as productive as females at all other sub-populations and a small number of females up to eight years old continued to produce young. Productivity from year five was due to just five females, two of which produced 17 young. A decline in productivity at Ile aux Aigrettes and Bel Ombre after year two was apparent, but may be an artifact of small sample sizes.

Table 6.5 Female productivity at different sub-populations (total number reared).

Age	No. females paired				Mean no. fledged per paired female			
(years)	PW	BF	BO	IAA	PW	BF	BO	IAA
0	11	39	25	25	0.95	0.66	0.66	1.18
1	18	52	30	31	1.24	0.82	0.65	1.90
2	18	39	20	21	0.99	0.76	0.76	1.30
3	16	27	6	12	1.30	0.67	0.47	0.66
4	13	14	2	5	1.37	0.65	0.00	0.46
5	10	9	-	-	2.08	0.14	-	-
6	7	5	-	-	0.64	0.00	-	-
7	3	2	-	-	0.50	0.00	-	-
8	2	-	-	-	3.00	-	-	-
9	2	-	-	-	0.00	-	-	-
10	1	-	-	-	0.00	-	-	-
11	1	-	-	-	0.00	-	-	-

Productivity of released and wild females

Productivity of wild females was significantly higher than productivity of released females in all age groups (Figure 6.4 (a)). A comparison of productivity between wild-fledged and released females at Ile aux Aigrettes and at Brise Fer supported the general trend (Figure 6.4 (b) and (c)). The difference was not as consistent at Brise Fer as it was at Ile aux Aigrettes but for some age groups at Brise Fer, e.g. years two and three, the difference was marked. A comparison of productivity at Pigeon Wood and Bel Ombre could not be carried out, as sample sizes of released and wild females at these sites were too small.

Recruitment of wild-fledged birds into the breeding population

Of 377 wild-fledged birds (excluding those censored as alive and less than one year old) 231 (61%) did not breed. Of these non-breeding birds, 142 (61%) died at less than one year old, which was considered breeding age (Chapter 4). Although some of these non-breeding

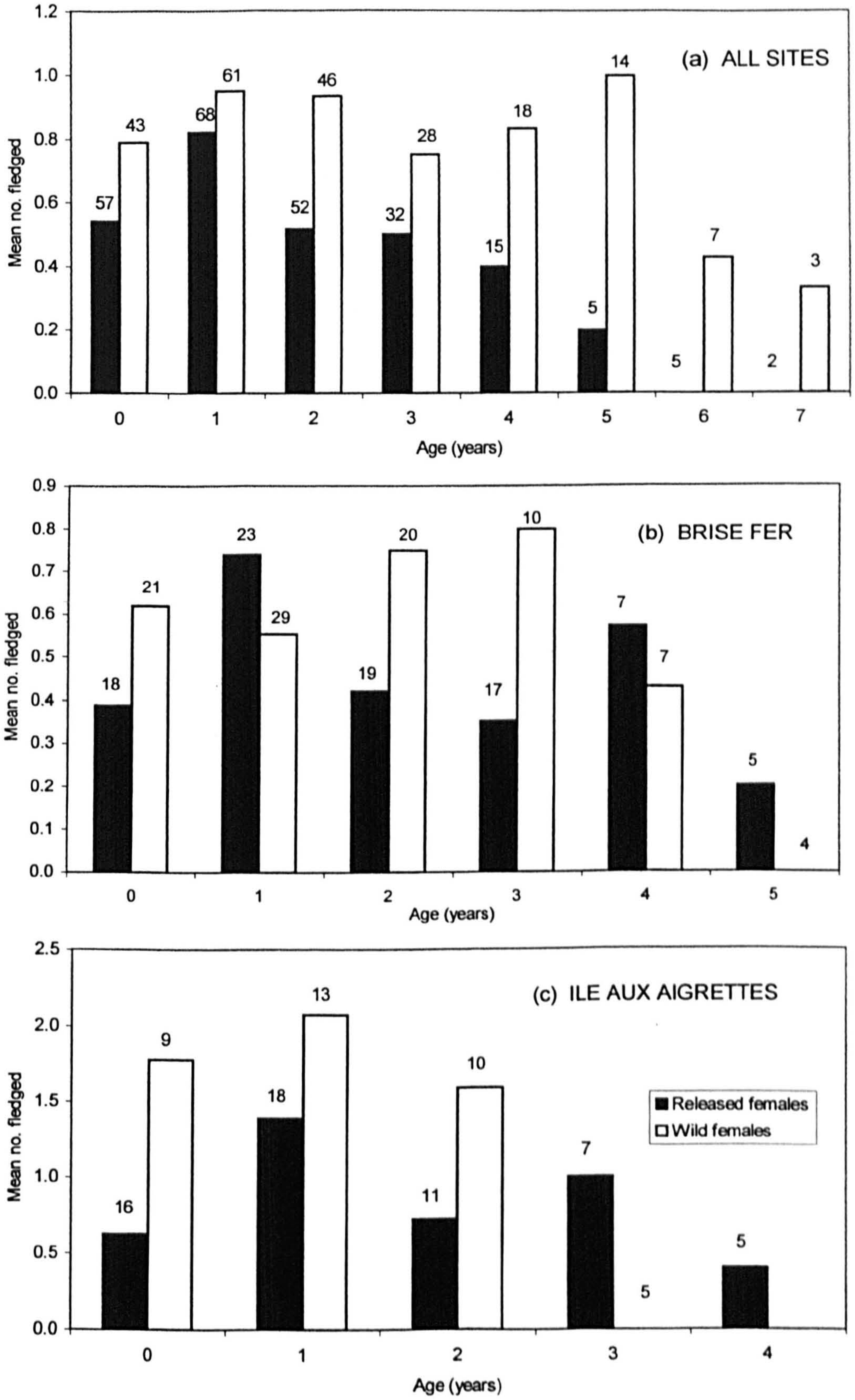

Figure 6.4 Productivity of released and wild females, (a) data for all sites pooled, 1988-98 (b) at Brise Fer 1988-98 (c) at Ile aux Aigrettes 1994-98. Bars represent the mean number of young fledged per paired female. Figures are the number of paired females per age category. Productivity of wild females was significantly better than productivity of released females ($F_{1,7} = 28.58$, $P < 0.001$). Sample size for all sites: 78 released and 78 wild, at Brise Fer 26 released and 33 wild, at Ile aux Aigrettes 20 released and 15 wild.

birds may yet still breed (56 were alive at the end of the study period, between one and two years old) this provided an indication of the recruitment rate into the breeding population.

DISCUSSION

Certain generalisations have been made about reproductive success in birds: (a) a large proportion of fledglings die before they can breed, (b) not all individuals which attempt to breed produce offspring and (c) individuals which breed successfully vary greatly in productivity (Newton 1989*a*). These patterns were seen in wild and released pink pigeons and similar patterns were seen in captive birds (Jones 1995). Although some birds were still alive at the end of the study and had not achieved their full reproductive potential, the variation in individual productivity was believed to reflect the pattern of lifetime reproductive success that would probably be seen over a longer study period. It was difficult to determine if high productivity was due to one individual within the pairing more than the other as young were mostly produced within a single pairing. It may be the combination of mates that comprise the pairing which influenced productivity rather than individual birds. Captive birds are notoriously difficult to pair and compatibility of captive pairs is a key feature for successful breeding (Jones *et al.* 1983), with the result that in the captive population there is a genetic over- representation of certain founder individuals (Jones *et al.* 1989, Lind 1993, Jones 1995).

There were some shortcomings to this study. Total productivity of males and females in different age classes, at different sites and in different years may be slightly over-estimated because there may have been some unknown pairs breeding and young which fledged from undetected nests were assigned to known pairs. Known productivity, including individual productivity, productivity in relation to pairing length and survival time and lifetime reproductive success, is underestimated because not every nest of monitored pairs was found and young that fledged from undetected nests were not assigned to monitored pairs. There was likely some mortality of young between fledging and ringing, although this was probably minimal. However, the number of breeding pairs and the total number of young trapped and ringed were sufficiently known that estimations of productivity were considered good.

Age-specific productivity

For the first four years, productivity in each age group was poorer than for captive birds. This is not surprising as most captive young were foster-reared (which in captivity is more successful than parent-rearing) and captive pairs were not under the same pressures as wild birds. However, the pattern of productivity in captive birds was similar. In Mauritius, the mean productivity of captive females was highest in the second year (year two to three) (2.71 young fledged per paired female) and productivity declined to 0.75 young per female in year five (Jones 1995). Similar patterns were seen in captive populations elsewhere despite different management practises. Captive males showed a greater reproductive life-span than females, up to 16 years for males and 11 years for females (Taynton & Lind 1991, Lind 1993). In 1993 the European captive population held two males breeding at 17 years old.

Some wild females continued to breed at an older age. Two females at Pigeon Wood fledged young at 7.4 years and 8.9 years old, and one still laid eggs (which did not hatch) at 11.4 years old. Most old females which bred were at Pigeon Wood because the survival of birds was higher at this site and because the released sub-populations were established more recently, and fewer birds had achieved older ages by the end of the study. Johnston & Janiga (1995) suggests that senescence may not be important to pigeons as domestic pigeons show a decrease in productivity only at about seven years old, which is probably near the end of their life-span. Captive female pink pigeons show a decline in fertility, hatchability and rearing success after four years old, which was thought to be due to intensive management (Jones 1995). There was some indication in this study that a similar pattern was happening in the wild but further studies of longer-lived birds are required.

The release and management programme enabled a rapid population increase over the study period and up until 1998, the population comprised more than 50% of birds less than two years old (Figure 6.5). At the end of 1998, the population was still relatively young, about 80% less than four years old. Productivity patterns may change in future years as a more stable age distribution is achieved.

Productivity, life-span and breeding life-span

In previous studies breeding life-span has been the major demographic determinant of lifetime reproductive success (Newton 1989*a*). This study provided some evidence for this. Productivity increased with survival time and time paired, although some short-lived birds produced large numbers of young and some long-lived birds produced no young. Productivity is therefore influenced by factors that determine the duration of a pairing and the survival of individuals. Pairings which were disrupted by the death of a mate (42% of pairings ended in death of a mate) or divorce (29% of pairings ended in divorce) may show poor productivity, particularly if pairings had been compatible and productive (see Chapter 4). In previous studies, variation in productivity can be partly accounted for by variation in age at first breeding (Newton 1989*b*, Dhondt 1989). In some birds productivity of first-

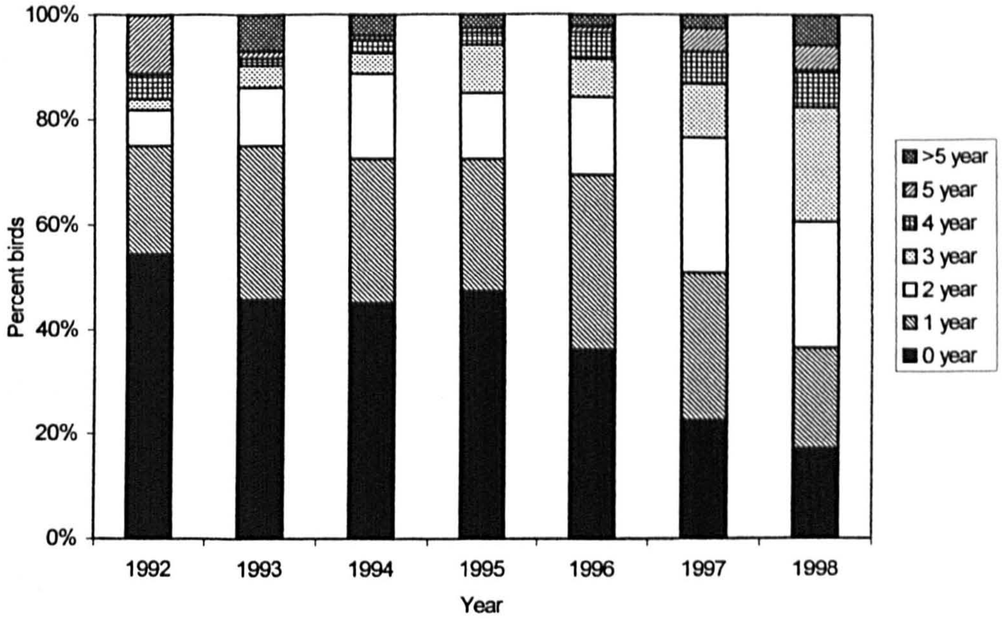

Figure 6.5 Age distribution of pink pigeons, all sites 1992-98.

year breeders is lower but the breeding life-span of second-year breeders is shorter and subsequent lifetime productivity lower (Sternberg 1989). Pink pigeons paired as young as 3.1-3.9 months old and most birds paired between 9-10 months old (Chapter 4). Mortality of first-year birds may disrupt pairing and prolong the onset of breeding, with subsequent effects on productivity. The reasons why some pairings are highly productive and the effect of pairing disruption on subsequent productivity deserves further study.

Lifetime productivity and replacement

On average, pink pigeons which attempted to breed produced enough young to replace themselves by three years old (end of year two) although this varied between sites. However, lifetime reproductive success estimates indicated that a bird did not produce enough young to replace itself within its lifetime. Lifetime productivity was underestimated in this study because it was calculated from birds that had already died within the study period and was therefore biased towards shorter-lived birds. Also lifetime productivity was obtained from known pairs and not all nests of each pair were found. The sample did not include many of the more productive birds, only six out of 19 of the most productive females (each of which produced five or more young each) and only one out of nine males (each of which produced seven or more young each). This may have biased the estimates towards less productive birds. More accurate estimates of lifetime reproductive success will be possible only after more years of study.

The Pigeon Wood population has not been supplemented with released birds, although five immigrant females from released sub-populations bred at this site from 1995. This population increased from 16 birds in 1992 to 77 birds in 1998, suggesting that productivity more than replaced individuals that died. However, releases stopped in 1997 (only five birds were released in January 1997) and the released sub-populations only increased from 217 birds at the end of 1996 to 220 birds at the end of 1998. This is a relatively short time in which to assess sustainability without releases, and Brise Fer suffered a poor breeding season in 1998. However, productivity may not be sufficient to increase the population size rapidly enough so as to minimise any deleterious stochastic and genetic effects, and further releases may be needed.

Productivity of wild and released breeding pairs

Productivity and nest success (Chapter 5) of wild birds was significantly better than for released birds. However, differences between sub-populations may be partly explained by the unequal distribution of wild-fledged breeding birds within each sub-population and habitat may have had an additive effect (Chapter 5).

Providing an enriched social environment is of critical importance for the development of reproductively normal adults (Shepherdson 1994). Captive-bred released birds probably showed poor socialisation and reproductive behaviour due to inadequate rearing methods (Chapter 4). The acquisition of behaviours from the foster-parent species may also cause problems. Cross-fostered black stilts *Himantopus novaezelandiae* in New Zealand migrated with their foster-parent pied stilts *Himantopus himantopus* and did not return to breed, and therefore did not increase recruitment to the black stilt population (Reed *et al.* 1993). Another example from New Zealand included a Chatham Island black robin *Petroica traversi* which nested with its foster-species the Chatham Island tomtit *Petroica macrocephala chatamensis* and gave similar calls (Reed & Merton 1991). It has also been suggested that behavioural traits of a foster-parent species can be exhibited by first generation born progeny of foster-reared released birds (Merton pers. comm.). The depressed productivity of captive-reared pink pigeons may be partly due to long-term socialisation problems in these birds, even after release. The high productivity of wild-fledged birds suggests that productivity may improve as the proportion of wild-fledged birds increases.

Productivity and predation

Reproductive traits in many columbids have evolved in response to predation pressure and selection for efficient seasonal multiple-brooding (Blockstein & Westmoreland 1993) (Chapter 5). Pink pigeons have evolved in the absence of mammalian predators but some avian predators existed such as the green heron *Butoroides striatus*, Mauritius kestrel, harrier *Circus alphonsi* (only known from sub-fossil remains) and vagrant falcons including the peregrine falcon *Falco peregrinus*, although their impact would probably have been small.

Pink pigeons show typical anti-predator behaviours such as the defensive-threat display, 'sleeking', 'freezing', distress calls, nest distraction display and they retain the ability to lose their tail feathers when grabbed (McKelvey 1976, Goodwin 1977). Half-feathered squabs display in response to intrusion into the nest by puffing or rearing themselves up and snapping their bill and older squabs will leap off the nest. It is not clear how these behaviours protect birds and their nests against mammalian predators but many fledged birds have survived attempted predation by macaques due to the ability to lose their tails. Pink pigeons may show other strategies in response to predation pressure. In captive birds, fertility and hatchability of eggs is higher when inter-clutch intervals are shorter (about two weeks after the previous egg-laying date) but this decreases after an inter-clutch interval of more than two months (Jones 1995). This suggests a short-term seasonal response to predation pressure, but which the deleterious effects of cumulative egg production may offset (see below). Despite this, nest success and productivity of pink pigeons is poor when compared to other columbids (Chapter 5). Some of the traits seen in pink pigeons may be remnant behaviours of the ancestral pigeon and their effectiveness is probably reduced due to evolution in the absence of mammalian predators. Pink pigeons may have also developed traits that prevent them from breeding successfully under predation pressure. Jones (1995) suggested that pink pigeons lay larger eggs than expected and invest more in their eggs owing to the lack of predation pressure on pristine Mauritius.

Pink pigeons showed a potential towards longevity and better survival rates than other pigeon species (with predator control and supplemental feeding) (Chapter 3) and some bred in older age. On pristine Mauritius, pink pigeons probably had a longer reproductive life-span and a lower annual productivity.

Supplemental feeding

Supplemental feeding may advance or extend the breeding season, increase breeding intensity of females, increase productivity, body weight and growth rate of juveniles and increase the survival of adults and juveniles (review in Boutin 1990). In this study, supplemental feeding was successful in increasing productivity and facilitating rapid population growth. However, supplemental feeding may also encourage repeated re-nesting, multiple broods and brood overlap which may, together with high nest predation rates, contribute to a shorter breeding life-span of females. Cumulative egg production reduced fertility in captive eggs, which was additional to age effects, and the poor productivity of females over four years old was believed due to intensive management (Lind 1989, Jones 1995).

Genetic implications of variation in individual productivity

The most successful individuals contribute disproportionately to the next generation and in a stable population, the proportion of contributing individuals is likely to remain more or less constant. However, the contribution that an individual makes to a future population will also depend on the population status and trend. A given number of offspring will form a greater proportion of the next generation in a low or declining population than in a large or increasing one (Fisher 1930 *in* Newton 1989*a*). Similarly in expanding populations, where offspring more than replace parents, an offspring produced early in the life-span is more valuable than one produced later because it forms a higher proportion of its cohort (Newton 1989*a*).

In the pink pigeon, disproportionate productivity of individuals that bred early in the recovery programme when the population size was small may have reduced the genetic diversity of the population. This effect may be greatest in the Pigeon Wood population, which was reduced to five original breeding females, only two of which were very productive. In the Brise Fer sub-population, this problem was reduced by the ten-year supplementation of this population with released birds, which were chosen to maximise genetic variability within the population. However, birds that were released and bred later in the programme would have contributed fewer genes than those which were released earlier in the programme. At the Bel Ombre and Ile aux Aigrettes released sub-populations, a larger number of birds were released over a shorter time-period so that larger populations were initially established.

Birds that dispersed between sub-populations also contributed to the genetic diversity of each sub-population (Lande & Barrowclough 1987). Between 1993 and 1998, 12 birds dispersed between mainland sites, eight of which bred (all females) and five produced a total of 18 young (one female produced 12 young). As sub-populations increase in size and the distance between sub-populations decreases, more birds will probably disperse between sub-populations to breed.

The majority of birds which fledge die without producing young themselves and any over-representation of individuals that fledge may be not be apparent in the subsequent breeding population. In this study, recruitment of wild-fledged young into the breeding population was 39%. As an example, at Pigeon Wood between 1990 and 1992, 20 fledged young were produced by five original wild females, 13 of which were produced by just two females. Of these progeny, nine subsequently bred and produced fledged young. The total number of young fledged was 59, but two birds that were not descendants of the two highly productive females produced 30 (51%) of these young. Where lifetime reproductive success of an individual is measured as the number of recruits to the breeding population, the survival of young between fledging and recruitment is important and factors affecting pre-breeding survival of an individual may affect the lifetime reproductive success of its parents. Management to improve pre-breeding survival and to maximise opportunities for birds to enter the breeding population may therefore be a practical way to encourage the maintenance of genetic variation.

Conclusions

Productivity in pink pigeons reflected general trends known in other bird species, namely that a small number of individuals produced a large proportion of young, and productivity was determined by life-span. Productivity was generally poor in pink pigeons, but varied between sub-populations. Productivity of wild birds was better than released birds, and productivity in released sub-populations may not be sufficient to ensure that the pink pigeon population increases to a level required to reduce the effects of demographic and stochastic events. To some extent, poor nesting success and productivity may be offset by the birds' ability to lay multiple clutches and rear several broods in one season. On pristine Mauritius, the pink pigeon was probably longer lived, and had a longer reproductive life-span and lower annual productivity. Management, including predator control, maintained current levels of productivity and without management, productivity may be even poorer. It is anticipated that as the proportion of wild-fledged birds increases, productivity will also increase.

Chapter 7

Parasites, pathogens and disease

INTRODUCTION

The mortality and morbidity of pink pigeons has been closely monitored in captive and free-living birds. Studies of captive birds have identified many causes of sickness and death (Cooper 1987, Jones *et al.* 1989). Studies of free-living birds identified three important diseases and these are investigated here. Trichomoniasis is a transmissible flagellated protozoan parasitic disease primarily affecting pigeons and turkeys. It is characterised by necrotic ulceration of the mouth, oesophagus, crop and proventriculus (Stabler 1954). The parasite, *Trichomonas gallinae*, infects the upper digestive tract and may invade other tissues. Mouth lesions prevent feeding and result in severe emaciation and eventually death. Transmission is directly via crop milk, regurgitated food, during mutual feeding between individuals, or indirectly through water sources. *Leucocytozoon* is a vector transmitted blood parasite that completes part of its lifecycle in the avian host's blood and tissues. The parasite produces an anti-erythrocyte factor that causes intravascular haemolysis and anaemia, which are the principal clinical signs (Garnham 1966), although diagnosis is by screening blood from infected birds. Avian pox (genus *Avipox*) is a viral disease characterised by wart-like scabs on the feet, beak and eyes or diptheritic patches on the mucous membranes. Transmission occurs from latently infected birds and by biting arthropods, in most areas by mosquitoes *Aedes* spp. and *Culex* spp. (Tudor 1991).

METHODS

Trichomoniasis and avian pox

Signs of trichomoniasis and avian pox were looked for in squabs in the nest and in juvenile and adult birds each time they were caught. In pink pigeons signs included yellowish cheesy nodules in the throat and mouth, stringy mucous in the mouth, foul smelling breath, a swollen throat and swelling around the eyes, nares and sinuses. Signs of avian pox included lesions (dry or suppurating) on the feet, tarsi, beak, vent or around the eye, a dry flaky bill usually associated with loss of keratin and creamy nodules on the tongue. Scarring from healed pox lesions and twisted or over-extended mandibles usually indicated a previous infection in fledged birds although mandibles could also be disfigured after recovery from trichomoniasis. Pox lesions from infected birds were sent to the University of Giessen, Germany, for isolation of the virus.

Squab growth

Squab growth was monitored on Ile aux Aigrettes. Body mass of squabs was measured every two or three days from hatch. Most squabs were not weighed beyond about 15 days because disturbance caused squabs to leave the nest. Squabs were weighed on a digital balance to the nearest 0.1g up to 10 days old and with a spring balance to the nearest gram after this age.

***Leucocytozoon* studies**

Captive, released and wild birds were screened for infection with the *Leucocytozoon* blood parasite between 1994 and February 1999. Samples were collected from released birds pre and post-release, wild-fledged birds when trapped and ringed, or from squabs on the nest. Between August and September 1996 and in February 1999 birds were trapped for intensive screening surveys. A blood sample was taken from the brachial vein or the medial metatarsal vein and two blood smears were prepared per sample. Blood smears were fixed in methanol and Giemsa stained (Peirce & Prince 1980) and sent to a specialist for reading. Parasites were recorded as either present or absent on each smear. The sample from each bird was recorded as infected (at least one smear with parasites present) or not infected (both smears with no parasites present). In samples collected in 1996 and 1999, each smear was also scored according to the number of parasites present. A post-mortem examination was carried out on birds found dead in the field and samples collected. Tissue samples from captive and released birds were examined histologically (Wheler & Riddle 1996 *in litt.*).

Treatment

Where trichomoniasis was detected or suspected, birds were individually treated with an antiprotozoal, carnidazole (brand name "Spartrix"). One dose of 10 mg (one tablet) was administered to adults and juveniles. From 1994 some wild-fledged juveniles were treated at ringing as a routine precaution. On Ile aux Aigrettes squabs were administered 5 mg on alternate days for as long as symptoms persisted. In June and September 1996, the whole population on Ile aux Aigrettes was treated via the drinking water with a seven-day course of ronidazole (brand name "Ronitrol"). Further treatments were carried out in November 1996 (with dimetridazole (brand name "Harkanker") for five days and a repeat treatment with ronidazole owing to the poor acceptability of Harkanker) and October 1997. Between September 1998 and January 1999, the island population was again treated once a month via the drinking water. Some severely affected individuals were removed to captivity for treatment.

Avian pox was not treated but a few severely affected individuals were removed to captivity for supportive treatment. In February 1994, seven pigeons awaiting release on Ile aux Aigrettes were vaccinated with a live domestic pigeon pox vaccine (Intervet: Nobilis). A further 62 captive birds were vaccinated in May 1994 20 of which were later released, 18 at Ile aux Aigrettes and two at Bel Ombre. Vaccine was brushed over open feather follicles on the thigh from which three to four feathers had been plucked. Reaction to the vaccine was recorded as negative, mild (characterised by scabs forming in the plucked follicles but little reaction under the skin) or strong (characterised by scabs in the plucked follicles and granulomas under the follicle skin).

Analysis

The term pathogen and pathogenic are used to mean an organism capable of causing disease. The term 'disease' is not synonymous with infection and birds may be infected with pathogens but not diseased. Disease here means a clinically abnormal state resulting from infection that may affect physiological function or performance. Clinical signs are objectively observed changes in the body or bodily function that indicate disease. Sub-clinical infections may only be detected at post-mortem examination. The prevalence rate is the number of affected birds at a point in time and the incidence rate is the number of new cases over a time period. Trichomoniasis and leucocytozoonosis are the manifestation of the disease and are not synonymous with infection with the parasite.

Incidence and prevalence rates of infection were investigated in squabs and free-living birds. Data from captive birds were used to substantiate effects found in wild birds. The Kaplan-Meier method (Chapter 3) was used to investigate squab survival with trichomoniasis and the survival of fledged birds infected with *Leucocytozoon*. Squabs removed to captivity were treated as censored data. Cox's proportional hazards model was used to test the differences in survival (Chapter 3). In studies of trichomoniasis Chi-squared analysis was used to test the relationship between seasonality of incidence and the effect of treatment on the number of birds fledged. ANOVA (MINITAB 8.21, 1991) was used to test for differences in squab growth. In *Leucocytozoon* studies, Chi-squared analysis was used to test the prevalence rates in captive, released and wild birds, the prevalence of infection at different sites, prevalence and age of birds and prevalence and seasonality. All mean values are followed by the standard deviation (± SD).

RESULTS

Trichomoniasis

Trichomoniasis was first found in a wild squab at Pigeon Wood in July 1992. At mainland sites a total of 17 cases were recorded: five at Pigeon Wood, five at Brise Fer and seven at Bel Ombre. Only one further case of trichomoniasis in a squab was recorded at Brise Fer in 1996 and all other cases were in fledged birds between 1996 and 1998. Of the 16 cases recorded in fledged birds, eight survived. Incidence of trichomoniasis was highest at Ile aux Aigrettes where it was found in a wild-fledged bird and in a brood of two squabs in October 1994. Squabs, fledglings and adult birds showed signs of disease and subsequent analysis has focussed on this sub-population.

Trichomoniasis in squabs on Ile aux Aigrettes

Trichomoniasis was recorded in 48.6% of squabs (Table 7.1). There were no significant seasonal differences (hot and wet: January to April, cool winter: May to August, hot and dry: September to December) in the incidence of squabs with trichomoniasis ($\chi^2_2 = 0.89$, $P > 0.05$). Disease incidence in squabs in single broods and broods of two was similar. It was likely that some squabs which showed no obvious signs of disease were infected, which may partly account for the lower incidence in second-hatched squabs. Of the 48 cases where disease was not recorded, 21 squabs (44%) died between 0 and two days old. Signs of disease were detected between one and 24 days old (mean 8 ± 4.8 days) and diseased squabs which died before fledging died between two and 25 days old (mean 11 ± 5.9 days).

Table 7.1 Incidence of trichomoniasis in squabs on Ile aux Aigrettes, 1994-98. In a brood of two, squab 1 was the first-hatched and squab 2 was the second-hatched.

	Single Squab	Brood of two Squab 1	Brood of two Squab 2	All squabs
No. not diseased	50	24	30	114
No. diseased	46	31	22	108
No. not recorded	24	9	12	48
Total no. squabs	120	64	64	270
% diseased of known	47.9	56.4	42.3	48.6

Trichomoniasis was widespread in the offspring of breeding pairs, 30/35 males and 26/33 females produced squabs which became diseased. In the remaining five males and seven females, too few squabs were produced to confirm infection. Of the parent birds that produced diseased squabs, all produced some diseased young but the proportion of squabs that became diseased differed between pairs. Only two out of 19 squabs examined from one pair became diseased. In contrast, 16 out of 18 squabs examined from one female and six squabs examined out of seven produced by one male became diseased.

Survival

Table 7.2 shows the number of diseased and treated squabs that fledged. No diseased squabs survived if not treated but in 13 cases, disease was detected on the day of death. The relationship between the number of squabs which fledged or died and were diseased or treated was significant ($\chi^2_3 = 36.5$, $P < 0.001$). Figure 7.1 shows Kaplan-Meier estimates of survival for squabs that were diseased or showed no signs of disease and were treated or not treated, the differences in squab survival were highly significant. The number of squabs surviving that did not show signs of disease was significantly better when squabs were treated than when not treated ($\chi^2_1 = 16.4$, $P < 0.001$). Survival of all treated squabs (62%) was significantly better than survival all of untreated squabs (27%) (Wald = 29.9, df = 1, $P < 0.0001$).

Table 7.2 Number of diseased squabs and squabs that showed no signs of disease which survived to fledge on Ile aux Aigrettes, 1994-98. Kaplan-Meier estimates of squab survivorship are presented.

	No. squabs	No. fledged	No. died	No. removed	% survival to fledge
Diseased / untreated	19	0	18	1	0.0
Diseased / treated	89	47	34	8	54.2
No disease / untreated	84	28	45	11	36.7
No disease / treated	30	24	5	1	82.4
All squabs	222	99	102	21	-

Seasonality of survival

The percentage of squabs that fledged was lowest in the dry season (September to December) and highest in the wet season (January to April) than during other times of the year (Table 7.3). In the dry season, fewer untreated squabs survived (12/58, 20.7%) than at other times of the year (16/45, 35.6%).

Table 7.3 Number of diseased squabs and those that showed no signs of disease, that hatched each season and survived to fledge on Ile aux Aigrettes, 1994-98. Seasons are January-April (hot, wet), May-August (cool winter) and September-December (hot, dry). Rem = removed.

	January - April					May - August					September - December				
	No. squabs	No. fledged	No. died	No. rem	% fledged	No. squabs	No. fledged	No. died	No. rem	% fledged	No. squabs	No. fledged	No. died	No. rem	% fledged
Diseased/ Untreated	2	0	2	0	0.0	6	0	6	0	0.0	11	0	10	1	0.0
Diseased/ Treated	23	13	7	3	56.5	25	13	9	3	52.0	41	21	18	2	51.2
No disease/ Untreated	16	6	7	3	37.5	21	10	10	1	47.6	47	12	28	7	25.5
No disease/ Treated	8	6	1	1	75.0	7	5	2	0	71.4	15	13	2	0	86.7
Total	49	25	17	7	51.0	59	28	27	4	47.4	114	46	58	10	40.3

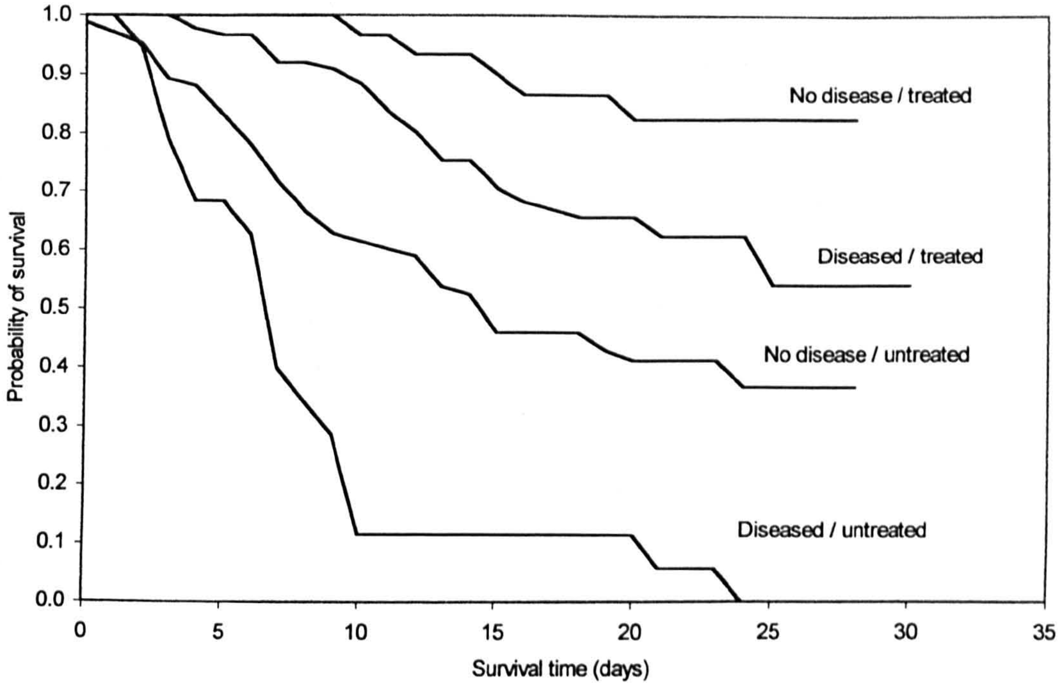

Figure 7.1 Survival of squabs on Ile aux Aigrettes where squabs showed signs if trichomoniasis and were treated, 1994-98. Kaplan-Meier estimates of survivor function are plotted. Sample size: 222 squabs (54% censored). The differences in survival were highly significant (Wald = 53.01, df = 3, P < 0.0001).

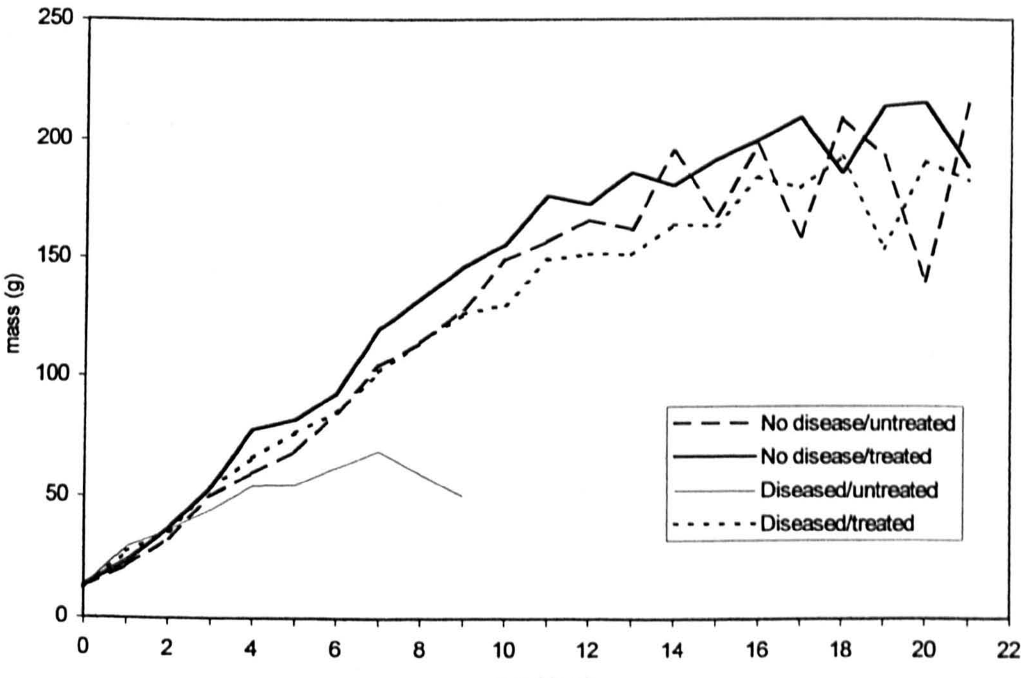

Figure 7.2 Squab growth on Ile aux Aigrettes where squabs did or did not show signs of trichomoniasis and were or were not treated, 1994-98. Sample size: 205 squabs. Excluding those squabs that were diseased and not treated, differences in growth were not significant.

Squab growth

Excluding squabs that were diseased and not treated, there was no significant difference in squab growth (Table 7.4 and Figure 7.2) and there was no significant difference in the mean age at fledging. Growth of diseased untreated squabs was poor and most squabs did not survive for more than 10 days, achieving only 50-70g at 7-10 days old. Diseased untreated squabs were excluded from the analysis as sample sizes were small.

Table 7.4 Comparison of squab growth on Ile aux Aigrettes, 1994-98, where squabs did or did not show signs of trichomoniasis and were or were not treated (results presented with means, standard deviations, ranges and sample sizes).

Variable	No disease/ Not treated	No disease/ Treated	Diseased/ Treated	ANOVA
Mass at 6 days (g)	85.1 ± 27.3 (43 - 130) 19	93.2 ± 13.1 (70 – 115) 9	85.0 ± 23.2 (70 - 100) 31	F=0.46, df=2,56, P > 0.05
Mass at 12 days (g)	166.1 ± 36.1 (90 - 220) 9	173.2 ± 21.0 (130 – 202) 11	151.5 ± 38.4 (117 - 205) 24	F=1.66, df=2,41, P > 0.05
Mass at 18 days (g)	209.2 ± 54.3 (110 - 260) 6	186.3 ± 19.5 (164 – 200) 3	193.1 ± 32.0 (130 - 225) 11	F=0.53, df=2,17, P > 0.05
Fledging age (days)	22.5 ± 3.2 28	23.0 ± 3.2 24	22.7 ± 3.7 47	F=0.14, df=2,96, P > 0.05

Post-fledging survival on Ile aux Aigrettes

Kaplan-Meier estimates of post-fledging survival was recorded for 95 birds (Table 7.5). Survival estimates were from fledging to the end of each age group and 32% were censored. Of the 95 birds which fledged, 53 (56%) died at less than 150 days old and 46 (48%) died at less than 70 days old, 35 of which were treated for trichomoniasis as squabs and 11 of which were not treated. Post-fledging survival of squabs in the three cohorts was not significantly different (Wald = 1.85, df = 2, P > 0.05) but the sample sizes were small.

Table 7.5 Kaplan-Meier estimates of post-fledging survival of birds that did or did not suffer from trichomoniasis as squabs, Ile aux Aigrettes 1994-98.

Age (years)	No disease / untreated			No disease / treated			Diseased / treated		
	No. birds	No. died	% survival	No. birds	No. died	% survival	No. birds	No. died	% survival
0	24	12	50.0	24	16	33.3	47	32	31.9
1	11	1	45.4	6	1	27.8	15	2	27.1
2	9	0	45.4	1	0	27.8	10	0	27.1
3	4	0	45.4	-	-	-	5	1	20.3

Trichomoniasis was recorded in four recently fledged birds at Pigeon Wood (in one of which infection had been diagnosed as a squab) of which three died between 29 and 37 days old. Two juveniles at Bel Ombre were diagnosed one of which died but as an adult at 163 days old.

Mortality of birds more than 150 days old

Trichomoniasis was detected in 21 birds more than 150 days old in all four sub-populations and was the cause of death in eight cases (Table 7.6). Birds that died of the disease died between 0.4 to 2.6 years old (mean 1.3 ± 0.7 years). Trichomoniasis did not always cause death and birds that lived for several years after disease was detected probably became carriers. Two birds diagnosed at Ile aux Aigrettes in 1996 at 38 and 44 days old and treated were still alive at the end of the study period. Two birds at mainland sites were found with signs at 2.5 and 5.5 years old.

Table 7.6 Number of cases of trichomoniasis recorded in birds more than 150 days old, all sites, 1992-98.

Site	No. diseased and survived	No. diseased and died	All birds
Brise Fer	4	1	5
Pigeon Wood	0	1	1
Bel Ombre	3	3	6
Ile aux Aigrettes	6	3	9
All birds	13	8	21

Leucocytozoonosis

Leucocytozoon marchouxi was the species that infected pink pigeons. On average 36% of birds were infected and there was no significant difference in the prevalence rates between captive, released and wild birds ($\chi^2_2 = 0.088, P > 0.05$) (Table 7.7). This analysis included 66 samples from 65 birds from which only one smear was screened, which may have given a false negative result.

Table 7.7 Number of birds infected with *Leucocytozoon marchouxi*, all sites 1994-99.

	No. samples	No. birds	No. +ve samples	No. +ve birds	% +ve samples	% +ve birds
Captive birds	33	33	10	10	30.3	30.3
Released birds	121	92	39	35	32.2	38.0
Wild birds	112	96	37	35	33.0	36.5
All birds	266	220	86	80	32.3	36.4

Degree of infection

Samples taken in 1996 and 1999 were scored to assess the degree of parasitaemia in infected birds. Two blood smears per sample were screened in 184 samplings from 167 birds (Table 7.8). Samples with 11 or more parasites per smear indicated high levels of parasitaemia and was found in 12 cases (6.5%) representing 11 birds, one of which was sampled twice. The results suggested that high parasitaemias were always indicated in both blood smears but that in low parasitaemias, the number of parasites was sometimes too low to be detected in both smears.

Table 7.8 Degree of parasitaemia of *L. marchouxi* in two blood smears per sample, 1996 and 1999.

Level of parasitaemia					Slide 2			
			L (+)	L+	L++	L+++	L++++	Negative
Slide 1	L(+)	1 parasite	6	3				14
	L+	2-5 parasites	3	10				2
	L++	6-10 parasites		2	4			
	L+++	11-20 parasites				8		
	L++++	over 21 parasites					4	
	Negative							128

Prevalence and site

The prevalence of infection per sample was not significantly different between sites ($\chi^2_4 = 4.65, P > 0.05$) (Table 7.9).

Table 7.9 Prevalence of *L. marchouxi* at different sites, 1994-99.

Site	No. samples	No. Birds	No. +ve samples	No. +ve birds	% +ve samples	% +ve birds
Brise Fer	39	36	11	11	28.2	30.5
Pigeon Wood	16	15	8	8	50.0	53.3
Bel Ombre	80	60	30	27	37.5	45.0
Ile aux Aigrettes	98	78	27	24	27.5	30.8
Black River aviaries	33	33	10	10	30.3	30.3
All sites	266	220	86	80	32.3	36.4

Prevalence and age

Infection in samples taken from birds less than one year old was significantly higher (37%) than samples taken from birds more than one year old (25%) ($\chi^2_1 = 4.27, P < 0.05$) (Table 7.10). Parasites were recorded in five out of 18 squabs and all positive squabs were at Ile aux Aigrettes. The youngest squab in which infection was recorded was six days old from Ile aux Aigrettes.

Table 7.10 Prevalence of *Leucocytozoon* infection with age, all sites 1994-99.

Age (years)	No. samples	No. birds	No. +ve samples	No. +ve birds	% +ve samples	% +ve birds
0	165	144	61	58	37.0	40.3
1	51	50	16	16	31.4	31.4
2	29	29	4	4	13.8	13.8
3	11	11	3	3	27.3	27.3
4	4	4	2	2	50.0	50.0
≥5	6	6	0	0	0.0	0.0

Seasonality

The prevalence of *Leucocytozoon* per sample was not significantly different between seasons ($\chi^2_2 = 2.79, P > 0.05$) (Table 7.11).

Table 7.11 Seasonality of *Leucocytozoon* prevalence, all sites 1994-99

Season	No. samples	No. birds	No. +ve samples	No. +ve birds	% +ve samples	% +ve birds
January-April (hot wet)	72	72	23	23	31.9	31.9
May-August (cool winter)	82	79	32	30	39.0	38.0
September-December (hot dry)	112	105	31	33	27.7	31.4

Survival and mortality

Kaplan-Meier estimates of survival to five years old was 44% in uninfected birds and 37% in infected birds but these differences were not significant (Figure 7.3). There was also no significant difference in the post-sample survival time of infected and uninfected birds between 1994 and 1998 (Wald = 0.137, df=1, $P > 0.05$, n = 190, 60% censored). Mean age at death of infected birds was 1.4 ± 1.2 years (n = 29) and of uninfected birds was 1.8 ± 1.3 years (n = 50). Mean post-sampling survival time of infected birds which died was 0.8 ± 0.9 years (n = 29) and of uninfected birds which died was 0.9 ± 0.9 years (n = 50).

Of the 13 birds which showed high parasitaemia (11 or more parasites per slide), mean survival after the sample was taken was 1.7 ± 1.1 years and mean survival time was 1.9 ± 1.2 years old. One bird which showed high parasitaemia at 16 days old and again at 219 days old was still alive at 2.9 years old.

Leucocytozoonosis was recorded in 20 of 45 pink pigeon samples submitted post-mortem for histology (11 captive birds and nine wild or released birds), five of which were from squabs. The youngest birds to die from leucocytozoonosis were two captive squabs that died at 16 and 18 days old. A squab that tested positive for parasites at six days old died at 13 days old although leucocytozoonosis was not confirmed as the cause of death at post-mortem. Leucocytozoonosis was the primary cause of death in 15 birds. In three additional cases (all wild birds) leucocytozoonosis was recorded along with other disease (avian pox and aspiration pneumonia, coccidiosis, parasite eggs in the ureters) and in two cases with accidental death (oesophageal obstruction and a gastric foreign body). Most birds affected were juveniles (mean age at death 63 ± 24 days, n = 14) with only one adult (1.7 years old at death). Mean age of squabs at death was 19 ± 6 days (n = 5).

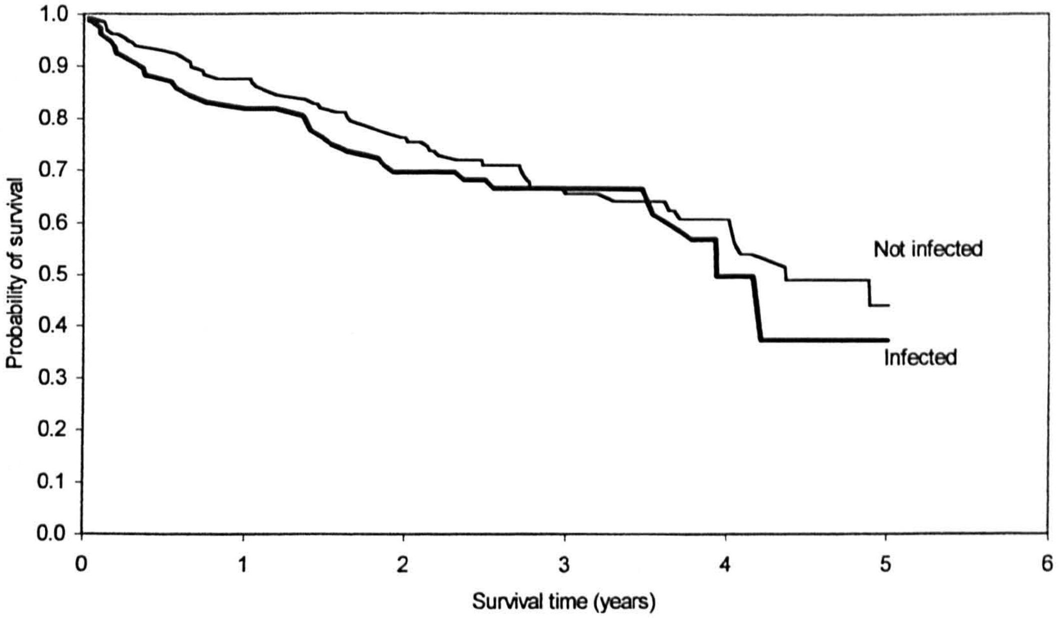

Figure 7.3 Survival to five years old of fledged birds infected with *Leucocytozoon marchouxi*, 1994-98. Data for all sites pooled. Kaplan-Meier estimates of survivor function are plotted. Sample size: infected birds 79, uninfected birds 136 (63% censored). There was no significant difference in survival of infected and uninfected birds (Wald = 0.389, df = 1, $P > 0.05$). Data included a sample of 31 birds taken in February 1999. For the purpose of the analysis it was assumed that the infection status of these birds was the same at the end of December 1998.

Birds sampled twice

Forty-two birds were sampled twice. Repeat samples were taken between eight days to 2.4 years apart (mean 1.0 ± 0.9 years, n = 46 repeat samples). Of birds sampled twice, 24 were negative in both samples and six were positive in both samples. Twelve were positive for only half the samples, in six cases the infection was lost and in six cases an infection was gained.

Leucocytozoon in exotic Columbiformes

From 1994 to February 1999, 79 samples were collected from exotic Columbiformes, six (7.6%) of which were positive for *L. marchouxi* (Table 7.12) and no other blood parasite was identified.

Table 7.12 *Leucocytozoon* infection in exotic Columbiformes, 1994-98. Site abbreviations are IAA = Ile aux Aigrettes, BO = Bel Ombre, BR = Black River, BF = Brise Fer, unk = unknown origin. In 38 samples (34 from Madagascar turtle doves) only one blood smear per sample was screened.

Species	No. samples	No. +ve samples	% +ve samples	Site sampled
Madagascar turtle dove *Streptopelia picturata*	53	4	7.5	40 from IAA, 5 BO, 8 unk
Barred ground dove *Geopelia striata*	13	1	7.7	9 from BR, 2 BF, 1 IAA
Spotted dove *Streptopelia chinensis*	6	1	17	4 from BR, 2 IAA
Barbary dove *Streptopelia risoria*	7	0	0	All from BR (captive)

Avian pox

Avian pox was first recorded in a captive pink pigeon in July 1993. Subsequently, at the captive-breeding centre, 22 birds became infected over the following six months, 18 of which were in October and November. A further seven birds were infected in 1994, two of which showed signs after vaccination. Avian pox was first recorded in the wild in October 1993 in a wild-bred bird at Brise Fer. In total, 69 cases of avian pox have been documented, 11 squabs, 34 juveniles and 24 adult birds, 54 of which were observed between 1995 and 1997. Avian pox was observed only in the three released sub-populations, although one possible case of a bird showing scars from an old pox infection was documented at Pigeon Wood. Of fledged birds, 23 cases were observed in released birds and 35 in wild birds. Pox was the believed to be the primary cause of death in 20/69 (29%) cases and only seven birds (10%) lived for more than one year after infection was detected.

Reaction to vaccination

A negative reaction to the vaccine suggested that the birds were already immune. Only five birds were known to have suffered from pox prior to vaccination and may have developed an immunity. Birds in captivity from July to December 1993 would have been exposed to the virus and may have developed sub-clinical disease. Of the 13 birds that showed no reaction, none hatched after December 1993 and were therefore all likely exposed to the virus. Of the 56 birds that showed a mild or strong reaction, 28 hatched after the outbreak in 1993 and prior to the 1994 outbreak and may not have been exposed. Nine birds reacted to the vaccine, despite being previously infected with pox less than one year prior to vaccination. Two birds developed pox after vaccination, one of which was caused by the vaccine and the other developed pox only two months after vaccination (Table 7.13).

Table 7.13 Reaction to the vaccine for domestic pigeon pox.

Reaction	No previous pox	Previous pox infection	Pox post vaccination	All birds
Negative	8	5	0	13
Mild	18	6	0	24
Strong	27	3	2	32
Total	53	14	2	69

Infection with several pathogens

During their lifetime, infections with more than one pathogen was recorded in 26 wild or released birds. Eight birds were infected with *L. marchouxi* and suffered from avian pox, eight birds were infected with *L. marchouxi* and suffered from trichomoniasis, nine birds suffered from trichomoniasis and avian pox and one bird suffered from all three. Mean age at death of 16 birds was 0.8 ± 1.1 years old. Mean age of 10 birds still alive at the end of the study period was 3.2 ± 1.6 years old.

DISCUSSION

Infectious and parasitic diseases play an important part in regulating animal populations by affecting breeding success and mortality. Parasites reduce breeding success of birds, either by affecting the condition of the adults or affecting the condition and survival of chicks (review in Møller *et al.* 1990 and Newton 1998). Disease as a cause of adult mortality in wild birds is difficult to assess owing to a difficulty in obtaining a random cross-section of deaths, and the interaction of disease with other variables affecting survival, e.g. food shortages and predation. In some species parasites and disease cause high mortality (Bellrose 1980). In a summary by Dobson & May (1991) of causes of mortality in four large scale post-mortem analyses of birds, between 6.1% and 24.7% mortality was due to viral, bacterial, fungal and parasitic diseases.

The impacts of disease on a population are unlikely to be wholly additive to other causes of mortality because contributing causes and interactions with other causes of mortality are apparent. For example, individuals weakened by starvation might be vulnerable to disease and individuals with high levels of intestinal parasites may be more susceptible to food shortages. Disease may predispose individuals to predation that in turn may reduce the spread of disease (Hudson 1992). The effects of disease are probably compensatory to other causes of mortality so that, in the absence of deaths from disease, a similar number of deaths would occur from other causes. Even if a large proportion of deaths is attributable to disease, this does not provide conclusive information about the effects of disease at the population level because of interactions with other causes of mortality.

Disease in threatened populations

The role of pathogens in threatened populations and the possibility that it may cause the decline and extinction of small populations has been reviewed (Cooper 1989*b*, Peirce 1989). One of the most significant threats is the introduction and spread of alien bird species to new areas which may expose indigenous species to diseases with which they have had no previous contact and may have little resistance (Stabler 1954, Conti & Forrester 1985, Harmon *et al.* 1987). Isolated or oceanic island populations are particularly vulnerable. Introduced diseases may have caused the extinction of up to half of the indigenous land birds of Hawaii (Warner 1968) and continue to restrict the distribution of extant native species (van Riper *et al.* 1986).

In addition, because endangered or rare species often exist in small populations, they are unlikely to sustain disease infections and may acquire them only from other more common host species (Dobson & May 1991). Because individuals may rarely be exposed to a pathogen, they do not acquire immunity and when an epidemic does occur it therefore may kill a large proportion of the population (Newton 1998).

Another threat to endangered populations are generalist parasites able to utilise a range of species as hosts. In small relict populations, benign host-specific parasites may have become extinct due to lack of host access. Endangered species may be more vulnerable to infection with less host-specific parasites as they are probably also suffering from stress factors such as food shortages and habitat loss (Peirce 1989, Dobson & May 1991). In addition reduced genetic variability and inbreeding may increase susceptibility to disease (Ralls *et al.* 1980, Thorne & Williams 1988, May 1988). Genetic impoverishment may also reduce the chance of withstanding future disease challenges.

Disease in the pink pigeon

There have been several investigations of disease, developmental deformities and causes of mortality in captive adult pink pigeons and squabs (Flach 1984, Cooper *et al.* 1987, Jones *et al.* 1989, Flach & Cooper 1991, Spencer 1993). In a review of captive birds, Jones *et al.* (1989) attributed mortality of fledged birds due to infectious disease in only 10/79 (12.7%) of cases.

In the pink pigeon, several possibilities may explain the apparent susceptibility to pathogens observed in wild birds. The most likely scenario is that pathogens have been introduced with exotic species, to which the pink pigeon has little immunity. Another possibility is that the vector for *Leucocytozoon* and pox did not arrive with the ancestral pink pigeon, the disease died out and the pigeon lost its immunity. A third possibility is that pathogens could not persist within the small population, and because of poor exposure to the pathogen, any immunity was lost. These scenarios are complicated by inbreeding, the effects of habitat degradation and loss and the distribution of alien hosts and vectors that may have changed over the centuries. Three species of dove were introduced to Mauritius in the eighteenth century, all of which overlap in range with the pink pigeon. Feral pigeons *Columba livia* were not mentioned before 1859 (Cheke 1987) and do not overlap with the current pink pigeon distribution, although they do overlap with the range of other introduced doves.

In 1999 13 wild and nine captive pink pigeons were screened for a range of viruses (avian reovirus, avian adenovirus, paramyxovirus, pigeon herpesvirus and pigeon pox). All tests were negative (Greenwood pers. comm. 1999) suggesting that these birds had not been previously exposed to many viruses commonly found in other pigeon species (Johnston & Janiga 1995). Mortality of captive pink pigeon squabs due to a herpesvirus transmitted by foster domestic pigeons was recorded at Albuquerque Zoo (USA) (Snyder *et al.* 1985) and Harewood Bird Park, UK (Greenwood pers. comm.).

Trichomoniasis

Trichomonas gallinae is probably the most common parasite in pigeons. The primary host is the domestic pigeon but the parasite has been recorded from a range of pigeon species (Stabler 1954, Murton 1965, Rowan 1983). Clinical disease is usually only found in young birds and adults probably do not die from the disease alone. Mortality can be high when birds are compromised by other factors such as concurrent disease or if a virulent strain is encountered. In feral pigeons incidence rates of between 54% and 64.5% are recorded (Stabler 1954, Johnston & Janiga 1995). In three species of wild Colorado columbids, incidence was 36.6% (Stabler 1951). Incidence and mortality in squabs may be higher and up to 75% mortality (of 200 squabs) has been recorded (review in Stabler 1954).

Different strains of *T. gallinae* may exist within a population and particularly virulent strains may cause massive mortality. An epizootic in Alabama in 1951 and 1952 may have caused deaths of between 25-50,000 mourning doves *Zenaida macroura* per year (Haugen & Keeler 1952). An avirulent infection or the survival of a virulent one may provide protective immunity against further exposure to a virulent strain (Stabler 1954). However resistant birds may be carriers of virulent strains without developing lesions and are possible sources of infection to susceptible birds. In California, a lethal strain of *T. gallinae* was responsible for the deaths of at least 16,000 native band-tailed pigeons *Columba fasciata* in 1988 (Conti 1993).

Trichomoniasis in pink pigeons

Trichomoniasis was first recorded in pink pigeons by McKelvey (1976) in a captive squab foster-reared by Madagascar turtle doves *Streptopelia picturata.* No further cases were known in captivity or in the wild until free-living birds came into contact with exotic birds. Jones *et al.* (1989) reported at least six cases of mortality due to trichomoniasis, including two released females and their young, at Pamplemousses Botanical Gardens. Trichomoniasis quickly became established in pink pigeons at Ile aux Aigrettes owing to the high numbers of exotic birds at this site and the lack of fresh water. Before trichomoniasis was perceived as a potential problem, water was provided for birds on Ile aux Aigrettes from which pink pigeons and introduced species drank but it is possible that the limited natural sources were also contaminated. The parasite was found from crop swabs in all three species of exotic doves, with no signs of disease. Lesions from trichomoniasis have been seen in barred ground doves *Geopelia striata*, feral pigeons and Mauritius kestrels *Falco punctatus* on Mauritius.

In pink pigeons, different signs were seen which may have been associated with different strains or variation in the squab's immunity. Squabs typically showed either mouth lesions (yellow cheesy nodules) or inflammation of the sinuses, tissue around the eyes and head, with mouth lesions scarce or absent. Stabler (1954) records that certain strains have a predilection for certain tissues.

Parent birds that produced diseased squabs were themselves likely infected with the parasite. However, it was possible that parents could transmit the parasite (e.g. through water) without becoming infected. Infection in birds that did not show signs of disease could only be determined using crop swabs, but detection of the parasite was generally poor. The 48.6% of squabs that showed signs of disease was probably an underestimate of the true prevalence of infection. Survival of squabs that did not show signs of disease was significantly better when squabs were treated than when not treated. Because treatment improved survival this suggested that both groups of squabs were probably infected.

Not all treated squabs survived, and the age of the squab and the extent of the disease when treatment started may explain some of the differences in survival. Other disease such as avian pox and infection with *Leucocytozoon* compromised the survival of some squabs. In contrast, treatment with antiprotozoals for trichomoniasis may have improved the squab's condition and reduced mortality due to other disease. Second-hatched squabs were less likely to survive than first-hatched squabs (Chapter 5) and, although disease incidence in second-hatched squabs was not different, inanition and poor growth further compromised the survival of diseased second-hatched squabs. In eight broods of two where both squabs were treated, one squab died of trichomoniasis while the other fledged. In seven of these broods, both squabs showed signs of disease but in one brood only the second squab showed signs. Different strains may affect squab survival but there was no evidence that possible virulent strains were associated with seasonality. The severity of the disease differed between squabs and about half of the diseased squabs developed a chronic infection. The 37% survival of untreated squabs that did not develop the disease suggests that these squabs may have been resistant or did not become infected at all. The survival of

18/84 of these squabs may been improved by treatment of the parents. From 1997 to 1998 a further 19 birds fledged which had not been monitored on the nest (and not treated), nine of which may have benefited from treatment of the parents. Some parents may have better resistance than others and the differences in squab survival between pairs may also be due to a lower number of parasites transmitted by the parents.

Mortality from trichomoniasis may depend on the immunocompetency of the bird, which in turn may be affected by previous exposure, inbreeding, nutrition, body condition and infection with other disease. Mouth lesions compromised feeding and malnutrition affected survival. The lack of any difference in squab growth was surprising but may be partly because squabs that had mouth lesions that restricted feeding died before growth was markedly affected. This would be especially acute in very young squabs. Death of chronically infected squabs was usually within two to three days after disease was first detected.

Leucocytozoonosis

The blood parasite *Leucocytozoon* is a cause of serious disease in domestic poultry and waterfowl and has been documented as a cause of localised epizootics in Canada geese *Branta canadensis* and other wild waterfowl populations (Herman *et al.* 1975, Atkinson & van Riper 1991). *Leucocytozoon marchouxi* is the only species of the genus occurring in Columbiformes where it is widely distributed (Bennet & Peirce 1990, Bennett *et al.* 1994). In columbids, it has been reported only once as being pathogenic, which was in an emerald-spotted wood dove *Turtur chalcospilos* which also had an infection with *Haemoproteus columbae* (Peirce 1984*a*). *Leucocytozoon* was identified in Mauritian columbids (in barred ground doves) by Maya (1912). In a survey of avian haematozoa in Mauritius (Peirce *et al.* 1977), *Leucocytozoon marchouxi* was recorded from the barred ground dove and spotted dove *Streptopelia chinensis* but was not reported in pink pigeons until later (Peirce 1984*b*, Jones *et al.* 1989). During this study histopathological samples identified *L. marchouxi* as pathogenic in pink pigeons and presented the first description of the endogenous development of the parasite in the host (Peirce *et al.* 1997)

Ornithophilic blackflies (Diptera: Simuliidae) are the only known vectors of *Leucocytozoon* except for one species *L. caulleryi* for which the vector is an ornithophilic species of *Culicoides*. Only one species of blackfly *Simulium ruficorne* is known from Mauritius (Peirce *et al.* 1997). Blackflies may be absent from coral islands devoid of fast-flowing freshwater streams which are the breeding grounds of the vectors (Peirce 1989). It was expected to find a higher prevalence of *L. marchouxi* in Pigeon Wood and Bel Ombre, where good habitat for blackflies exists, and a low prevalence or lack of parasites at Ile aux Aigrettes, which has no running water. Prevalence was higher at Bel Ombre and Pigeon Wood but the evidence was not conclusive. Prevalence at Ile aux Aigrettes was similar to Brise Fer and the captive population at Black River, both of which are drier sites. Blackflies may travel several kilometers in search of hosts and it is conceivable that flies travel across the lagoon to Ile aux Aigrettes (Peirce pers. comm.) but the relatively high prevalence at Ile aux Aigrettes was surprising. It is possible that other vectors on Ile aux Aigrettes may be involved. *Culicoides* spp. has been suggested as a vector for *L. toddi* to sparrowhawks *Accipiter nisus* in the apparent absence of *Simulium* spp. (Ashford *et al.* 1990).

There was no marked seasonality in prevalence. A higher prevalence was expected in the wet season (January to April) which is probably the main breeding period for the simuliids. A larger sample size from each sub-population may show seasonal differences within sites.

Infection with *Leucocytozoon* did not appear to affect survival of fledged birds. Chicks may become infected soon after hatching and by 14 days lots of gametocyctes may appear in the peripheral blood without any apparent pathogenicity (Peirce & Marquiss 1983). Infections with *Leucocytozoon* may persist for years and possibly for the lifetime of infected birds. Infected hosts develop some degree of resistance and may exhibit chronic or latent infections that may only be detectable in blood smears during seasonal 'relapse' or under environmental and physiological stresses (Atkinson & van Riper 1991). Seasonal relapse in temperate climates is usually associated with spring and is possibly related to the reproductive activity of the host. Of 23 samples that showed high parasitaemia (more than 11 parasites per slide), 18 were between August and November, which is during the pink pigeon breeding season.

Some birds showed clinical signs thought to be due to high parasitaemias or tissue phases. Birds suffered convulsions which resulted in opisthotonus, paralysis and death. This was more frequently observed in squabs and juveniles but also in some adults and apparently healthy captive juveniles suffered "sudden death". In squabs, anaemia, blackness and puffiness to the skin and general weakness were all thought due to the disease. Anaemia was thought a typical sign of infection in fledged birds.

Some birds survived for several years after high parasitaemias were detected. Mortality may be caused by high parasitaemias or when the bird is compromised by other factors such as concurrent disease or food shortages. Infection with the parasite may also lower resistance to other disease. In some cases, Leucocytozoonosis was reported as the only cause of death but in other cases there was concurrent disease. Other factors affecting survival such as inbreeding or body condition were not accounted for. Most cases of mortality due to Leucocytozoonosis were in juveniles and squabs and prevalence was also higher in birds less than one year old. Larger samples from squabs and from birds with high parasitaemias may indicate a greater effect on survival.

Introduced pigeons and doves to Mauritius probably act as reservoir hosts for *L. marchouxi*. A low prevalence of *L. marchouxi* in exotic doves suggests that they may be resistant to the parasite but more samples are needed from doves and feral pigeons in different habitats to confirm their role as hosts.

Avian pox

The genus avipox is restricted to birds and most members are genus or family specific but some pox viruses can pass the species, genus or even family barrier. Pigeon pox virus has experimentally affected other avian species and other types of pox virus may affect pigeons but cross immunity may not be inducible (Tudor 1991, Gerlach 1997). Pigeon pox has been reported from several wild pigeon species (Murton 1965, Cottam & Trefethen 1968, Rowan 1983, Conti 1993). Its effects on survival are not clear, in Cape turtle doves *Streptopelia capicola* 10% of juveniles were actively suffering from the disease but several recovered (Rowan 1983).

In pink pigeons the cutaneous form (dry pox) was the most commonly observed, characterised by variable-sized nodules on the beak, at the gape or at the base of the upper mandible, feet, tarsi, around the eyes and on the eye-lids. Lesions on the beak, particularly at the gape, restricted feeding and eye lesions restricted vision so that malnutrition and risk of predation were increased. In severe cases lesions were found all over the body, on the wing, vent, pygial gland and head. Lameness associated with swelling at the joints was also thought caused by pox. The diptheritic form (wet pox) was only observed in a few cases and typically small creamy nodules were found on the tongue and back of the throat, resembling trichomoniasis. Pox was only detected in birds where lesions were obvious and many birds may have been infected but showed mild or no clinical signs.

Pox had not been recorded in pink pigeons prior to this study. It was not clear where the virus originated from as both captive and wild birds contracted the disease at the same time and there was no evidence to suggest that one population infected the other by the transfer of birds between sites. There is a possibility that it is an unknown virus unique to

Mauritius. All attempts to isolate the virus and determine the strain failed and the pink pigeon pox virus behaved differently from all of the other pox viruses circulating in domestic pigeons (Kaleta 1994 *in litt.*). The nine birds that should have had immunity to pox but which reacted to the vaccine and the bird that developed pox after vaccination also suggested that the pox virus they were previously infected with was not a domestic pigeon pox. One case of pox was seen in a feral pigeon on Mauritius but the lesions were very different to those seen in pink pigeons. Pox-like lesions have been recorded from common mynhas *Acridotheres tristis*, Mauritius kestrels, house sparrows *Passer domesticus* and captive barbary doves on Mauritius (*pers. obs.*). Mortality is more likely when infection is with concurrent disease and there may be interactions between diseases. In Hawaii, both pox and malaria were found in more birds than expected, either because infection with one lowered resistance to the other or because twin-infected birds received greater attention from mosquitoes, which transmit both (van Riper *et al.* 1986).

Other parasites and pathogens in pink pigeons

Three other blood parasites were identified in three pigeons. An unknown *Rickettsia* species was identified in a blood smear in 1996 from an adult at Bel Ombre; a trypanosome was identified in a blood smear from a juvenile bird at Ile aux Aigrettes in February 1999 and an unidentified microfilaria was found post mortem in a 47 day old bird in 1995 which had been rescued from Bel Ombre. These were the first infections recorded in pink pigeons. The prevalence of the trypanosome is probably higher but the level of infection too low to show up on blood smears (M. Peirce pers. comm.) and the significance of the other parasites is unknown. Trypanosomes and microfilaria were previously found in exotic passerines and in the barred ground dove (Maya 1912).

Low to medium infestations of coccidia oocysts were found in group samples from wild and released birds in 1995 at Brise Fer. Coccidiosis is a transmissible intestinal parasitic disease caused by a protozoan parasite. Birds may develop immunity but it is not known if infestation with coccidia together with other disease affects survival.

Pink pigeons suffered from infestations of hippoboscid flies *Ornithoctona plicata* and squabs were attacked by the tropical nest fly *Passeromyia heterochaeta*. Severely bitten squabs suffered anaemia, which together with other disease, could result in death. Tropical nest flies caused mortality in a few cases of captive squabs and were a regular cause of mortality in wild echo parakeets *Psittacula eques* (Jones & Duffy 1993). Hippoboscid flies are vectors for *Haemoproteus*, trypanosomes and microfilaria, microfilaria may also be transmitted by blackflies (Ledger 1968, Tudor 1991).

Disease effects on survival and reproductive success, general comments

Disease probably affected the survival of all age groups on Ile aux Aigrettes but had its greatest effect on survival of wild juveniles from fledging up to one year old. On Ile aux Aigrettes, where many birds were not released until about five months old, survival of wild-fledged juveniles (36%) was much poorer than survival of released juveniles (84%) (Chapter 3). Most of the effects were within one to two months after fledging and probably involved birds which retained infections accrued as a squab and which were re-infected by parents that were still feeding them. The older age at release on Ile aux Aigrettes and the lack of exposure to disease as a squab may have increased the chances of survival for captive-reared birds. However, a wild-fledged bird on Ile aux Aigrettes that survived its first year may be better able to resist disease than a released bird. On Ile aux Aigrettes survival of first-year wild adults was 84% and survival of first-year released adults was 67%. Between years one and three, survival of wild-fledged adults (88.6% per year) was better than survival of released adults (76.1% per year) (see Chapter 3 for more details).

At Ile aux Aigrettes reproductive success was similar to mainland sites (Chapter 5). Disease as a limiting factor has to some degree replaced the effects of predation at mainland sites. Levels of reproductive success on Ile aux Aigrettes are maintained by treatment of squabs and some breeding adults, without which disease would have a far more severe impact. In July 2000 there was some evidence that trichomoniasis was an increasing problem for squab survival at Brise Fer when 10/24 squabs died from the disease.

Disease and management practices

Two management practices may risk increasing the spread of disease between birds. Supplemental feeding and watering stations increase contact between birds and vectors, and the feeding station itself may be a source of contamination. This was demonstrated at Ile aux Aigrettes with a common water source. Feeding hoppers are designed to exclude exotic pigeons from feeding but they still pick up spilt grain from the platform. Mortality due to local outbreaks of trichomoniasis in mourning doves in Oregon was associated with "backyard" bird feeders and waterers (Conti 1993). The spread of salmonellosis among wild birds concentrated at garden feeding tables is well recognised (Wilson & Macdonald 1967). Feeding stations need to be situated so that high densities of birds are not clustered around them. Control of predators may increase the survival of diseased birds and encourage disease spread. Hudson (1992) showed that disease in red grouse *Lagopus l. scoticus* was a limiting factor because of predator control. Predators reduced parasite transmission by preying upon heavily parasitised birds. Low levels of predation were sufficient to reduce disease effects but at higher levels predation itself reduced grouse density.

Disease and the re-introduction programme

The introduction of disease into wild populations through re-introduction and translocation programmes is serious cause for concern (Woodford & Rossiter 1994, Cunningham 1996, Ballou 1999). This is usually because captive populations, particularly *ex situ*, are in close contact with other species and exposed to a range of diseases. For the pink pigeon re-introduction programme, most birds were captive-bred on Mauritius and were probably exposed to similar diseases as wild birds which has so far proved to be true. Only three birds were bred *ex-situ* at Jersey Zoo and underwent quarantine and screening prior to arrival. The risk of introducing new diseases into the remaining wild population was considered low. Up to 1993, all pink pigeons were individually screened prior to release. Since then, a more general approach to disease monitoring was adopted whereby captive and wild pink pigeons and exotic hosts were screened and management practises introduced where necessary. During the recovery programme, sub-populations of birds were established for several reasons, one of which was to reduce the risk of an epidemic disease affecting the whole population. This has happened to some extent as avian pox is rare in the Pigeon Wood population and trichomoniasis is rare at mainland sub-populations.

Conclusions

This study has presented data on the parasites and pathogens present in pink pigeons and made some attempts to investigate their effect on survival. It has also highlighted disease as a contributing factor to the pink pigeon's original decline, particularly from lowland areas, that had not previously been fully understood. It is probable that these pathogens affect other aspects of reproductive success which have not yet been investigated (Hudson 1986, Norris *et al.* 1994, Richner *et al.* 1995, Oppliger *et al.* 1997).

In small populations the effect of pathogens may be masked by other factors such as predation. In the pink pigeon, disease effects became clearer once other limiting factors were controlled and a larger population size was achieved. There is no doubt that disease will continue to play an important role in limiting the size and distribution of the population.

Chapter 8

Project evaluation and a long-term prognosis for the pink pigeon

INTRODUCTION

In the face of increasing biodiversity loss and species extinction rates (Wilson 1988, Stattersfield *et al.* 1998), re-introduction is increasingly being used to restore extirpated species to their native habitats. Such has been the interest that in 1989, the IUCN Species Survival Commission established a Re-introduction Specialist Group (RSG) to co-ordinate and guide efforts in re-introductions and to establish a set of guidelines for acceptable protocols (IUCN 1987, 1998). The conservation of the pink pigeon has been a good example of how captive-breeding and re-introduction of a critically endangered species can be important management options when used together with other management techniques.

HAS THE RE-INTRODUCTION AND MANAGEMENT PROGRAMME BEEN A SUCCESSFUL CONSERVATION TOOL FOR THE PINK PIGEON?

The success of the pink pigeon programme can be evaluated in several ways, depending on short-term and long-term goals. The immediate goal of the programme was to prevent the species' extinction in the wild. This it did and, as a result of the programme, pink pigeons have survived and bred in the wild since 1987 and the species has been down-listed from critically endangered (Collar *et al.* 1994) to endangered (Stattersfield & Capper 2000). Extinction in the wild is no longer a threat and the population has been successfully re-established.

In the long-term, the goal was to achieve a self-sustaining population but it was recognised that some management would be necessary. Between 1997 and 1998, productivity was sufficient to maintain the population and to contribute to population growth, which increased from 282 birds to 297 birds without releases (Chapters 3 and 6, and Appendix 2). This is a relatively short time in which to assess self-sustainability and further releases in 1999 and 2000 has since increased the population to 420 birds at end 2000 (C. Jones pers. comm.). To assess to likelihood of the population becoming self-sustaining, life history data from this study was used to predict the future population trend without further releases for the next five years (Table 8.1).

The number of birds in each age class in 1998 was obtained from a census carried out on 31st December 1998 (Chapter 6). This census included birds of different ages that were distributed within each age group, for example birds in year 0-1 included birds that were two months old, six months old and 11 months old. The number of birds that would have been alive at the start of each age group was calculated as (number of birds that survived to a specific age x 100 ÷ per cent survival of the individual), where survival estimates were known for each bird at a specific number of days old. This gave an adjusted age distribution of birds alive at the start of each age group on the census date (1998 adjusted). To calculate the proportion of birds in each age group that would survive to the next age group the following year, age-specific survivorship rates for fledged birds (Chapter 3) were applied to the birds in each age group. For example, of 62 birds that were alive at the beginning of year 0 in 1998, 42 (68%) would survive to the start of the next age group (year 1) in 1999.

Birds in each age group will contribute to the total number of young produced each year at a rate specified by age-specific productivity. Because productivity was calculated only for paired birds (Chapter 6) and only a proportion of the total population bred each year (Chapter 5), an adjusted productivity was calculated as (productivity x the percentage of birds that bred ÷ 100). This value could then be applied to all birds in the table to obtain the number of young produced each year by each age group. The total number of young produced each year was the sum of the number of young produced by each age group.

Table 8.1 Life history data and projected population trends for free-living pink pigeons. Age-specific survival is the mean survival for all birds. Productivity was calculated as the average of the mean number of young fledged per paired female and per paired male, and assumed that the sex ratio was 1:1 and that a male and female contributed 50% to each gamete.

Age	Age-specific survival	Productivity	% bred	Adjusted productivity	Number of birds per year						
					1998	1998 adjusted	1999	2000	2001	2002	2003
0	0.675	0.40	35.7	0.14	51	62	100	117	127	128	128
1	0.801	0.60	72.4	0.43	58	65	42	68	79	86	86
2	0.852	0.46	80.6	0.37	71	78	52	34	55	63	69
3	0.814	0.35	80.4	0.28	65	71	66	44	29	47	54
4	0.799	0.41	84.0	0.34	21	25	58	54	36	24	38
5	0.772	0.55	100.0	0.55	14	16	20	46	43	29	19
6	0.889	0.35	85.7	0.30	11	12	12	15	36	33	22
7	0.900	0.15	50.0	0.08	2	2	11	11	13	32	29
≥8	0.690	0.00	00.0	0.00	4	4	5	13	19	25	46
Total population					297	335	366	403	437	467	491

This analysis suggested that the population will increase on average by 31 ± 5.6 birds per year over the next five years, without further releases, and that the age structure of the population will become more stable. The predicted number of recruits to the population is relatively low, particularly as this is for the whole metapopulation and each sub-population may only achieve on average an increase of between six and 10 birds per year. Although the survivorship estimates do include two periods of exceptionally high mortality at Pigeon Wood in 1992 and Brise Fer in 1996 (Chapter 3), the number of birds recruited each year may not be sufficient to withstand periods of catastrophic mortality such as cat predation, a disease epidemic or a major cyclone.

Analysis of the net reproductive rate (R_o) for female pink pigeons also suggested that the population will increase under current rates of survivorship and productivity (Table 8.2).

Table 8.2 Calculations of the net reproductive rate (R_o) for female pink pigeons, 1992-98. Female survivorship values were obtained from Chapter 3. In year 0-1, survival rates for all juveniles (sexed and unsexed) were used owing to the inaccurate estimation of survival rates for juvenile females. For years ≥ 8, survival rates for all birds were used owing to the small sample size of females. Productivity values for females were obtained from Chapter 6. If the population size remains constant, Ro = 1, when Ro is less than one the population decreases and when Ro is more than one, the population increases.

Age (x)	Survivorship (l_x)	Age-specific survival ($l_x + 1 / l_x$)	Productivity (m_x)	Expected offspring ($l_x m_x$)
0-1	0.68	0.68	0.43	0.29
1-2	0.70	0.78	0.58	0.41
2-3	0.61	0.86	0.47	0.29
3-4	0.48	0.79	0.41	0.20
4-5	0.36	0.75	0.40	0.14
5-6	0.26	0.74	0.51	0.13
6-7	0.23	0.88	0.17	0.04
7-8	0.16	0.71	0.13	0.02
≥ 8	0.15	0.69	0.00	0.00
			Ro =	1.52

Predicted population trends in Table 8.1 and the net reproductive rate shown in Table 8.2 may be underestimated as productivity of birds seven years old or more may be underestimated. In the analyses it was assumed that there was no productivity for birds eight years and older. Productivity declined in females after five years old and in males after six years old (Chapter 6). However, two females produced five young at eight years old and two males produced three young in years seven and eight but it is not known if this was exceptional or if birds that achieve older age are productive. In Table 8.1, the proportion of birds breeding per age group may be underestimated owing to possible undetected breeding pairs, which will have contributed to an overall underestimation of the population trend. In contrast the proportion of birds surviving older than seven years may be overestimated. Data suggested that survival between eight and 11 years old was 69%, but sample sizes were small (16 birds were known).

The projected population trends and the net reproductive rate for pink pigeons assumes that current levels of management will be maintained. The pink pigeon population is currently unlikely to be self-sustaining without some management and therefore does not fulfil the criteria of Beck *et al.* (1994) that requires a population free of human support for a successful re-introduction (Chapter 1). The intensity of management will undoubtedly decrease as the population increases, and may depend on the ability of the birds to use non-native habitats. The remaining habitat available on Mauritius and the impact of predators will mean that some supplementary feeding and predator control may always be required. However ongoing habitat restoration and the permanent exclusion of some exotic species may mean that management of the pink pigeon population will decline over time. Where management is needed, it may only be required in core areas to maintain nest success, productivity and survival, which will act as "sources" of birds.

Another indicator of success is how well released individuals or re-established populations are doing compared with wild birds. There are some problems inherent in this when few wild individuals remain which are themselves suffering from environmental stresses. In the pink pigeon, both released and wild populations required management, which may have reduced any differences that existed between them. A comparison of survival between wild birds at Pigeon Wood (mean 84.5% for years 0-7) and released birds (80.1%) did not suggest large differences. There was some evidence that the survival of wild birds (including wild-bred progeny of released birds) was significantly better than the survival of released birds but habitat and the pre-release captive period of released birds confounded the results (Chapter 3). Reproductive ecology and nesting behaviour of birds at Pigeon Wood and in re-introduced sub-populations was similar (Chapter 4) but nest success and productivity of released birds was significantly poorer than wild birds (Chapters 5 and 6). Released birds undoubtedly suffered from inadequate social and survival skills. However careful nurturing and management of released birds in the wild to improve survival and reproductive success resulted in wild-born progeny that helped re-establish the population.

During the programme, recovery techniques suitable for other species were developed. Egg and brood manipulations were used (Cade 1977, Fyfe *et al.* 1977) including egg harvesting, fostering and cross-fostering of eggs and squabs and brood reduction. Some of these techniques have been successfully applied to other endangered species (Jones & Duffy 1993, Jones *et al.* 1995, Merton *et al.* 1999). The effectiveness of re-introduction and species oriented projects, compared to more traditional methods of wildlife conservation such as habitat preservation and ecosystem management, has been critically debated (Myers 1979, Csuti *et al.* 1987, Hutto *et al.* 1987) and discussions still continue

(Snyder *et al.* 1996, Wolf *et al.* 1996, Simberloff 1998). The recovery of the pink pigeon was part of a larger programme to restore and conserve the native biodiversity of Mauritius, with the ultimate aim of whole ecosystem restoration. This programme, along with that of the Mauritius kestrel *Falco punctatus* and echo parakeet *Psittacula eques*, stimulated the Government of Mauritius to establish the Black River Gorges National Park (Anon 1998) and has also stimulated habitat and island restoration. The release of pink pigeons on Ile aux Aigrettes fulfilled both the requirements for the species' recovery and the need for a site that provided an educational experience for visitors and school children. The successful re-establishment of the pink pigeon and its sister programmes have indicated that re-introduction and associated recovery techniques are valuable conservation tools, and that species oriented projects can galvanise the development of further conservation measures such as habitat restoration and protection.

REASONS FOR SUCCESS

Several factors have been identified as criteria for a successful recovery project: releases into the core of the historical range, releases into excellent habitat, releases of wild-caught animals rather than captive-reared ones, releases of large numbers of individuals (≥ 100, often synonymous with the length of the programme), and the removal of the original cause of decline (Griffith *et al.* 1989, Beck *et al.* 1994, Wolf *et al.* 1996, Fischer & Lindenmayer 2000). Other factors included species-specific behaviours and an omnivorous diet that allowed species flexibility, supportive measures during releases and human-related elements (e.g. public relations, education, program methodology, species protection from hunting, trapping or human disturbance) (Beck *et al.* 1994, Wolf *et al.* 1996, Fischer & Lindenmayer 2000). Genetic considerations have rarely been cited as influencing the outcome of a re-introduction.

The pink pigeon programme fulfilled several of these criteria, namely: releases into the core range, releases in good quality habitat with ongoing habitat improvement, release of a large number of individuals and management to reduce the effects predation, disease and habitat degradation which were the original causes of decline. Other factors influencing success included the release of birds into several discrete sub-populations (suggested by Griffith *et al.* 1989 as increasing the chances of success), and long-term population monitoring. The influence of human-related reasons should not be underestimated. The Mauritius conservation project in general has been very successful, a large part due to the establishment of an in-country non-governmental organisation (the Mauritian Wildlife Foundation), long-term commitment and funding and support from the Government. The successful economic development of Mauritius as a country has no doubt also contributed to the success of the conservation programmes, since more resources and a well developed infrastructure were available.

CURRENT CONCERNS FOR THE PINK PIGEON

In the pink pigeon, management has reduced the likelihood that the population will become extinct because of demographic variation and environmental effects, and close monitoring of the population will ensure that future threats are counteracted by appropriate management. Predator control appears to have effectively reduced predation on fledged birds and survival was higher than expected (Chapter 3). However, nest success and productivity was poor, some of which can be attributed to nest predation. Despite the control of rats within nesting areas, mean annual nest success was still only 18.4%. On average a pair of birds in their lifetimes need to produce three young for two of them (i.e. minimum replacement) to survive to one year old and have the potential to breed (assuming 68% juvenile survival, Chapter 3). Mean annual productivity per female (1.18) and per male (1.14) (Chapter 6) suggested that three young could be produced in three years. To produce three young in two years would require a nest success rate of 23.8% per year (using 1.16, the mean for males and females), which is lower than currently observed at Pigeon Wood. Analysis of age-specific productivity suggested that on average a bird did not produce three young until the end of year two (2.9 young) or during year three (Chapter 6). In addition, only 76% of birds that reached breeding age actually bred (Chapter 5). However, because of the pink pigeons ability to re-nest and have multiple broods within a breeding season, the 'poor' nest success does not necessarily reflect inadequate productivity. Undoubtedly nest predation by introduced mammals has had an impact and nest success may be even poorer without rat control but further improvement in predator control may result in better productivity.

Genetic considerations

Small populations are challenged by a number of factors that increase the risk of extinction (Ballou 1991, Foose *et al.* 1995). Stochastic problems affecting the long-term persistence of small populations can be environmental, demographic and/or genetic. Random demographic variation (e.g. in survival, reproductive success, biased sex ratios, fertility) and environmental catastrophes can be severe enough to cause population extinction. Genetically, small populations can rapidly lose the diversity necessary for fitness and for their adaptation to future environmental changes (Lacy *et al.* 1995). Demographic and genetic problems can interact to create the "extinction vortex" (Gilpin & Soulé 1986) caused by negative feedback effects of inbreeding. As the population becomes more inbred, reduced survival and reproduction are likely and the population decreases.

One of the main concerns for the pink pigeon has been the potential genetic problems associated with the small population size and the population bottleneck through which the species passed. Population estimates were lowest after cyclone Gervaise in 1974, at just 10-20 birds (Chapter 1) before the captive programme began. The captive population has descended from just eleven original founders and it is likely that some or all of the secondary founders, from which many released birds and all wild birds at Pigeon Wood were descended, are also descendants of the original founders (see Chapter 2). Evidence in support of genetic depletion through the bottleneck has been shown for the pink pigeon (Bruford *et al.* 1991, Wayne *et al.* 1994) and has been suggested as a possible reason for low genetic diversity in the founder population (Groombridge 2000). Bruford *et al.* (1991) and Groombridge (2000) also suggested that there were relationships between birds in the original founder population.

Genetic management of the captive pink pigeon population has followed guidelines to preserve genetic diversity (Ralls & Ballou 1983) by maximising founder representation and minimising inbreeding (see Jones 1995) and efforts were made to establish released populations with birds of diverse lineages. To retain as much of the original genetic diversity of the founder population, all founders should contribute equally to successive generations (Frankel & Soulé 1981). In the early years of the captive-breeding programme, some founders contributed disproportionately to the captive population owing to the difficulty of identifying compatible pairs and the urgent need to establish captive breeding. Between 1988 and 1992, productivity of the captive population in Mauritius was not sufficient to provide many surplus birds for the release programme as most captive females were too old to breed (Jones 1995). Consequently most released birds are in part descended from secondary founders established in captivity since 1989 (Chapter 2).

Effective population size

A concern for the future of the pink pigeon is the minimum population size required to preserve genetic diversity and whether genetic management of the free-living population will be required. The effective population size *Ne* required to minimise the loss of genetic diversity has been suggested as 500 individuals (Franklin 1980). Although this figure has often been used in management plans for threatened species (Foose *et al.* 1995), including the pink pigeon (Bruford *et al.* 1991), it will differ between species depending on the departure from an "ideal" population (e.g. sex ratios, overlapping generations, differential reproductive success, changes in population size) (Soulé 1997). The effective population size may be the "census" size or only a proportion. Mace and Lande (1991) suggest a general *Ne/N* (total population size) ratio of 0.2, which for an effective population size of

500 would require a total population of 2500 individuals. Owing to the effect of the bottleneck and the consequent low genetic diversity remaining in the pink pigeon population, an effective population size smaller than expected may be sufficient to maintain the remaining diversity. In addition, distinct sub-populations and migration between them may help to maintain genetic diversity of the metapopulation (Lande & Barrowclough 1987).

Inbreeding depression

The extent to which a population suffers inbreeding depression depends largely on the demographic history of the population. In a small population, most deleterious mutations have been purged by selection and further decreases in population size due to catastrophic events may result in only a low rate of inbreeding depression (Tanaka 1997). Evidence for low genetic diversity in post-bottleneck pink pigeon founders has been shown, although there is some suggestion that this might be normal for pigeons (Groombridge 2000). Evidence for inbreeding depression in the pink pigeon has been discussed for survival (Chapter 4), reproductive success (Chapter 5) and in captive birds (Jones *et al.* 1989, Jones 1995). Inbreeding effects were not always clear and in some cases, effects were only seen where inbreeding coefficients were ≥ 0.25. The effects of inbreeding may not be deleterious to the population as a whole, as long as there are sufficient non-inbred individuals to maintain population growth. As an example, analysis of the productivity of 19 sibling pairings showed that 10 pairings produced 19 progeny. Of 12 progeny that could be traced, three bred but only one produced one young which died at less than two months old. These inbred progeny did not therefore contribute to subsequent generations.

The Ile aux Aigrettes sub-population originated from 46 captive-bred birds released between 1994 and 1996, and whose mean inbreeding coefficient was 0.024 ± 0.033. At the end of 1998, the mean inbreeding coefficient for all birds alive was 0.054 ± 0.068 (n = 46) and for wild-bred progeny was 0.073 ± 0.075 (n = 31). Fourteen wild-bred progeny were of unknown pedigree at end 1998. The mean inbreeding coefficient of birds on Ile aux Aigrettes has increased in two to three generations. Increasing inbreeding with subsequent generations in the mainland population may be offset by migration between sub-populations, a larger carrying capacity and a more diverse founder population. In contrast, the population at Pigeon Wood was reduced to eight or nine secondary founders in 1993 (Chapter 2, Figure 2.3) some of whom were probably related to each other. However, this sub-population showed better survival and reproductive success than other sites and better productivity than other mainland sites.

One of the main potential consequences of inbreeding that may affect the population's viability is infertility (Chapter 5). It has been assumed that the high rates of infertility are due to inbreeding and Jones (1995) provided some evidence. Other causes of infertility are possible (such as pathogens) and further study is urgently needed as it could be a major factor limiting the recovery of this species.

Genetic management

In Chapter 6 the possibility was suggested that the pink pigeon population may require genetic management to reduce the potential problems caused by differential productivity. An example from Pigeon Wood indicated that disproportionate production of progeny by certain breeding pairs may not be reflected in subsequent generations owing to other factors affecting pre-breeding survival. However, data from Ile aux Aigrettes may indicate otherwise. Ile aux Aigrettes originated from 11 released females of which four produced 65% of the first generation (Table 8.2). Analysis of second and third generation breeding birds (second generation breeding was achieved in 1995 and third generation of at least one parent was achieved in 1997) suggests that the original females that left most young were more likely to be represented in subsequent generations. This only represents productivity up to end 1998 when three of the original females were still breeding. But it may indicate that, at least on Ile aux Aigrettes, some genetic management may be necessary to counteract the effects of individual variation in productivity if genetic variation is to be maintained.

Table 8.2 Contribution of known females and their progeny to subsequent generations on Ile aux Aigrettes, 1994-98. F1 = first generation progeny, F2 = second generation progeny, F3 = third generation progeny.

Female ID	Status 1998	No. fledged	% contribution to F1	No. F1 bred	No. fledged	% contribution to F2	No. F2 bred	No. fledged	% contribution to F3
514	Dead	2	3.7	0	0	0	0	0	0
523	Dead	4	7.4	0	0	0	0	0	0
532	Dead	6	11.1	3	6	12.8	0	0	0
537	Dead	9	16.7	2	18	38.3	3	6	33.3
539	Dead	3	5.6	0	0	0	0	0	0
540	Alive	8	14.8	2	12	25.5	2	12	66.7
543	Dead	12	22.2	2	11	23.4	0	0	0
550	Dead	2	3.7	0	0	0	0	0	0
553	Alive	4	7.4	0	0	0	0	0	0
563	Dead	1	1.8	0	0	0	0	0	0
735	Alive	3	5.6	0	0	0	0	0	0
Total		54	100	9	47	100	5	18	100

LONG-TERM PROGNOSIS FOR THE PINK PIGEON

In 1991 a Population Viability Assessment for the pink pigeon recommended that the wild population would require intensive management in order for it to survive over the next hundred years (Bruford *et al.* 1991). Population figures for the 1980s and 1990s suggested that the species would become extinct in the wild at about year 2002 (Chapters 1 and 3). Recommendations made at the PVA (see Bruford *et al.* 1991 for details) were incorporated into the management plans for the species, the most important of which was to improve productivity. This was achieved by increasing productivity of breeding birds and increasing the number of birds released. Forest restoration has improved the habitat quality for pink pigeons that, together with supplemental feeding, has increased the carrying capacity of the remaining habitat and the population numbered 420 birds in the wild on 31st December 2000 (C. Jones pers. comm.). In Mauritius, the maintenance of self-sustaining populations is presently unattainable and the damage caused by habitat destruction and the introduction of exotic species may not be fully reversible (Safford & Jones 1997). Management of the pink pigeon and its habitat is therefore considered essential if the species is to persist in the face of habitat degradation and predation.

Chapter 9

Developing re-introduction guidelines, experiences from the pink pigeon programme

INTRODUCTION

The planning and implementation of a re-introduction is complex and needs to incorporate biological and non-biological factors. Stanley Price (1989) provided a model for re-introductions developed from experience with the Arabian Oryx *Oryx leucoryx*, (Figure 9.1) which was proposed as applicable to all re-introductions and which have subsequently been incorporated into the IUCN Re-introduction Guidelines (1998). The planning and execution of the pink pigeon recovery programme has followed this model and some of the issues have been investigated and discussed in this thesis.

Some species may be better candidates for re-introduction than others, owing to their ecology and flexibility. Stanley Price (1989) identified classes of animals that were most 're-introducible'. For example the re-introduction of species with an omnivorous diet, species tolerant of a wide range of habitat conditions and species whose behaviour can be manipulated may have a greater chance of success (see also Wolf *et al.* 1996). Similarly, some situations will predispose a recovery programme to greater chances of success, for example if the original causes of decline have been removed or if re-introduced species are protected. Many aspects of the pink pigeons' biology, behaviour and habitat favoured the birds' re-establishment. Recovery techniques applied during the programme also facilitated its success, some of which were highlighted in Chapter 8 (see *Reasons for success)*. Experiences from the pink pigeon programme can be used to develop the IUCN Re-introduction Guidelines, and are summarised below.

WORKING WITH THE IUCN RE-INTRODUCTION GUIDELINES

The IUCN Re-introduction Guidelines (1998) set out detailed points to be considered when planning and implementing a re-introduction programme. The guidelines encompass all plant and animal taxa in a range of geographical regions, and are unsurprisingly very general. Guidelines for re-introducing individual groups of animals and plants are much needed. Some problems arose during the pink pigeon programme when trying to apply the IUCN guidelines, and are discussed below. Recommendations made in the guidelines are presented in italics.

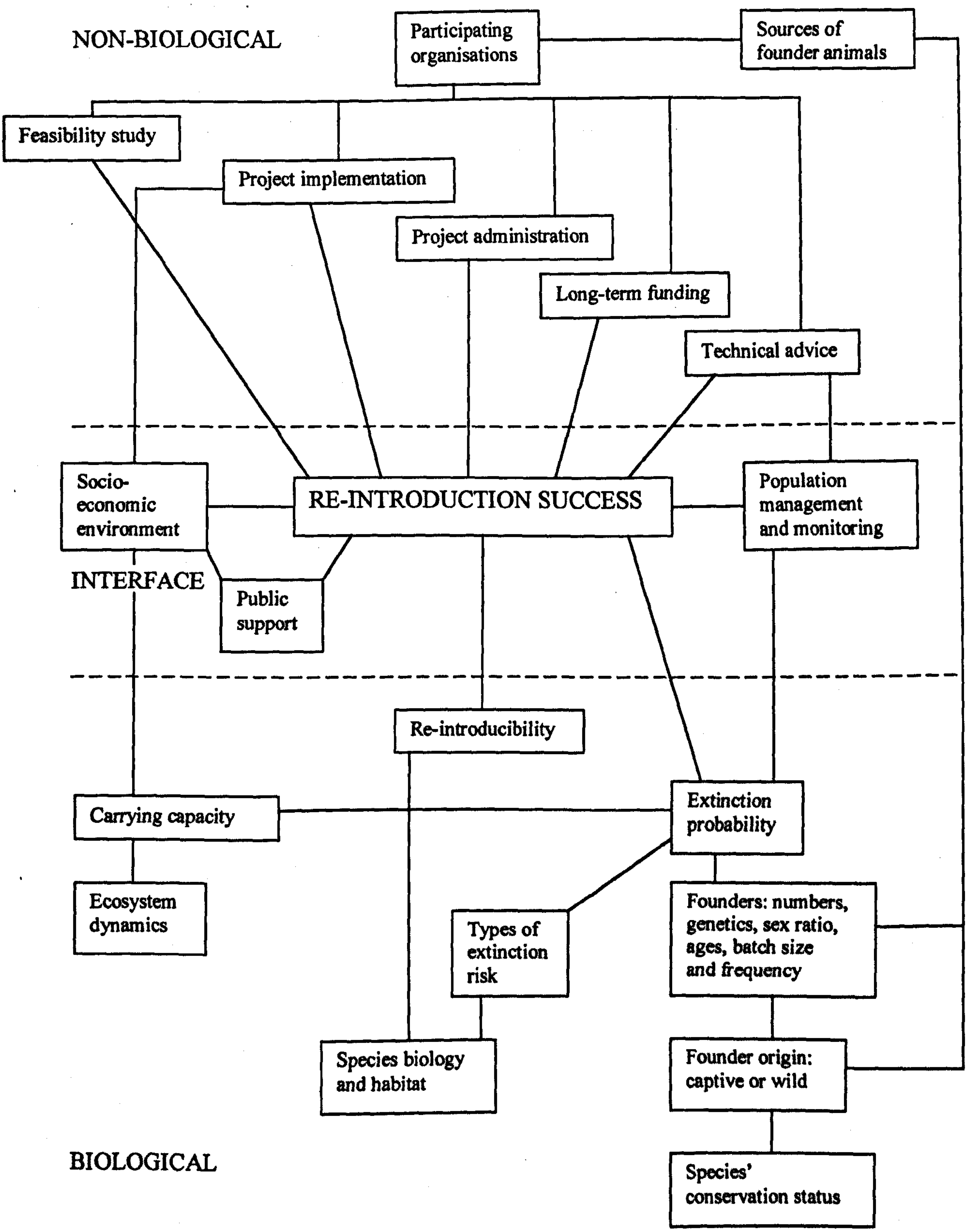

Figure 9.1 Factors relevant to a successful re-introduction. The main concerns can be classified into biological, non-biological and an interface between the two to achieve re-introduction success. The arrows are one way, with exception of a dialogue between the re-introducing agency and the sources of founder animals. Extracted from Stanley Price (1989).

'Detailed studies of the species status and biology should be made prior to release to determine the species' needs'. In the pink pigeon, the remaining population of wild birds was so small that evaluation of the species' biology and its habitat requirements was not possible. The information that was available came from a few historical observations, and from studies of the wild population in non-native and modified habitat. The birds were facing ongoing threats from food shortages and predation and their ecology was unlikely to reflect that found on pristine Mauritius. It was only through releasing and studying birds during the recovery programme that this information was gained. It is likely that many endangered species would be in a similar situation by the time a re-introduction is contemplated.

'Re-introductions should only take place where the habitat and landscape requirements of the species are satisfied'. Assuming again that a species has become so rare as to warrant a re-introduction, specific habitat requirements of a species may be poorly known. The existence of a rare species in a particular habitat may only be because this is where the pressures are the least. In the pink pigeon, the remnant wild population in the 1970s (and up to 1997) nested in an exotic plantation of Japanese red cedar *Cryptomeria japonica*, mainly because nest predation was lower there than other areas. The habitat occupied by a remnant wild population may not be suitable for a re-introduction, which will need to be accessible and enable close monitoring of the released animals. For example, the last wild Przewalski horses *Equus przewalski* lived in the remote Gobi Altai of Mongolia (Weeks 1977), but re-introduction into part of their historical range in Europe and Asia may be more practical. In some situations, optimal habitat may not be available and re-introduced animals may do just as well in modified habitats. In pink pigeons, survival and breeding success of the remaining wild population in Japanese red cedar and pine *Pinus* spp. is better than birds at Brise Fer, which has the best native forest remaining on Mauritius. The Hawaiian goose *Branta sandvicensis* is unable to be re-introduced to formerly occupied lowland areas owing to mosquitoes and avian pox to which they are susceptible (Kear & Berger 1980). In New Zealand, the transfer of native birds from mainland sites to offshore islands required balancing their habitat needs with providing a site free from predators (Butler & Merton 1992, Merton *et al.* 1999).

'Identification and elimination, or reduction to a sufficient level, of previous causes of decline'. This recommendation is also inherent in a successful re-introduction programme where the species is self-sustaining and needs no further support (Beck *et al.* 1994). An example of complete elimination of the cause of decline leading to successful re-establishment of a species can be found in the Lord Howe island woodhen *Tricholimnas*

sylvestris. This species declined to 10 breeding pairs in 1975, restricted to summits of the two highest mountains by predation by feral pigs (Miller & Mullette 1985). Eradication of nearly all the pigs between 1979 and 1981 and a captive-breeding and re-introduction programme enabled the woodhen population to recover to between 50 and 60 pairs in 1993 (Caughley & Gunn 1996).

This programme was unusual in that a single limiting factor was identified which was subsequently overcome. Other examples, where the historical cause of decline was largely removed prior to recovery, includes the peregrine falcon *Falcon peregrinus* into the USA, and the red kite *Milvus milvus* and white-tailed sea-eagle *Haliaeetus albicilla* into the United Kingdom (Cade 2000). However, it is more likely that the causes of decline or rarity in a species will be many, and some may be obscure, and that complete elimination will not be possible. The re-introduction programme for the Hawaiian goose has been hampered by an array of limiting factors including predation by mongooses, disease, sub-optimal habitat, poor post-release monitoring owing to difficult high altitude terrain, ecological specialisation, and road kills (Kear & Berger 1978, Stanley Price 1989, Caughley & Gunn 1996). On Fregate island in the Seychelles, elimination of cats had little effect on the population of Seychelles magpie robin *Copsychus sechellarum*, as land changes associated with increasing tourism, and more recently invasion by rats (*Rattus* spp.), have caused new threats (Caughley & Gunn 1996).

In the pink pigeon, a suite of factors limiting the population was identified, and evaluation was only possible through controlling their impact. Proximate factors included predation by exotic mammals and food shortages, but the ultimate factor is probably poor fertility of eggs. More than anything, the pink pigeon programme has emphasised the need to look beyond the obvious causes of decline and rarity.

Caughley (1994) cited the rescue of the Lord Howe Island woodhen *Tricholimnas sylvestris* (Miller & Mulette 1985, Fraser 1985) as a good example of diagnosis and treatment of a problem (his declining-population paradigm) followed by a captive-breeding programme (small-population paradigm) to solve a conservation problem. The pink pigeon project is another successful example but the recovery strategy was slightly different to that of the woodhen. The recovery programme itself enabled the evaluation of the causes of decline, through experimental releases in different habitats and long-term monitoring of the free-living population, and appropriate management was applied to counteract the limiting factors and improve population growth. In the pink pigeon, the problem has not been entirely solved, as some management will be needed to ensure its continued survival.

In the face of increasing pressures on wildlife, it is rare that the threats to endangered species can be completely eliminated, as in the woodhen, and most species and their habitats will require management if they are to persist at all.

DEVELOPING RE-INTRODUCTION GUIDELINES USING EXPERIENCES FROM THE PINK PIGEON PROGRAMME

Many lessons have been learnt from the pink pigeon re-introduction programme and from similar programmes for the Mauritius kestrel *Falco punctatus* and Echo parakeet *Psittacula eques*. Aspects of the pink pigeons' life-history favoured the birds re-establishment, and management techniques applied during and post-release contributed towards its success. These have been summarised below. The points are not exhaustive, but are additional to or expand upon the re-introduction guidelines, and may be in particular applicable to birds. I have only dealt with the biological factors, as the non-biological factors (e.g. funding, project administration, participating organisations and partnerships) are considered necessary for any re-introduction programme.

Aspects of the recovery programme particular to Mauritius that facilitated re-establishment

- The establishment of an in country captive-breeding programme removed many of the problems associated with importing animals for release, e.g. disease concerns, logistics, increased costs of shipping animals.
- Mauritius is a small island and access to release sites was relatively easy. Similarly, the distance between the captive-breeding facility and release sites was no more than two hours by a vehicle.
- The establishment of on site aviaries and on site field stations at each release site where staff were permanently based to monitor released birds.
- The release sites were within protected areas and no indigenous people lived in them. Human persecution of re-introduced birds was a minor concern.
- The forest is relatively short (at mainland sites 18 to 25 m, at Ile aux Aigrettes five to ten metres) and the interior accessible, which facilitated post-release monitoring.

Aspects of pink pigeon biology that favoured re-establishment

- Causes of the pink pigeons' decline were known, although had not been evaluated.
- Detailed information about the reproductive biology and management of the pink pigeon was available from captive birds by the time re-introduction was considered.
- The ability of captive birds to lay multiple clutches and the development of foster-rearing methods provided large numbers of birds for the programme.

- Rapid growth of captive young meant that birds could be released at two to three months old.
- The lack of a complex social system meant that social grouping prior to release was not a priority.
- Juveniles remained in cohesive groups once released and adults did not disperse widely once released, but whether the latter is a natural behaviour or encouraged by supplemental feeding stations (see below) is uncertain. Both behaviours facilitated post-release monitoring and management.
- The ability to breed in their first year, lay multiple clutches and rear multiple broods facilitated rapid establishment of the birds in the wild.
- The ability to use non-native species for nesting (and to some extent as food although this has not yet been investigated).
- Birds did not show negative behavioural responses to frequent trapping and handling, or to regularly accessing nests.

Aspects of the recovery programme particular to management techniques that facilitated re-establishment.

- The development of soft release techniques (based on hacking techniques used for falcons) whereby birds were kept in an aviary on site prior to release and given gradual independence.
- The release of large numbers of birds (256 were released, 195 (76%) over a period of three years), which enabled quick establishment of the population, thereby reducing the effects of mortality caused by demographic and stochastic events.
- The release of juveniles, which reduced territorial and captivity-related behavioural problems associated with releasing adults.
- Releases of four to eight birds per release group.
- Establishment of discrete sub-populations prevented disease epidemics and tested habitat flexibility in birds.
- Regular trapping and ringing, which enabled a regular population census and constant health monitoring.
- Post-release management practices, which included supplemental feeding stations, predator control and disease control, reduced the effects of food shortages, predation and mortality due to disease as these factors could not be eliminated entirely.
- Establishment of supplemental feeding stations at the release site which encouraged birds to develop a long-term release site attachment and facilitated post-release monitoring.

- Intensive post-release monitoring allowed constant reassessment of release procedures and management practices, which were regularly modified to improve survival and reproductive success.
- The development of micro-manipulative techniques (egg harvesting, fostering and cross-fostering and other egg and brood manipulations) to maximise productivity. Harvesting eggs from the remaining wild population for captive-rearing was particularly important early in the programme, to provide young birds for captive-breeding and to retain as much as possible of the wild gene pool.

One of the most crucial components of the pink pigeon programme was the development of post-release monitoring and management activities. In 1999, the Re-introduction Specialist Working Group recognised that the post-release phase of a re-introduction has received the least attention in past re-introduction projects relative to the pre-release phase. This has largely been because locating released animals is difficult, but also because release has been seen as an end rather than a beginning. Lessons learnt from the pink pigeon programme (many of which have been discussed in this thesis) were used to develop post-release monitoring and management activities, and are summarised below. More detail can be found in Roth *et al.* (1999).

- Questions of primary importance during post post-release monitoring should relate to the survival, behaviour and productivity of released individuals, and the dynamics of the released population. Variables to be monitored should include survival, mortality, breeding success, habitat use, diet and foraging behaviour, social behaviour, inter-specific interactions and population size.
- It is possible that in some cases the re-introduced population may become the best source of information about the behavioural ecology of the species, because re-introductions often result in a known size, age sex population of individually marked animals.
- For a highly endangered species, survival can be maximised through intensive post-release support, including provision of supplementary food, water and veterinary care. A move away from strictly non-interventive policy for re-introductions was suggested.
- Due to habitat fragmentation and the limited size of many re-introduction sites, some form of post-release management of populations may be necessary in perpetuity.
- There is a need for increased consideration of application of captive management techniques to free-ranging populations.

- Through monitoring and manipulation of variables, re-introductions provide opportunities to test ecological theory in field experiments. Manipulations should be undertaken in a systematic manner so that conclusions may be drawn.
- Management of re-introduced populations may also entail future further releases.

The main features of the pink pigeon recovery programme, that contributed to its success.

Summarising the points discussed above, the most important features of the pink pigeon recovery programme that facilitated its success are as follows.

- Development of an in country captive-breeding programme, that provided birds for re-introduction.
- The release of large numbers of birds to quickly establish the population, thereby reducing the effects of demographic and stochastic events.
- Application of soft-release techniques where birds were given gradual independence.
- Intensive post-release support and management of birds, including supplemental feeding, predator control and disease control, to maximise survival and reproductive success.
- Intensive post-release research relating to the survival, behaviour, reproductive success and ecology of released and wild individuals. This information is required to plan for the future management of the species and its habitat.

The pink pigeon programme has shown that captive-breeding and re-introduction can be used to successfully restore a declining population, but critical analysis of such programmes is needed to improve upon the re-introduction guidelines and provide practical information for future programmes. It is hoped that the data presented in this thesis, and the issues discussed, will contribute to the development of re-introduction theory and practice, will emphasise the need to develop sound research-oriented recovery programmes for endangered species and contribute to the future survival of the pink pigeon.

References

Anon [Middleton, G.] 1998. Black River Gorges National Park Management Plan. National Parks and Conservation Services, Ministry of Agriculture, Fisheries and Co-operatives.

Archibald, G.W. 1977. Supplemental feeding and manipulation of feeding ecology of endangered birds, a review. In: S.A. Temple (ed.). *Endangered Birds. Management techniques for preserving threatened species*, pp. 131-134.

Ashford, R.W., Green, E.E., Holmes, P.R. & Lucas, A.J. 1991. *Leucocytozoon toddi* in British sparrowhawks *Accipiter nisus*: patterns of infection in nestlings. *J. Nat. Hist.* 25: 269-277.

Atkinson, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. In: Moors, P.J. (ed.), *Conservation of Island Birds*, pp. 35-81. ICBP Technical Publication No. 3, Cambridge.

Atkinson, I.A.E. 1996. Introductions of wildlife as a cause of species extinctions. *Wildl. Biol.* 2: 135-141.

Atkinson, C.T. & van Riper, C. 1991. Pathogenicity and epizootiology of avian haematozoa: *Plasmodium*, *Leucocytozoon*, and *Haemoproteus*. In: J.E. Loye & M. Zuk (eds.), *Bird-Parasite Interaction: ecology, evolution and behaviour*, pp. 19-48. Oxford University Press.

Ballou, J. 1983. Calculating inbreeding coefficients from pedigrees. In: C.M. Schonewald-Cox, S.M. Chambers, B. Macbryde & L. Thomas (eds.), *Genetics and Conservation: a reference for managing wild animal and plant populations*, pp. 509-520. Benjamin/Cummings, Menlo Park, CA, USA.

Ballou, J. 1991. Small population overview. In: U.S. Seal, & M.W. Bruford (eds.), *Pink Pigeon Conservation Viability Assessment*, IUCN/SSC Captive Breeding Specialist Group.

Ballou, J.D. 1999. Infectious disease risk assessment in captive propagation, reintroduction and wildlife conservation. *Proc. 7th World Conf. on Breeding Endangered Species*, pp. 63-76. Cincinnati, OH, USA.

Ballou, J., & Ralls, K. 1982. Inbreeding and juvenile mortality in small populations of ungulates: a detailed analysis. *Biol. Cons.* 24: 239-272.

Baskett, T.S., Sayre, M.W., Tomlinson, R.E. & Mirarchi, R.E. (eds.) 1993. *Ecology and Management of the Mourning Dove.* Wildlife Management Institute, Stackpole books, Harrisburg, PA, USA.

Barbour, M., Burk, J. & Pitts, W. 1987. *Terrestrial Plant Ecology.* Cambridge University Press, Cambridge.

Beck, B.B., Rapaport, L.G., Stanley Price, M.R. & Wilson, A.C. 1994. Re-introduction of captive-born animals. In: P.J.S. Olney *et al.* (eds.), *Creative Conservation*, pp. 265-286.

Bell, D.J. & Hartley, J.R.M. 1987. An investigation into current captive breeding problems with the pink pigeon *Nesoenas mayeri*: a report on the first years' results. *Dodo, J. Jersey Wildl. Preserv. Trust* 24: 86-102.

Bellrose, F.C. 1980. *Ducks, Geese and Swans of North America.* Stackpole books, Harrisburg, PA.

Bennet, G.F. & Peirce, M.A. 1990. The haemoproteid parasites of pigeons and doves (Columbidae). *J. Nat. Hist.* 24: 311-325.

Bennet, G.F., Peirce, M.A. & Earle, R.A. 1994. An annotated checklist of the valid avian species of *Haemoproteus*, *Leucocytozoon* (Apicomplexa, Haemosporida) and Hepatozoon (Apicomplexa, Haemogregarinidae). *Systematic Parasitology* 29: 61-73

Birkhead, T.R. & Møller, A.P. 1996. Monogamy and sperm competition in birds. In: J.M. Black (ed.), *Partnerships in Birds: the study of monogamy*, pp. 323-343. Oxford University Press, Oxford.

Black, J.M. 1996. Pair bonds and partnerships. In: J.M. Black (ed.), *Partnerships in Birds: the study of monogamy*, pp. 3-20. Oxford University Press, Oxford.

Blockstein, D.E. & Westmoreland, D. 1993. Reproductive strategy. Chapter 6 *in* Baskett *et al.* (eds.), *Ecology and Management of the Mourning Dove*, pp. 105-116.

Boutin, S. 1989. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. *Can. J. Zool.* 68: 203-220.

Brownie, C., Hines, J.E. & Nichols, J.D. 1986. Constant parameter capture-recapture models. *Biometrics* 42: 561-574.

Brouard, N.R. 1963. A history of woods and forests in Mauritius. Port Louis, Mauritius: Government Printer.

Bruford, M.W., Jones, C.G. & Seal, U.S. 1991. Pink pigeon (*Nesoenas mayeri*) PVA. In: U.S. Seal, & M.W. Bruford (eds.), *Pink Pigeon Conservation Viability Assessment*, IUCN/SSC Captive Breeding Specialist Group.

Bruford, M.W., Krupa, A.P. & Burke, T. 1991. Genetic variation in the Jersey captive population of the pink pigeon (*Nesoenas mayeri*) revealed by DNA fingerprinting. In: U.S. Seal, & M.W. Bruford (eds.), *Pink Pigeon Conservation Viability Assessment*, IUCN/SSC Captive Breeding Specialist Group.

Burger, L.W., Dailey, T.V., Kurzejeski, E.W. & Ryan, M.R. 1995. Survival and cause-specific mortality of northern bobwhite in northern Missouri. *J. Wildl. Manage.* 59: 401-410.

Burley, N. & Moran, N. 1979. The significance of age and reproductive experience in the mate preference of pigeons *Columba livia*. *Anim. Behav.* 27: 686-698.

Burn, R.W. 1990. The pink pigeon database system in Mauritius. Progress report. Unpublished report to the Mauritius Wildlife Appeal Fund.

Cade, T.J. 1977. Manipulating the nesting biology of endangered birds, a review. In: S.A. Temple (ed.), *Endangered Birds. Management techniques for preserving threatened species*, pp.167-182. The University of Wisconsin Press, Madison, Wisconsin & Croom Helm Ltd., UK.

Cade, T. 2000. Progress in translocation of diurnal raptors. In: R.D. Chancellor & B.U. Meyburg (eds.), *Raptors at Risk. Proc. World Working Group on Birds of Prey*, pp. 343-372. Hancock House.

Cade, T., Enderson, J.H., Thelander, C.G. & White, C.M. (eds.) 1988. *Peregrine Falcon Populations, their management and recovery.* The Peregrine Fund Inc., Boise, Idaho.

Campbell, S. 1980. Is re-introduction a realistic goal? In: M.E. Soulé & B.A. Wilcox (eds.), *Conservation Biology, an evolutionary-ecological perspective*, pp. 263-269. Sinauer, Sunderland Mass., USA.

Carter, S. 1998. Mammalian predation on endangered Mauritian birds: predator identification, impacts and refuges in exotic vegetation. BSc. thesis, Royal Holloway, University of London, Egham, Surrey, UK.

Carter, S. & Bright, P. 2000. Exotic trees protecting endemic birds. Unpubl. abstract from the conference, *Evolution and Conservation in the Mascarene Islands - 2*, Nat. Hist. Mus., London.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* 63: 215-244.

Caughley, G & Gunn, A. 1996. *Conservation Biology in Theory and Practice*. Blackwell Science, Oxford.

Cheke, A.S. 1987. An ecological history of the Mascarene Islands with particular reference to extinctions and introductions of land vertebrates. In: A.W.Diamond (ed.), *Studies of Mascarene Island Birds*, pp. 5-89. Cambridge University Press, Cambridge.

Clobert, J. & Lebreton, J.D. 1991. Estimation of demographic parameters in bird populations. In: C.M. Perrins *et al.* (eds.), *Bird Population Studies,* pp. 75-104.

Clout, M.N., Gaze, P.D. & Hay, J.R. 1988. Clutch overlap by a New Zealand pigeon. *Notornis* 35: 59-62.

Clout, M.N., Karl. B.J., Pierce, R.J. & Robertson, H.A. 1995. Breeding and survival of New Zealand pigeons *Hemiphaga novaeseelandiae*. *Ibis* 137: 264-271.

Clutton-Brock, T.H. (ed.) 1991. *Reproductive Success: studies of individual variation in contrasting breeding systems*. The University of Chicago Press, Chicago & London.

Collar, N.J. & Stuart, S.N. 1985. *Threatened Birds of Africa and Related Islands.* ICBP/IUCN Red data book, Part 1. ICBP and IUCN, Cambridge.

Collar, N.J., Crosby, M.J., & Stattersfield, A.J. 1994. *Birds to Watch 2, the world list of threatened birds.* Birdlife Conservation Series No. 4. Birdlife International, Cambridge.

Collett, D. 1994. *Modelling Survival Data in Medical Research.* Chapman & Hall, London.

Conti, J.A. 1993. Diseases, parasites and contaminants. Chapter 12 *in* Baskett *et* al. (eds.), *Ecology and Management of the Mourning Dove*, pp. 205-224.

Conti, J.A., & Forrester, D.J. 1981. Interrelationships of parasites of white-winged doves and mourning doves in Florida. *J. Wildl. Dis.* 17: 529-536.

Cooch, E.G. & Cooke, F. 1991. Demographic changes in a snow goose population: biological and management implications. In: C.M Perrins *et al.* (eds.), *Bird Population Studies*, pp. 168-189.

Cooper, J.E., Needham, J.R., Applebee, K. & Jones, C.G. 1987. Clinical and pathological studies on the Mauritian pink pigeon (*Columba mayeri*). *Ibis* 130: 57-64.

Cooper, J.E. (ed.) 1989*a*. *Disease and Threatened Birds*. ICBP Technical Publication No. 10, Cambridge.

Cooper, J.E. 1989*b*. The role of pathogens in threatened populations: an historical review. In: J.E. Cooper (ed.), *Disease and Threatened Birds*, pp. 51-68.

Cottam, C. & Trefethen, J.B. 1968. *Whitewings, the life history, status and management of the white-winged dove*. D. van Nostrand Co. Inc..

Cox, D.R. 1972. Regression models and life tables (with discussion). *J. Roy. Stat. Soc.*, B, 74: 187-220.

Cox, D.R. & Oakes, D. 1984. *Analysis of Survival Data*. Chapman & Hall, London.

Cramp, S. (ed.) 1985. *The Birds of the Western Palearctic. Vol IV: terns to woodpeckers*. Oxford University Press.

Crome, F.H.J. 1975. The ecology of fruit pigeons in tropical northern Queensland. *Aust. Wildl. Res.* 2: 155-185.

Crow, J.F. & Kimura, M. 1970. *An Introduction to Population Genetics Theory*. Harper & Row, New York.

Csuti, B.A., Scott, J.M. & Estes, J. 1987. Looking beyond species-oriented conservation. *Endangered Species Update* 5:4.

Cunningham, A.A. 1996. Disease risks of wildlife translocations. *Cons. Biol.* 10: 349-353.

Dhondt, A.A. 1989. Blue tit. In: Newton, I. (ed.), *Lifetime Reproduction in Birds*. pp. 15-33, Academic Press, London.

Diamond, J.M. 1984. 'Normal' extinction of isolated populations. In: M.H. Nitecki (ed.), *Extinctions*, pp. 191-246. Chicago University Press, Chicago.

Diamond, J. 1989. Overview of recent extinctions. In: D. Western & M. Pearl (eds.), *Conservation for the Twenty-first Century*, pp. 37-41. Oxford University Press, New York..

Dingwall, P.R., Atkinson, I.A.E. & Hay, C. (eds.) 1978. *The Ecology and Control of Rodents in New Zealand Nature Reserves*. Dept. Lands & Survey Information Series 4, Wellington.

Dobson, A.P. & May, R.M. 1991. Parasites, cuckoos, and avian population dynamics. In: C.M. Perrins (ed.), *Bird Population Studies*, pp. 391-412.

Dulloo, M.E., Verburg, J., Paul, S.S., Green, S.E., de Boucherville Baissac, P. & Jones, C. 1997. Ile aux Aigrettes Management Plan 1997-2001. *MWF Technical Series No. 1/97*, Mauritius.

Durrell, G. 1977. Golden Bats and Pink Pigeons. Collins.

Durrell, G. & Durrell, L.M. 1980. Breeding Mascarene wildlife in captivity. *Int. Zoo Yearbook* 20: 112-119.

Edgerley, L.F. 1962. The conifers in Mauritius. *Proc. Roy. Arts. Sci.* Mauritius 2: 190-202.

Ens, B.J., Choudhury, S. & Black, J.M. 1996. Mate fidelity and divorce in monogamous birds. In: J.M. Black (ed.), *Partnerships in Birds: the study of monogamy*, pp. 344-401. Oxford University Press, Oxford.

Fischer, R.W. 1930. *The Genetical Theory of Natural Selection.* Oxford University Press.

Fischer, J. & Lindenmayer, D.B. 2000. An assessment of the published results of animal relocations. *Biol. Cons.* 96: 1-11.

Flach, E.J. 1984. Observations, clinical examinations and post-mortem examinations on two Mayer's pink pigeons, *Nesoenas mayeri*, with locomotor disorders. Report of Summer School Project, *Jersey Wildl. Preserv. Trust.*

Flach, E.J. & Cooper, J.E. 1991. Clinical and pathological findings in two Mauritian pink pigeons (*Columba mayeri*). *Vet. Record* 29: 48-51.

Foose, T.J., de Boer, L., Seal, U.S. & Lande, R. 1995. Conservation management strategies based on viable populations. In: J.D. Ballou, M. Gilpin & T.J. Foose (eds.), *Population Management for Survival & Recovery: analytical methods and strategies in small population conservation*, pp. 273-294. Columbia University Press, USA.

Frankel, O.H. & Soulé, M.E. 1981. *Conservation and Evolution.* Cambridge University Press, Cambridge.

Franklin, I.R. 1980. Evolutionary change in small populations. In: M.E. Soulé & B.A. Wilcox (eds.), *Conservation Biology, an evolutionary-ecological perspective*, pp. 135-149. Sinauer, Sunderland Mass., USA.

Fraser, G.L. 1985. Successful woodhen project – a brief overview. *Aust. Avicult.* November, pp. 255-271.

Frith, H.J. 1982. *Pigeons and Doves of Australia.* Rigby Publishers.

Fyfe, R.W., Armbruster, H., Banasch, U & Beaver, L.J. 1977. Fostering and cross-fostering of birds of prey. In: S.A. Temple (ed.), *Endangered Birds. Management techniques for preserving threatened species*, pp. 167-182. The University of Wisconsin Press, Madison, Wisconsin & Croom Helm Ltd., UK.

Garnham, P.C.C. 1966. *Malaria Parasites and Other Haemosporidia.* Blackwell, Oxford.

Gerlach, H. 1997. Viruses. In: B.W. Ritchie, G.J. Harrison, L.R. Harrison (eds.), *Avian Medicine: principles and application* (abridged edition), pp. 471-519. Wingers Publishing Inc..

Gilpin, M.E. & Soulé, M.E. 1986. Minimum viable populations: processes of species extinction. In: M.E. Soulé (ed.), *Conservation Biology, the science of scarcity and diversity*, pp. 19-34. Sinauer, Sunderland, Mass..

Goodwin, D. 1977. *Pigeons and Doves of the World.* British Museum (Natural History). Cornell University Press, Ithaca & London, second edition.

Gorman, M. 1999. Oryx go back to the brink. *Nature*, 398: 190.

Griffith, B., Scott, M., Carpenter, J.W. & Reed, C. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245: 477-480.

Groombridge, J.J. 2000. Conservation genetics of the Mauritius kestrel, pink pigeon and echo parakeet. Ph.D. thesis, QMW University of London, UK.

Harmon, W.M., Clark, W.A., Hawbecker, A.C. & Stafford, M. 1987. *Trichomonas gallinae* in Columbiform birds from the Galapagos Islands. *J. Wildl. Dis.* 23: 492-494.

Hartley, J.R.M. 1977. The Mauritius pink pigeon *Columba mayeri*. *Dodo, J. Jersey Wilidl. Preserv. Trust* 14: 23-26.

Haugen, A.O. & Keeler, J.E. 1952. Mortality of mourning doves from trichomoniasis in Alabama during 1951. *Trans. N. Amer. Wildl. Conf.* 17: 141-151.

Herman, C.M., Barrow, J.H. Jr., & Tarshis, I.B. 1975. Leucocytozoonosis in Canada geese at the Seney National Wildlife Refuge. *J. Wildl. Dis.* 11: 404-411.

Hernandez, M.A., Martin, A., & Nogales, M. 1999. Breeding success and predation on artificial nests of the endemic pigeons Bolle's laurel pigeon *Columba bollii* and white-tailed laurel pigeon *Columba junoniae* in the laurel forest of Tenerife (Canary Islands). *Ibis* 141: 52-59.

Hosany, R. 1998. Analysis of flora of Ile aux Aigrettes. B.Sc. thesis, University of Nottingham, UK.

Hudson, P.J. 1986. The effect of a parasitic nematode on the breeding production of red grouse. *J. Anim. Ecol.* 55: 85-92.

Hudson, P.J., Newborn, D. & Dobson, A.P. 1992. Regulation and stability of a free-living host-parasite system, *Trichostrongylus tenuis* in red grouse. 1: monitoring and parasite reduction experiments. *J. Anim. Ecol.* 61: 477-486.

Hutto, R.L., Reel, S. & Landres, P.B. 1987. A critical evaluation of the species approach to biological conservation. *Endangered Species Update* 4: 1-4.

IUCN 1987. Position Statement on the Translocation of Living Organisms: Introductions, Re-introductions, and Re-stocking. IUCN Council, Gland, Switzerland.

IUCN 1998. *IUCN Guidelines for Re-introductions*. Prepared by the IUCN/SSC Re-introduction Specialist Group, Gland, Switzerland and Cambridge, UK.

Jamieson, I.G. & Ryan, C.J. 2000. Increased egg infertility associated with translocating inbred takahe (*Porphyrio hochstetteri*) to island refuges in New Zealand. *Biol. Cons.* 94: 107-114.

Jeggo, D. 1977. Preliminary notes on the Mauritius pink pigeon at the Jersey Zoological Park. *Dodo, J. Jersey Wilidl. Preserv. Trust* 14: 26-30.

Jeggo, D. 1978. The Mauritius pink pigeon at the Jersey Zoological Park. *Avicult. Mag.* 84: 112-114.

Jeggo, D. 1979. Breeding the Mauritius pink pigeon at Jersey Zoological Park. *Avicult. Mag.* 85 (1): 1-2.

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

Johnson, T.H. & Stattersfield, A.J. 1990. A global review of island endemic birds, *Ibis* 132: 167-80.

Johnston, R. & Johnson, S. (1990). Reproductive ecology of feral pigeons. In: J. Pinowski & D. Summers-Smith (eds.). *Granivorous Birds in the Ecological Landscape*, pp 237-252. Polish Ecological Publ., Warsaw.

Johnston, R.F. & Janiga, M. 1995. *Feral Pigeons*. Oxford University Press.

Jones C.G. 1979. Mauritius/Rodrigues conservation project report for January 22nd-June 20th 1979. Unpubl. report to ICBP.

Jones C.G. 1980. The conservation of the endemic birds and bats of Mauritius and Rodrigues. A progress report and proposal for future activities. ICBP, Washington.

Jones, C.G., Jeggo D.F. & Hartley, J. 1983. The maintenance and captive breeding of the pink pigeon *Nesoenas mayeri. Dodo, J. Jersey Wildl. Preserv. Trust* 20: 16-20.

Jones, C.G. & Owadally, A.W. 1985. The status, ecology and conservation of the Mauritius kestrel. In: I. Newton and R.D. Chancellor (eds.), *Conservation Studies on Raptors*, pp. 211-222. ICBP Technical Publication No. 5, Cambridge.

Jones, C.G. 1987. The larger land-birds of Mauritius. In: A.W. Diamond (ed.), *Studies of Mascarene Island Birds*, pp. 208-300. Cambridge University Press, Cambridge.

Jones C.G. & Owadally, A.W. 1988. The life histories and conservation of the Mauritius kestrel *Falco punctatus*, pink pigeon *Columba mayeri* and echo parakeet *Psittacula eques*. *Proc. Royal Soc. Arts & Sci. Mauritius* 5: 79-130.

Jones, C.G., Todd, D.M., Swinnerton, K.J., Mungroo, Y. 1988. The release and management at liberty of captive-bred pink pigeons *Columba mayeri* on Mauritius. *Proc. 5th World Conf. on Breeding Endangered Species in Captivity*, pp 393-411. Cincinnati, OH.

Jones, C.G. Todd, D.M. & Mungroo, Y. 1989. Mortality, morbidity and breeding success of the pink pigeon (*Columba* (*Nesoenas*) *mayeri*). In: J.E. Cooper (ed.), *Disease and Threatened Birds*, pp. 89-113.

Jones, C.G., Heck, W., Lewis, R.E., Mungroo, Y. & Cade, T.J. 1991. A summary of the conservation management of the Mauritius kestrel *Falco punctatus* 1973-1991. *Dodo, J. Jersey Wildl. Preserv.* Trust 27: 81-99.

Jones C.G., Swinnerton, K.J., Taylor, C.J. & Mungroo, Y. 1992. The release of captive-bred pink pigeons *Columba mayeri* in native forest on Mauritius. A progress report July 1987-June 1992. *Dodo, J. Wildl. Preserv. Trusts* 28: 92-125.

Jones, C.G. & Duffy, K. 1993. Conservation management of the echo parakeet *Psittacula eques echo*. *Dodo, J. Wildl. Preserv. Trusts* 29: 126-148.

Jones, C.G., Heck, W., Lewis, R.E., Mungroo, Y., Slade, G. & Cade, T. 1994. The restoration of the Mauritius kestrel *Falco punctatus* population. *Ibis* 137: S173-180.

Jones C.G. 1995. Studies on the biology of the pink pigeon *Columba mayeri*. Ph.D. thesis, University College of Swansea, University of Wales, UK.

Jones C.G., & Hartley, J. 1995. A conservation project on Mauritius and Rodrigues: an overview and bibliography. *Dodo, J. Wildl. Preserv. Trusts* 31: 40-65.

Jones, C.G., Swinnerton, K., Hartley, J. & Mungroo, Y. 1999. The restoration of the free-living populations of the Mauritius kestrel (*Falco punctatus*), pink pigeon (*Columba mayeri*) and echo parakeet (*Psittacula eques*). *Proc. 7th World Conf. on Breeding Endangered Species*, pp. 77-86. Cincinnati, OH., USA.

Kaplan, E.L. & Meier, P. 1958. Nonparametric estimation from incomplete observations. *J. Am. Statist.* 53: 457-481.

Kear, J. & Berger, A.J. 1980. *The Hawaiian Goose – an experiment in conservation.* T & A.D. Poyser, Calton.

King, W.B. 1985. Island birds: will the future repeat the past? In P.J. Moors (ed.), *Conservation of Island Birds*, pp. 3-15. ICBP Technical Publication No. 3, Cambridge.

Koenig, P. 1926. Re-afforestation in Mauritius. *Empire Forestry J.*, 5: 218-222.

Krebs, C.J. 1989. *Ecological Methodology*, pp. 411-444. HarperCollins, NY.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. Chapman & Hall, London.

Lacy, R.C., Ballou, J.D., Princée, F., Starfield, A. & Thompson, E.A. 1995. Pedigree analysis for population management. In: J.D. Ballou, M. Gilpin & T.J. Foose (eds.), *Population Management for Survival & Recovery: analytical methods and strategies in small population conservation*, pp. 273-294. Columbia University Press, USA.

Lande, R. & Barrowclough, G.F. 1987. Effective population size, genetic variation, and their use in population management. In: M.E. Soulé (ed.), *Viable Populations for Conservation*, pp. 87-123. Cambridge University Press, Cambridge.

Ledger, J.A. 1968. Notes on the Hippoboscidae. *Bokmakerie, S.A. Ornithol. Soc.* 20: 66-67.

Levi, W.M. 1974. *The Pigeon*. Levi Publ. Co., Sumter, SC.

Lind, C.R. 1989. The effects of multiple clutching on the size, fertility and hatchability of the eggs of the pink pigeon. *Dodo, J. Jersey Wildl. Preserv. Trust* 26: 93-98.

Lind, C.R. 1993. Pink pigeon *Columba* (*Nesoenas*) *mayeri* EEP studbook, No. 1. Jersey Wildl. Preserv. Trust.

Lohoefener, R. & Lohmeier, L. 1986. Experiments with gopher tortoise (*Gopherus polyphemus*) relocation in southern Mississippi. *Herp. Review* 17: 37-40.

Lorence, D.H. & Sussman, R.W. 1986. Exotic species invasion into Mauritius wet forest remnants. *J. Trop. Ecol.* 2:147-162.

Lorence, D.H. & Sussman, R.W. 1988. Diversity, density, and invasion in a Mauritian wet forest. *Monogr. Syst. Bot. Missouri Bot. Gard.* 25: 187-204.

Mace, G.M. & Lande, R. 1991. Assessing extinction threats: towards a reevaluation of IUCN threatened species categories. *Cons. Biol.* 5: 148-157.

Martin, F.W. & Sauer, J.R. 1993. Population characteristics and trends in the eastern management unit. Chapter 17 *in* Baskett *et al. (eds.), Ecology and Management of the Mourning Dove*, pp. 281-304.

Maxwell, J. & Jamieson, I.G. 1997. Survival and recruitment of captive-reared and wild-reared takahe in Fiordland, New Zealand. *Cons. Biol.* 11: 683-691.

May, R.M. 1988. Conservation and disease. *Cons Biol.* 2: 28-30.

Maya, E. 1912. Blood parasites of birds. Notes of various haematozoa of birds observed in Mauritius. *Colony of Mauritius: Ann. Rep. Bacteriol. Lab.* 1911: 16-17.

Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255-261.

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

McKelvey, D.S. 1976. A preliminary study of the Mauritian pink pigeon (*Nesoenas meyeri*). *The Mauritius Inst. Bull.* 8: 145-175.

McKelvey, D.S. 1977. Observations on the Mauritian pink pigeon. *Birds International* 2: 36-8.

Merton, D.V. 1977. Controlling introduced predators and competitors on islands. In S.A. Temple (ed.). *Endangered Birds. Management techniques for preserving threatened species*, pp. 121-128.

Merton, D., Reed, C. & Crouchley, D. 1999. Recovery strategies and techniques for three free-living, critically-endangered New Zealand birds: kakapo (*Strigops habroptilus*), black stilt (*Himantopus novaezelandiae*) and takahe (*Porphyrio mantelli*). *Proc. 7th World Conf. on Breeding Endangered Species*, pp. 151-162. Cincinnati, OH., USA.

Mills, J. 2000. The spoils of Africa's land wars. *BBC Wildlife* (October) Vol. 18, No. 10 pp. 41-42.

Møller, A.P., Allander, K., & Dufva, R., 1990. Fitness effects of parasites on passerine birds: a review. In: J. Blondel, A. Gosler, J.D. Lebreton & R.H. McCleery (eds.), *Population Biology of Passerine Birds: an integrated approach*, pp. 269-280. Springer-Verlag, Berlin.

Montaggioni, L. 1972. Géologie marine. Essai de chronologie relative des stationnements marin quaternaires à l'Ile Maurice (Archipel des Mascareignes, Océan Indien). *C.R. Acad. Sc. Paris* 274: 2936-2939.

Moors, P.J. 1978. Methods for studying predators and their effects on forest birds. In: P.R. Dingwall, I.A.E. Atkinson & C. Hay (eds.). *The Ecology and Control of Rodents in New Zealand Nature Reserves*, 4: 47-57. Dept. Lands & Survey Information Series 4, Wellington.

Moors, P.J. (ed.) 1985. *Conservation of Island Birds.* ICBP Technical Publication No. 3. ICBP, Cambridge.

Murton, R.K. 1965. *The Wood Pigeon.* New Naturalist Monograph Series, Collins, London.

Murton,, R.K. 1966. A statistical evaluation of the effect of wood pigeon shooting as evidenced by the recoveries of ringed birds. *Statistician* 16: 183-202.

Myers, N. 1979. *The Sinking Ark.* Collins, London.

Newlands, W.A. 1975. Mauritius Conservation Project. Monthly reports. February-October 1975.

Newton, I. 1989*a*. Synthesis. Chapter 26 *in* Newton I. (ed.), *Lifetime Reproduction in Birds*, pp. 441-469. Academic Press, London.

Newton, I. 1989*b*. Sparrowhawk. In: Newton, I. (ed.), *Lifetime Reproduction in Birds*, pp. 279-296, Academic Press, London.

Newton, I. 1998. *Population Limitation in Birds*, Academic Press, London.

Norris, K., Anwar, M. & Read, A.F. 1994. Reproductive effort influences the prevalence of haematozoan parasites in great tits. *J. Anim. Ecol.* 63: 601-610.

Olney, P.J.S., Mace, G.M. & Feistner, A.T.C. 1994. *Creative Conservation: interactive management of wild and captive animals.* Chapman & Hall, London.

Oppliger, A., Christe, P. & Richner, H. 1997. Clutch size and malarial parasites in female great tits. *Beh. Ecol.* 8: 148-152.

Padya, B.M. 1989. *Weather and Climate of Mauritius.* Mahatma Gandhi Institute, Moka, Mauritius.

Page, W. 1995. A preliminary survey of the indigenous forest vegetation of southwest Mauritius to locate priority areas for conservation management. Report to Mauritius Wildlife Appeal Fund and National Parks and Conservation Services, Govt. Mauritius.

Papastravrou, V. 1999. Oryx suffering from success. *BBC Wildlife* (June), Vol. 17, No. 6, pp.55-56.

Parnell, J.A.N., Cronk, Q., Wyse Jackson, P. & Strahm, W. 1989. A study of the ecological history, vegetation and conservation management of Ile aux Aigrettes, Mauritius. *J. Trop. Ecol.* 5: 355-374.

Peirce, M.A. 1984*a*. Haematozoa of Zambian birds. I: general survey. *J. Nat. Hist.* 18: 105-122.

Peirce, M.A. 1984*b*. Haematozoa of African birds: some miscellaneous findings. *African J. Ecol.* 22: 149-152.

Peirce, M.A. & Marquiss, M. 1983. Haematozoa of British birds. VII: Haematozoa of raptors in Scotland with a description of *Haemoproteus nisi* sp. nov. from the sparrowhawk (*Accipiter nisus*). *J. Nat. Hist.* 17: 813-21.

Peirce, M.A. 1989. The significance of avian haematozoa in conservation strategies. In J.E. Cooper (ed.), *Disease and Threatened Birds*, pp. 69-76.

Peirce, M.A., Cheke, A.S. & Cheke, R.A. 1977. A survey of blood parasites of birds in the Mascarene Islands, Indian Ocean. *Ibis* 119: 451-461.

Peirce, M.A. & Prince, P.A. 1980. *Hepatozoon albatrossi* sp. nov. (Eucoccida: Hepatozoidae) from *Diomedea* spp. in the Antarctic. *J. Nat. Hist.* 14: 447-452.

Peirce, M.A., Greenwood, A.G. & Swinnerton, K. 1997. Pathogenicity of *Leucocytozoon marchouxi* in the pink pigeon (*Columba mayeri*) in Mauritius. *The Vet. Record* 140: 155-156.

Perez-Rivera, R. 1987. A preliminary study on squab behaviour of the pink pigeon and plains pigeon. Unpubl. J.W.P.T. Summer School Project.

Pollock, K.H., Winterstein, S.R. & Conroy, M.J. 1989a. Estimation and analysis of survival distributions for radio-tagged animals. *Biometrics* 45: 99-109.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989*b*. Survival analysis in telemetry studies: the staggered entry design. *J. Wildl. Manage.* 53 (1): 7-15.

Powlesland, R., grant, A., Tisdall, C., Dilks, P. & Flux, I. 1992. Ecology and breeding biology of Parea (Chatham Island pigeon) on southern Chatham Island, July 1991-April 1992. *Science & Research Internal Report* No. 134, Dept. of Conservation, Wellington, New Zealand.

Powlesland, R., Grant, A., Flux, I. & Dilks, P. 1994. Some aspects of the ecology and breeding biology of Parea on southern Chatham island, July 1992-April 1993. Dept. of Conservation, Science & Research Series No. 66. Wellington, New Zealand.

Prévost. 1843. In: Knip, Les Pigeons. Ed. 2.2 (1938-1843), p. 113, pl. 60.

Ralls, K., Brugger, K. & Glick, A. 1980. Deleterious effects of inbreeding in a herd of captive Dorcas gazelle *Gazzella dorcas*. *Int. Zoo Yearbook* 20: 137-146.

Ralls, K. & Ballou, J. 1983. Extinction: lessons from zoos. In: C.M. Schonewald-Cox, S.M. Chambers, B. Macbryde & L. Thomas (eds.), *Genetics and Conservation: a reference for managing wild animal and plant populations*, pp. 164-184. Benjamin/Cummings, Menlo Park, CA, USA.

Ralls, K., Harvey, P.H. & Lyles, A.M. 1986. Inbreeding in natural populations of birds and mammals. In: M.E. Soulé (ed.), *Conservation Biology: the science of scarcity and diversity*, pp. 35-56. Sinauer, Sunderland, Mass., USA.

Reed, C.E.M. & Merton, D.V. 1991. Behavioural manipulation of endangered New Zealand birds as an aid towards species recovery. *Acta Congr. Int. Ornithol.* 20: 2514-2522.

Reed, C.E.M., Nilsson, R.J., Murray, D.P. 1993. Cross-fostering in New Zealand's black stilt. *J. Wildl. Manage.* 57 (3): 608-611.

Reeves, H.M., Tomlinsons, R.E. & Bartonek, J.C. 1993. Population characteristics and trends in the western management unit. Chapter 19 *in* Baskett *et al.* (eds.), *Ecology and Management of the Mourning Dove*, pp. 341-376.

Reichner, H., Christe, P. & Oppliger, A. 1995. Parental investment affects prevalence of malaria. *Proc. Natl. Acad. Sci. USA.* 92: 1192-1194.

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

Rivera-Milan, F.F. 1996. Nest density and success of columbids in Puerto Rico. *The Condor* 98: 100-113.

Rivera-Milan, F.F. 1999. Population dynamics of Zenaida doves in Cidra, Puerto Rico. *J. Wildl. Manage*. 63: 232-244.

Robertson, H. 1985. Pigeons. In: C.M. Perrins & A.L.A. Middleton (eds.). *The Encyclopaedia of Birds*, pp. 216-219. G. Allen and Unwin, London.

Roth, T.L., Swanson, W.F. & Blattman, L.K. (eds.) 1999. *Seventh World Conference on Breeding Endangered Species: linking zoo and field research to advance conservation*, pp. 285-288. Cincinnati, OH, USA.

Rowan, M.K. 1983. *The Doves, Parrots, Louries & Cuckoos of Southern Africa*. Croom Helm Ltd, London & Canberra.

Roy, S.S., Jones, C.G. & Swinnerton, K. 1998. The feral cat in Mauritius. *Cat News* 28: 18-20.

Roy, S. S. 2001. The ecology and management of the lesser Indian mongoose *Herpestes javanicus* on Mauritius. Ph.D. thesis, University of Bristol, UK.

Safford, R.J. 1997*a*. Distribution studies on the forest-living native passerines of Mauritius. *Biol. Cons.* 80: 189-198

Safford, R.J. 1997*b*. A survey of the occurrence of native vegetation remnants on Mauritius in 1993. *Biol. Cons.* 80: 181-188.

Safford, R.J. 1997*c*. Nesting success of the Mauritius fody *Foudia rubra* in relation to its use of exotic trees as nest sites. *Ibis* 139: 555-559.

Safford, R.J. & Jones, C.G. 1993. Habitat management for conservation of the native passerine birds of Mauritius. *Proc. Roy. Soc. Arts Sci. Mauritius* 5: 21-32.

Sayre, M.W., Baskett, T.S., Mirarchi, R.E. 1993. Behaviour, Chapter 10 *in* Baskett *et al.* (eds.), *Ecology and Management of the Mourning Dove*, pp. 161-180.

Sayre, M.W. & Silvy, N.J. 1993. Nesting and Production. Chapter 5 *in* Basket *et al.* (eds), *Ecology and Management of the Mourning Dove*, pp. 81-104.

Schulz, J.H., Drobney, R.D., Sheriff, S.L. & Fuemmeler, W.J. 1996. Adult mourning dove survival during spring/summer in northcentral Missouri. *J. Wildl. Manage.* 60: 148-154.

Scott, D.K. 1988. Breeding success in Bewick's swans. In: T.H. Clutton-Brock (ed.), *Reproductive Success*, pp. 220-236.

Seymore, A. 2000. Spatial pattern of musk shrew *Suncus murinus* captures on the Ile aux Aigrettes. Unpubl. report. Mauritian Wildlife Foundation and Bristol University.

Sheperdson, D. 1991. The role of environmental enrichment in the captive breeding and reintroduction of endangered species. In P.J.S. Olney *et al.* (eds.), *Creative Conservation*, pp. 167-177.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biol. Cons.* 83: 247-257.

Skutch, A.F. 1991. *Life of the Pigeon.* Cornell University Press.

Snyder, B., Thilstead, J., Burgess, B. & Richard, M. 1985. Pigeon herpesvirus mortalities in foster reared Mauritius pink pigeons. *Abstracts and Papers - 1985 Annual Meeting, American Association of Zoo Veterinarians*, Arizona.

Snyder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Tooner, W.D. & Miller, B. 1996. Limitations of captive-breeding in endangered species recovery. *Cons. Biol.* 10: 338-348.

Soulé, M.E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In: M.E. Soulé & B.A. Wilcox (eds.), *Conservation Biology, an evolutionary-ecological perspective*, pp. 151-69. Sinauer, Sunderland Mass., USA.

Spencer, R. 1995. *The Ringer's Manual.* BTO, Norfolk, UK.

Spencer, S. 1993. Clinical investigation of the Mauritius pink pigeon. *Anim. Tech.* 44: 59-63.

Stabler, R.M. 1951. A survey of Colorado band-tailed pigeons, mourning doves and wild common pigeons for *Trichomonas gallinae*. *J. Parasitol.* 37: 471-472.

Stabler, R.M. 1954. Parasitological reviews. *Trichomonas gallinae*: a review. *Expermiental Parasitology* 111: 368-402.

Stanley Price, M.R. 1989. *Animal Re-introductions: the Arabian Oryx in Oman.* Cambridge University press, Cambridge.

Stattersfield, A.J., Crosby, M.J., Long, A.J., Wege, D.C. 1998. *Endemic Bird Areas of the World, priorities for biodiversity conservation.* Birdlife Conservation Series No. 7. Birdlife International, Cambridge.

Stattersfield, A.J. & Capper, D.R. 2000. *Threatened Birds of the World.* Birdlife International, Cambridge.

Staub, F.J.J. 1976. *Birds of the Mascarenes and Saint Brandon.* Port Louis, Mauritius. Organisation Normale des Enterprises.

Steele, F.N. 1979. Conservation of birds on Mauritius, final report for 1978. Unpubl. report to ICBP.

Sternberg, H. 1989. Pied flycatcher. In: Newton, I. (ed.), *Lifetime Reproduction in Birds*, pp. 55-74, Academic Press, London.

Stoddart, D.R., Taylor, J.D., Fosberg, F.R. & Farrow, G.E. 1971. Geomorphology of Aldabra Attoll. *Phil. Trans. Roy. Soc. Lond. B.* 260: 31-65.

Strahm, W.A. 1993. The conservation and restoration of the flora of Mauritius and Rodrigues. Ph.D. thesis, University of Reading.

Steele, F.N. 1979. Conservation of birds on Mauritius, final report for 1978. Unpubl. report to ICBP.

Stewart, G.R. 1999. A preliminary investigation into possible causes of parental failure in captive Mauritius pink pigeons. Report to Durrell Wildlife Conservation Trust.

Swinnerton, K.J., Jones, C.G., & Liddiard, T. 1993. Pink pigeon in Mauritius. *Re-introduction News. Newsletter of the Re-introduction Specialist Group of IUCN's SSC.* No. 7, pp. 12-13.

Swinnerton, K.J., Jones, C.G., Lam, R., Paul, S. Chapman R., Murray, K.A., Freeman, K. 2000. Conservation of the pink pigeon in Mauritius. *Re-introduction News, Newsletter of the re-introduction specialist group of IUCN's SSC.* No. 19: 10-13.

Tanaka, Y. 1997. Extinction of populations due to inbreeding depression with demographic disturbances. *Res. Popul. Ecol.* 39: 57-66.

Taynton, K.W. & Lind, C.R. 1991. Pink pigeon *Columba (Nesoenas) mayeri* International Studbook, No. 1. *Jersey Wildl. Preserv. Trust.*

Temple, S. A. 1975. The native faunas of Mauritius. I. The land birds. In: J. Proctor & R. Salm, *Conservation in Mauritius 1974*, q.v., appendix 6. Morges, Switzerland: IUCN,

Temple, S.A. 1976*a*.. Project 1082: Mauritius – promotion of conservation. *WWF Yearbook 1975-1976*, pp. 165-166.

Temple S.A. 1976*b*. Conservation of endemic birds and other wildlife on Mauritius (a progress report and proposal for future activities). Cornell University, Ithaca.

Temple, S.A. 1977. The status and conservation of endemic kestrels on Indian Ocean Islands. In: R.D. Chancellor (ed.), *World Conference on Birds of Prey, Vienna 1-3 October 1975, Report on proceedings*, pp. 74-81. ICBP, London.

Temple, S.A. 1977 (ed.). *Endangered Birds. Management techniques for preserving threatened species.* Univ. of Wisconsin Press, Croom Helm Ltd.

Temple. S.A. 1978. The life histories and ecology of the indigenous landbirds of Mauritius (kestrel, pink pigeon and parakeet). Unpubl. manuscript, Alexander library, Edward Grey Institute, Oxford (copy).

Thomas, C.S. & Coulson, J.C. 1991. Reproductive success of kittiwake gulls, *Rissa tridactyla.* In T.H. Clutton-Brock (ed.), *Reproductive Success*, pp. 251-278.

Thorne, E.T. & Williams, E.S. 1988. Disease and endangered species: the black-footed ferret as a recent example. *Cons. Biol.* 2: 66-74.

Thornhill, N.W. (ed.) 1993. *The Natural History of Inbreeding and Outbreeding*. Chicago. University of Chicago Press.

Todd, D.M. 1984. The release of pink pigeons *Columba (Nesoenas) mayeri* at Pamplemousses, Mauritius – a progress report. *Dodo, J. Jersey Wildl. Preserv. Trust* 21: 43-57.

Tomlinson, R.E. & Dunks, J.H. 1993. Population characteristics and trends in the central management unit. Chapter 18 *in* Baskett *et al.* (eds.), *Ecology and Management of the Mourning Dove*, pp. 305-340.

Tudor, D.C. 1991. *Pigeon Health and Disease.* Iowa State University Press, Ames, Iowa.

van Noordwijk, A.J. & van Balen, J.H. 1988. The great tit, *Parus major.* In: T.H. Clutton-Brock (ed.), *Reproductive Success*, pp. 119-153.

van Riper, C.I., van Riper, S.G., Goff, M.G., & Laird, M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56: 327-344

van Tyne, J. & Berger, A.J. 1976. *Fundamentals of Ornithology*. Second edition, John Wiley & Sons, NY.

Vaughan, R.E. & Wiehé, P.O. 1937. Studies on the vegetation of Mauritius I. A preliminary survey of the plant communities. *J. Ecol. 25*: 289-343.

Vaughan, R.E. & Wiehé, P.O. 1939. Note on 'The plant communities of Mauritius'. *J. Ecol.* 27: 281.

Vaughan, R.E. & Wiehé, P.O. 1941. Studies on the vegetation of Mauritius III. The structure and development of the upland climax forest. *J. Ecol.* 29: 127-160.

Veitch, C.R. 1985. Methods of eradicating feral cats from offshore islands in New Zealand. In: P.J. Moors (ed.), *Conservation of Island Birds*, pp. 125-141.

Warner, R.E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *The Condor* 70: 101-120.

Wayne, R.K., Bruford, M.W., Girman, D., Rebholz, W.E.R., Sunnucks, P. & Taylor, A.C. 1994. Molecular genetics of endangered species. In: P.J.S. Olney *et al.*, (eds.) *Creative Conservation*, pp. 92-117.

Weeks, M. 1977. *The Last Wild Horse*. Houghton Mifflin Company, Boston.

White, G.C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. *J. Wildl. Manage.* 47: 716-728.

Wiley, J.W. & Wiley, B.N. 1979. The Biology of the White-crowned Pigeon. Wildlife Monographs No. 64 (supplement to the *J. Wild. Manage.* 43 (1)), The Wildlife Society.

Williams, G.R. 1977. Marooning: a technique for saving threatened species from extinction. *Int. Zoo Yearbook* 17: 102-106.

Wilson, E.O. 1988. The current state of biological diversity. In: E.O. Wilson (ed.) *Biodiversity*, pp. 3-18.

Wilson, J.E. & Macdonald, J.W. 1967. Salmonella infection in wild birds. *Br. Vet. J.* 123: 212-219.

Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Cons. Biol.* 10: 1142-1154.

Woodford, M.H. & Rossiter, P.B. 1994. Disease risks associated with wildlife translocation projects. In: P.J.S. Olney *et al.* (eds.), *Creative Conservation*, pp. 178-200.

Appendix 1 Sample sizes for life history table analyses

(a) The number of pink pigeons in life history table analyses.

Age (years)	All birds	Released	Wild	Males	Females	Brise Fer	Pigeon Wood	Bel Ombre	Ile aux Aigrettes
0	689	248	441	240	212	230	132	139	176
1	420	184	236	205	190	152	84	64	79
2	286	134	152	150	128	102	60	66	49
3	176	86	90	98	78	70	43	33	24
4	87	40	47	47	40	34	28	10	13
5	47	17	30	25	22	22	20	-	-
6	23	10	13	12	11	11	12	-	-
7	11	-	-	-	-	-	-	-	-

(b) The number of released and wild pink pigeons at release sites in life history table analyses.

Age	Brise Fer		Bel Ombre		Ile aux Aigrettes	
(years)	Released	Wild	Released	Wild	Released	Wild
0	103	127	89	50	50	126
1	67	85	69	25	42	37
2	47	55	54	12	28	21
3	39	31	28	-	15	-
4	17	17	10	-	12	-
5	13	9	-	-	-	-
6	10	-	-	-	-	-

Appendix 2 Population trends for the pink pigeon, 1987-98.

(a) Population trends for the pink pigeon on Mauritius showing number released and number fledged, 1987-98.
BF = Brise Fer, BO = Bel Ombre, IAA = Ile aux Aigrettes, PW = Pigeon Wood.

		1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	Total
Number released	BF	11	4	4	2	18	16	3	1	29	20	0	0	108
	BO	0	0	0	0	0	0	0	7	49	34	5	0	95
	IAA	0	0	0	0	0	0	0	34	7	14	0	0	55
Total no. released		**11**	**4**	**4**	**2**	**18**	**16**	**3**	**42**	**85**	**68**	**5**	**0**	**256**
Number fledged	BF	0	0	1	0	0	0	25	26	9	36	27	3	127
	PW	12	1	0	2	3	17	10	8	13	23	25	20	122
	BO	0	0	0	0	0	0	0	0	8	16	12	18	54
	IAA	0	0	0	0	0	0	0	6	27	35	21	37	126
Total no. fledged		**0**	**1**	**1**	**2**	**3**	**17**	**35**	**40**	**57**	**110**	**85**	**78**	**429**
Total population	BF	8	4	6	6	16	26	47	57	86	87	91	79	
	PW	12	12	13	10	12	18	25	27	39	56	66	77	
	BO	0	0	0	0	0	0	0	7	46	79	73	81	
	IAA	0	0	0	0	0	0	0	33	36	51	52	60	
Total population		20	16	19	16	28	44	72	124	207	273	282	297	

(b) Population trends at Brise Fer, 1987-98.

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	Total
Number released	11	4	4	2	18	16	3	1	29	20	0	0	108
Number of males	6	1	1	2	9	5	1	0	18	8	0	0	51
Number of females	5	1	2	0	5	11	1	1	8	3	0	0	37
Number of unknown sex	0	2	1	0	4	0	1	0	3	9	0	0	20
Number fledged	0	0	1	0	0	0	25	26	9	36	27	3	127
Number died	3	8	3	1	7	6	6	17	10	56	23	15	153
Number removed	0	0	0	1	1	0	2	0	0	0	0	0	4
Number immigrated	0	0	0	0	0	0	1	0	1	1	1	0	4
Number emigrated	0	0	0	0	0	0	0	0	0	0	1	0	1
Total population	8	4	6	6	16	26	47	57	86	87	91	79	

(c) Population trends at Pigeon Wood, 1987-98.

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	Total
Number fledged	0	0	1	2	3	17	10	8	13	23	25	20	122
Number of males	5	0	1	0	2	4	4	6	9	9	7	1	48
Number of females	7	0	0	0	1	8	3	0	6	8	9	0	42
Number of unknown sex	0	0	0	2	2	3	3	2	0	7	6	19	44
Number died	0	0	0	5	1	11	2	6	5	7	17	9	59
Number immigrated	0	0	0	0	0	0	0	0	4	2	3	0	9
Number emigrated	0	0	0	0	0	0	1	0	0	1	1	0	3
Total population	12	12	13	10	12	18	25	27	39	56	66	77	

(d) Population trends at Bel Ombre, 1994-98

	1994	1995	1996	1997	1998	Total
Number released	7	49	34	5	0	95
Number of males	4	18	12	1	0	35
Number of females	3	21	17	2	0	43
Number of unknown sex	0	10	5	2	0	17
Number fledged	0	8	16	12	18	54
Number died	0	13	15	21	10	58
Number immigrated	0	0	1	0	0	1
Number emigrated	0	5	3	2	0	10
Total population	7	46	79	73	81	

(e) Population trends on Ile aux Aigrettes, 1994-98

	1994	1995	1996	1997	1998	Total
Number released	34	7	14	0	0	55
Number of males	17	1	9	0	0	27
Number of females	17	3	2	0	0	22
Number of unknown sex	0	3	3	0	0	6
Number fledged	6	27	35	21	37	126
Number died	6	31	33	20	29	119
Number removed	1	0	1	0	0	62
Total population	33	36	51	52	60	

Appendix 3 Breeding success on Ile aux Aigrettes, 1994-98.

(a) Summary of monthly production, fertility, hatchability and rearing success on Ile aux Aigrettes, 1994-98. Nest attempts where eggs were found before or during incubation.

Month	Number laid	Number fertile	Number infertile	Number known	Number unknown	% fertile of known	Number hatched	% hatched of laid	% hatched of fertile	Number fledged	% fledged of laid	% fledged of hatched
January	60	32	26	58	2	55.2	23	38.3	71.9	12	20.0	52.2
February	29	11	14	25	4	44.0	6	20.7	54.5	2	6.9	33.3
March	13	3	9	12	1	25.0	2	15.4	66.7	1	7.7	50.0
April	22	15	5	20	2	75.0	12	54.5	80.0	5	22.7	41.7
May	30	14	14	28	2	50.0	13	43.3	92.9	6	20.0	46.2
June	24	11	12	23	1	47.8	10	41.7	90.9	1	4.2	10.0
July	55	29	25	54	1	53.7	19	34.5	65.5	11	20.0	57.9
August	45	28	13	41	4	68.3	25	55.6	89.3	5	11.1	20.0
September	60	37	18	55	5	67.3	32	53.3	86.5	6	10.0	18.8
October	65	37	26	63	2	58.7	30	46.2	81.1	9	13.8	30.0
November	56	29	19	48	8	60.4	28	50.0	96.6	14	25.0	50.0
December	63	38	20	58	5	65.5	33	52.4	86.8	18	28.6	54.5
Total	522	284	201	485	37	58.6	233	44.6	82.0	90	17.2	38.6

(b) Summary of annual production, fertility, hatchability and rearing success on Ile aux Aigrettes, 1994-98. Nest attempts where eggs were found before or during incubation.

Year	Number laid	Number fertile	Number infertile	Number known	Number unknown	% fertile of known	Number hatched	% hatched of laid	% hatched of fertile	Number fledged	% fledged of laid	% fledged of hatched
1994	61	38	18	56	5	67.9	29	47.5	76.3	9	14.8	31.0
1995	195	104	84	188	7	55.3	87	44.6	83.7	28	14.4	32.2
1996	112	41	65	106	6	38.7	34	30.4	82.9	16	14.3	47.1
1997	83	52	18	70	13	74.3	43	51.8	82.7	21	25.3	48.8
1998	71	49	16	65	6	75.4	40	56.3	81.6	16	22.5	40.0
Total	522	284	201	485	37	58.6	233	44.6	82.0	90	17.2	38.6

Appendix 4 (a) Inbreeding coefficients of fledged birds. LSBN = local studbook number, GDEWS = Gerald Durrell Endemic Wildlife Sanctuary, Mauritius, BF = Brise Fer, BO = Bel Ombre, IAA = Ile aux Aigrettes, JERSEY = Jersey Zoo, Channel islands, WILD = wild-fledged.

LSBN	Sex	Hatch date	Sire LSBN	Dam LSBN	Where bred	Where released	Inbreeding coefficient
0377	M	09/09/86	0003	0124	GDEWS	BF	0.000000
0378	M	10/09/86	0003	0124	GDEWS	BF	0.000000
0387	F	12/11/86	0003	0124	GDEWS	BF	0.000000
0391	M	21/01/87	0003	0124	GDEWS	BF	0.000000
0392	M	01/02/87	0003	0124	GDEWS	BF	0.000000
0434	M	08/11/90	0420	0426	GDEWS	BF	0.000000
0435	M	09/11/90	0420	0426	GDEWS	BF	0.000000
0436	U	12/11/90	0381	0424	GDEWS	BF	0.000000
0437	U	30/11/90	0420	0426	GDEWS	BF	0.000000
0439	M	08/12/90	0430	0421	GDEWS	BF	0.000000
0441	M	29/12/90	0430	0421	GDEWS	BF	0.000000
0444	F	18/01/91	0420	0426	GDEWS	BF	0.000000
0447	M	17/02/91	0429	0423	GDEWS	BF	0.000000
0448	U	03/03/91	0381	0424	GDEWS	BF	0.000000
0449	M	12/03/91	0429	0423	GDEWS	BF	0.000000
0456	M	22/04/91	0429	0423	GDEWS	BF	0.000000
0459	U	09/05/91	0429	0423	GDEWS	BF	0.000000
0465	M	13/07/91	0381	0424	GDEWS	BF	0.000000
0469	F	15/09/91	0429	0423	GDEWS	BF	0.000000
0470	F	27/10/91	0381	0424	GDEWS	BF	0.000000
0471	M	13/11/91	0381	0424	GDEWS	BF	0.000000
0472	M	10/05/92	0384	0446	GDEWS	BF	0.000000
0473	M	11/05/92	0384	0446	GDEWS	BF	0.000000
0474	F	18/05/92	0381	0424	GDEWS	BF	0.000000
0475	M	19/05/92	0381	0424	GDEWS	BF	0.000000
0476	F	23/05/92	0429	0423	GDEWS	BF	0.000000
0478	F	08/06/92	0429	0423	GDEWS	BF	0.000000
0480	F	03/07/92	0384	0446	GDEWS	BF	0.000000
0481	M	08/07/92	0190	0424	GDEWS	BF	0.000000
0490	M	05/12/92	0430	0423	GDEWS	BF	0.000000
0491	F	07/12/92	0430	0423	GDEWS	BF	0.000000
0492	U	09/12/92	0190	0424	GDEWS	BF	0.000000
0503	M	27/04/93	0384	0446	GDEWS	IAA	0.000000
0506	M	20/05/93	0384	0446	GDEWS	IAA	0.000000
0514	F	25/07/93	0495	0426	GDEWS	IAA	0.000000
0515	M	30/07/93	0484	0423	GDEWS	IAA	0.000000
0516	M	02/08/93	0484	0423	GDEWS	IAA	0.000000
0523	F	20/08/93	0484	0423	GDEWS	IAA	0.000000
0524	F	03/08/93	0495	0426	GDEWS	IAA	0.000000
0533	F	22/11/93	0484	0424	GDEWS	IAA	0.000000
0538	M	11/01/94	0128	0423	GDEWS	IAA	0.000000
0540	F	16/01/94	0501	0482	GDEWS	IAA	0.000000
0541	M	16/01/94	0501	0482	GDEWS	IAA	0.000000
0542	M	20/01/94	0502	0424	GDEWS	IAA	0.000000
0544	M	24/01/94	0128	0423	GDEWS	IAA	0.000000
0550	F	06/03/94	0501	0482	GDEWS	IAA	0.000000
0552	F	07/03/94	0504	0482	GDEWS	BO	0.000000
0554	F	08/03/94	0128	0423	GDEWS	IAA	0.000000
0562	M	05/04/94	0128	0423	GDEWS	IAA	0.000000
0587	F	04/11/94	0530	0548	GDEWS	BO	0.000000
0592	U	16/11/94	0496	0509	GDEWS	BO	0.000000
0595	U	30/11/94	0530	0548	GDEWS	BO	0.000000
0596	M	30/11/94	0496	0509	GDEWS	BO	0.000000

LSBN	Sex	Hatch date	Sire LSBN	Dam LSBN	Where bred	Where released	Inbreeding coefficient
0597	M	01/12/94	0530	0548	GDEWS	BO	0.000000
0599	M	05/12/94	0502	0424	GDEWS	BO	0.000000
0601	F	07/12/94	0530	0548	GDEWS	BO	0.000000
0603	F	19/12/94	0530	0548	GDEWS	BO	0.000000
0604	F	29/12/94	0530	0548	GDEWS	BO	0.000000
0607	F	12/01/95	0496	0509	GDEWS	BO	0.000000
0612	M	01/02/95	0502	0518	GDEWS	BO	0.000000
0613	M	02/02/95	0502	0518	GDEWS	BO	0.000000
0618	F	28/04/95	0502	0518	GDEWS	BF	0.000000
0619	F	29/04/95	0502	0518	GDEWS	BF	0.000000
0620	M	01/05/95	0575	0482	GDEWS	BF	0.000000
0621	M	02/05/95	0575	0482	GDEWS	BF	0.000000
0624	U	09/05/95	0504	0446	GDEWS	BF	0.000000
0627	F	23/05/95	0430	0424	GDEWS	BO	0.000000
0633	F	21/06/95	0502	0518	GDEWS	BF	0.000000
0635	F	26/06/95	0575	0482	GDEWS	BO	0.000000
0636	M	29/06/95	0530	0548	GDEWS	BF	0.000000
0637	F	06/07/95	0530	0548	GDEWS	BF	0.000000
0639	M	16/07/95	0504	0446	GDEWS	BF	0.000000
0643	F	26/07/95	0502	0518	GDEWS	BF	0.000000
0644	M	29/07/95	0538	0589	GDEWS	BF	0.000000
0646	M	06/08/95	0575	0482	GDEWS	BF	0.000000
0649	M	01/08/95	0502	0518	GDEWS	BF	0.000000
0650	F	17/08/95	0530	0548	GDEWS	BF	0.000000
0651	M	18/08/95	0530	0548	GDEWS	BF	0.000000
0652	F	21/08/95	0575	0482	GDEWS	BF	0.000000
0660	M	04/10/95	0530	0548	GDEWS	BF	0.000000
0661	M	04/10/95	0530	0548	GDEWS	BF	0.000000
0666	M	21/10/95	0538	0589	GDEWS	BF	0.000000
0667	F	27/10/95	0128	0518	GDEWS	BO	0.000000
0668	F	28/10/95	0128	0518	GDEWS	BO	0.000000
0669	F	29/10/95	0530	0548	GDEWS	BO	0.000000
0670	U	31/10/95	0530	0548	GDEWS	BO	0.000000
0671	U	31/10/95	0454	0511	GDEWS	BO	0.000000
0672	F	08/11/95	0538	0589	GDEWS	BO	0.000000
0673	F	08/11/95	0579	0546	GDEWS	BF	0.000000
0674	M	08/11/95	0530	0548	GDEWS	BF	0.000000
0675	M	09/11/95	0530	0548	GDEWS	BF	0.000000
0676	U	11/11/95	0128	0518	GDEWS	BF	0.000000
0679	M	16/11/95	0454	0511	GDEWS	BF	0.000000
0680	F	17/11/95	0454	0511	GDEWS	BF	0.000000
0681	F	22/11/95	0530	0548	GDEWS	BO	0.000000
0682	U	28/11/95	0504	0482	GDEWS	BO	0.000000
0683	M	29/11/95	0504	0482	GDEWS	BO	0.000000
0684	M	30/11/95	0579	0546	GDEWS	BO	0.000000
0685	M	01/12/95	0579	0546	GDEWS	BO	0.000000
0688	M	08/12/95	0504	0482	GDEWS	BF	0.000000
0692	F	20/12/95	0530	0548	GDEWS	BF	0.000000
0694	U	30/12/95	0454	0511	GDEWS	BF	0.000000
0696	M	31/12/95	0504	0482	GDEWS	BO	0.000000
0698	U	13/01/96	0530	0548	GDEWS	BF	0.000000
0699	M	21/01/96	0504	0482	GDEWS	BO	0.000000
0700	U	23/01/96	0504	0482	GDEWS	BF	0.000000
0701	U	29/01/96	0530	0548	GDEWS	BF	0.000000
0702	F	31/01/96	0454	0511	GDEWS	BO	0.000000
0704	U	02/02/96	0454	0511	GDEWS	BO	0.000000
0707	U	10/02/96	0530	0548	GDEWS	BF	0.000000

LSBN	Sex	Hatch date	Sire LSBN	Dam LSBN	Where bred	Where released	Inbreeding coefficient
0708	M	16/02/96	0128	0518	GDEWS	BO	0.000000
0709	F	20/02/96	0504	0482	GDEWS	BO	0.000000
0713	F	25/03/96	0495	0634	GDEWS	BO	0.000000
0714	M	04/04/96	0504	0482	GDEWS	BO	0.000000
0720	M	19/05/96	0504	0482	GDEWS	BO	0.000000
0721	U	19/05/96	0504	0482	GDEWS	BO	0.000000
0722	F	03/06/96	0504	0482	GDEWS	BO	0.000000
0724	F	22/06/96	0454	0511	GDEWS	BO	0.000000
0728	F	10/07/96	0128	0518	GDEWS	BO	0.000000
0729	F	28/07/96	0495	0634	GDEWS	BO	0.000000
0730	M	05/08/96	0520	0498	GDEWS	BO	0.000000
0731	F	07/08/96	0520	0498	GDEWS	BO	0.000000
0732	F	14/08/96	0454	0511	GDEWS	BO	0.000000
0733	M	14/08/96	0520	0498	GDEWS	IAA	0.000000
0734	M	16/08/96	0520	0498	GDEWS	IAA	0.000000
0735	F	26/08/96	0454	0511	GDEWS	IAA	0.000000
0736	F	21/08/96	0495	0634	GDEWS	IAA	0.000000
0738	M	09/09/96	0454	0511	GDEWS	IAA	0.000000
0739	M	11/09/96	0454	0511	GDEWS	IAA	0.000000
0740	M	19/09/96	0520	0498	GDEWS	IAA	0.000000
0742	U	16/10/96	0454	0511	GDEWS	BO	0.000000
0743	U	01/11/96	0454	0511	GDEWS	BO	0.000000
0744	M	02/11/96	0454	0511	GDEWS	BO	0.000000
0747	F	20/11/96	0454	0511	GDEWS	BO	0.000000
2112	F	26/01/94	0456	0470	BF	BF	0.000000
2114	F	19/05/94	0456	0470	BF	WILD	0.000000
2366	M	05/05/96	0481	3068	BF	WILD	0.000000
2379	U	09/06/96	0447	0480	BF	WILD	0.000000
2380	U	09/06/96	0447	0480	BF	WILD	0.000000
4275	U	05/09/94	0535	0532	IAA	WILD	0.000000
4278	U	26/10/94	0544	0537	IAA	IAA	0.000000
4279	F	29/11/94	0562	0537	IAA	WILD	0.000000
4280	M	27/11/94	0535	0532	IAA	WILD	0.000000
4282	M	01/01/95	0562	0537	IAA	WILD	0.000000
4298	F	05/02/95	0562	0537	IAA	WILD	0.000000
4299	F	05/02/95	0569	0532	IAA	WILD	0.000000
4302	M	14/03/95	0569	0537	IAA	WILD	0.000000
4308	U	26/05/95	0517	0539	IAA	WILD	0.000000
4316	U	29/08/95	0517	0539	IAA	WILD	0.000000
4318	F	13/07/95	0569	0537	IAA	IAA	0.000000
4325	M	14/10/95	0569	0537	IAA	WILD	0.000000
4326	U	06/10/95	0535	0532	IAA	IAA	0.000000
4341	U	15/05/96	0569	0537	IAA	WILD	0.000000
4359	M	29/10/96	0517	0539	IAA	WILD	0.000000
4360	U	01/11/96	0569	0537	IAA	WILD	0.000000
4366	U	14/08/96	4338	0540	IAA	WILD	0.008698
4386	U	22/10/97	4338	0540	IAA	WILD	0.008698
4388	U	26/11/97	4338	0540	IAA	WILD	0.008698
4398	U	25/11/97	4338	0540	IAA	WILD	0.008698
4403	F	26/01/98	4338	0540	IAA	WILD	0.008698
0591	F	09/11/94	0538	0526	GDEWS	BO	0.015625
0594	M	28/11/94	0538	0526	GDEWS	BO	0.015625
0551	M	07/03/94	0190	0507	GDEWS	IAA	0.016602
0553	F	07/03/94	0190	0507	GDEWS	IAA	0.016602
0556	M	23/03/94	0190	0507	GDEWS	BO	0.016602
0561	M	05/04/94	0190	0507	GDEWS	IAA	0.016602
0563	F	13/04/94	0190	0507	GDEWS	IAA	0.016602

LSBN	Sex	Hatch date	Sire LSBN	Dam LSBN	Where bred	Where released	Inbreeding coefficient
0567	M	26/04/94	0190	0507	GDEWS	IAA	0.016602
0570	M	23/05/94	0190	0507	GDEWS	BO	0.016602
0571	M	24/05/94	0190	0507	GDEWS	BO	0.016602
0572	M	02/06/94	0190	0507	GDEWS	BO	0.016602
4274	U	30/08/94	0503	0543	IAA	WILD	0.023193
4277	U	23/11/94	0503	0543	IAA	WILD	0.023193
4281	U	26/12/94	0503	0543	IAA	WILD	0.023193
4301	U	05/03/95	0503	0543	IAA	WILD	0.023193
4303	M	04/04/95	0503	0543	IAA	WILD	0.023193
4307	M	05/05/95	0503	0543	IAA	WILD	0.023193
4313	F	30/07/95	0503	0543	IAA	WILD	0.023193
4319	U	02/09/95	0503	0543	IAA	WILD	0.023193
4330	F	18/12/95	0503	0543	IAA	WILD	0.023193
4331	F	19/12/95	0503	0543	IAA	WILD	0.023193
4333	U	28/01/96	0503	0543	IAA	WILD	0.023193
4343	U	16/05/96	0503	0543	IAA	WILD	0.023193
5250	M	07/09/95	0593	0605	BO	WILD	0.025391
0375	M	18/01/86	0121	0144	GDEWS	BF	0.031250
0440	F	26/12/90	0453	0361	GDEWS	BF	0.031250
0658	M	28/09/95	0520	0576	GDEWS	BO	0.031250
0663	U	07/10/95	0520	0576	GDEWS	BF	0.031250
0686	M	01/12/95	0520	0576	GDEWS	BF	0.031250
0687	F	03/12/95	0520	0576	GDEWS	BO	0.031250
0690	M	14/12/95	0520	0576	GDEWS	BF	0.031250
0703	U	31/01/96	0520	0576	GDEWS	BF	0.031250
2104	F	13/12/93	0434	1735	BF	WILD	0.033142
0389	F	09/01/87	0367	0360	GDEWS	BF	0.033203
0625	M	15/05/95	0384	0498	GDEWS	BF	0.033203
0631	F	15/06/95	0384	0498	GDEWS	BO	0.033203
0655	U	09/09/95	0384	0498	GDEWS	BO	0.033203
0656	U	10/09/95	0384	0498	GDEWS	BF	0.033203
0664	M	17/10/95	0384	0498	GDEWS	BF	0.033203
0677	M	13/11/95	0384	0498	GDEWS	BF	0.033203
0678	U	14/11/95	0384	0498	GDEWS	BF	0.033203
0691	M	17/12/95	0384	0498	GDEWS	BF	0.033203
0695	U	30/12/95	0384	0498	GDEWS	BF	0.033203
0705	M	06/02/96	0384	0498	GDEWS	BO	0.033203
0706	F	06/02/96	0384	0498	GDEWS	BO	0.033203
0711	F	27/02/96	0384	0498	GDEWS	BO	0.033203
0715	F	06/04/96	0384	0498	GDEWS	BO	0.033203
0716	U	07/04/96	0384	0498	GDEWS	BO	0.033203
0717	F	27/04/96	0384	0498	GDEWS	BO	0.033203
0718	F	28/04/96	0384	0498	GDEWS	BO	0.033203
2373	U	22/05/96	0649	5240	BF	WILD	0.036224
4412	U	03/08/98	0740	4312	IAA	WILD	0.037537
4413	U	04/08/98	0740	4312	IAA	WILD	0.037537
2108	F	19/01/94	0441	0479	BF	WILD	0.038086
4290	U	20/01/95	0506	0514	IAA	WILD	0.040527
4305	F	28/11/94	0561	0540	IAA	WILD	0.040771
4312	F	24/07/95	0561	0540	IAA	WILD	0.040771
4391	U	11/12/97	4361	0735	IAA	WILD	0.042175
4416	U	01/08/98	0738	4357	IAA	WILD	0.042175
0727	M	05/07/96	0556	0574	BO	BO	0.046875
4296	U	27/01/95	0549	0563	IAA	WILD	0.046875
5453	M	03/10/95	0556	0574	BO	WILD	0.046875
2368	F	05/05/96	0435	0474	BF	WILD	0.048828
2399	U	18/09/96	0435	0474	BF	WILD	0.048828

LSBN	Sex	Hatch date	Sire LSBN	Dam LSBN	Where bred	Where released	Inbreeding coefficient
2421	U	19/08/97	0435	0474	BF	WILD	0.048828
4336	F	21/01/96	4302	4312	IAA	WILD	0.049149
4383	M	18/10/97	0740	4336	IAA	WILD	0.054047
4384	U	19/10/97	0740	4336	IAA	WILD	0.054047
4396	U	21/12/97	0740	4336	IAA	WILD	0.054047
4402	F	23/01/98	0740	4336	IAA	WILD	0.054047
4409	U	05/07/98	0740	4336	IAA	WILD	0.054047
4377	U	18/07/97	0734	4352	IAA	WILD	0.054230
4380	F	18/09/97	0734	4352	IAA	WILD	0.054230
4395	U	16/12/97	0734	4352	IAA	WILD	0.054230
4414	U	04/08/98	0734	4352	IAA	WILD	0.054230
4415	U	04/08/98	0734	4352	IAA	WILD	0.054230
5198	U	04/10/96	0570	0591	BO	WILD	0.057617
5451	M	26/09/95	0570	0591	BO	WILD	0.057617
0801	U	01/11/96	0684	0706	BO	WILD	0.060608
0802	F	01/11/96	0684	0706	BO	BO	0.060608
2415	M	01/08/97	0664	0673	BF	WILD	0.060608
0519	M	07/08/93	0488	0487	GDEWS	IAA	0.062500
0534	M	24/12/93	0488	0487	GDEWS	IAA	0.062500
0535	M	24/12/93	0488	0487	GDEWS	IAA	0.062500
0539	F	12/01/94	0488	0487	GDEWS	IAA	0.062500
0549	M	05/03/94	0488	0487	GDEWS	IAA	0.062500
0569	M	20/05/94	0488	0487	GDEWS	IAA	0.062500
0574	F	11/06/94	0488	0487	GDEWS	BO	0.062500
0583	U	01/10/94	0488	0487	GDEWS	BO	0.062500
0584	M	09/10/94	0488	0487	GDEWS	BO	0.062500
0598	F	03/12/94	0488	0487	GDEWS	BO	0.062500
0600	U	05/12/94	0488	0487	GDEWS	BO	0.062500
0605	F	01/01/95	0488	0487	GDEWS	BO	0.062500
0608	M	22/01/95	0488	0487	GDEWS	BO	0.062500
0609	U	24/01/95	0542	0564	GDEWS	BO	0.062500
0610	F	31/01/95	0488	0487	GDEWS	BO	0.062500
0611	M	31/01/95	0488	0487	GDEWS	BO	0.062500
0615	M	03/02/95	0542	0564	GDEWS	BO	0.062500
0617	U	21/02/95	0488	0487	GDEWS	BO	0.062500
0622	M	05/05/95	0488	0487	GDEWS	BF	0.062500
0623	M	06/05/95	0488	0487	GDEWS	BF	0.062500
0630	F	29/05/95	0488	0487	GDEWS	BF	0.062500
0632	M	15/06/95	0542	0564	GDEWS	BF	0.062500
0641	M	21/07/95	0542	0564	GDEWS	BF	0.062500
0657	M	21/09/95	0542	0564	GDEWS	BO	0.062500
0659	F	01/10/95	0488	0487	GDEWS	BO	0.062500
4394	F	15/12/97	0488	0553	IAA	WILD	0.062500
0517	M	07/08/93	0457	0498	GDEWS	IAA	0.064453
0528	F	18/10/93	0457	0498	GDEWS	IAA	0.064453
0532	F	09/11/93	0457	0498	GDEWS	IAA	0.064453
0536	M	31/12/93	0457	0498	GDEWS	IAA	0.064453
0537	F	01/01/94	0457	0498	GDEWS	IAA	0.064453
0543	F	21/01/94	0457	0498	GDEWS	IAA	0.064453
0557	M	31/03/94	0457	0498	GDEWS	IAA	0.064453
0566	F	24/04/94	0457	0498	GDEWS	IAA	0.064453
0577	F	22/06/94	0457	0498	GDEWS	BO	0.064453
2365	M	04/05/96	0465	0480	BF	WILD	0.072266
0719	F	05/05/96	0465	0480	BF	BO	0.072266
4337	U	20/12/95	0567	4299	IAA	IAA	0.076874
0388	M	03/11/86	0368	0144	GDEWS	BF	0.078125
5195	M	25/08/96	0613	0605	BO	WILD	0.078125

LSBN	Sex	Hatch date	Sire LSBN	Dam LSBN	Where bred	Where released	Inbreeding coefficient
2375	M	25/05/96	0636	0618	BF	WILD	0.078735
1725	F	04/08/92	1978	1977	JERSEY	BF	0.079102
1735	F	27/08/92	1978	1977	JERSEY	BF	0.079102
0723	U	14/06/96	4307	4298	IAA	BO	0.080292
4323	F	07/10/95	4307	4298	IAA	WILD	0.080292
4328	U	10/12/95	4307	4298	IAA	WILD	0.080292
4329	U	12/12/95	4307	4298	IAA	WILD	0.080292
4335	F	11/01/96	4307	4298	IAA	WILD	0.080292
4347	U	13/06/96	4307	4298	IAA	WILD	0.080292
4351	M	17/07/96	4307	4298	IAA	WILD	0.080292
4357	F	19/09/96	4307	4298	IAA	WILD	0.080292
4361	M	27/10/96	4307	4298	IAA	WILD	0.080292
4367	U	30/12/96	4307	4298	IAA	WILD	0.080292
4368	U	01/01/97	4307	4298	IAA	WILD	0.080292
4387	U	26/10/97	4307	4298	IAA	WILD	0.080292
4400	U	05/01/98	4307	4298	IAA	WILD	0.080292
5474	M	01/01/96	0594	0605	BO	WILD	0.082031
5482	M	28/02/96	0594	0605	BO	WILD	0.082031
4310	U	18/07/95	0567	4298	IAA	WILD	0.084686
4273	U	04/09/95	0519	0523	IAA	WILD	0.093750
4283	U	06/01/95	0519	0523	IAA	WILD	0.093750
4304	U	15/04/95	0519	0523	IAA	WILD	0.093750
4327	M	09/12/95	0519	0523	IAA	WILD	0.093750
1729	F	13/08/92	1971	1970	JERSEY	BF	0.099243
0582	U	30/09/94	0495	0546	GDEWS	BO	0.101563
0586	M	28/10/94	0495	0546	GDEWS	BO	0.101563
0588	F	06/11/94	0495	0546	GDEWS	BO	0.101563
0590	M	07/11/94	0495	0546	GDEWS	BO	0.101563
0593	M	26/11/94	0495	0546	GDEWS	BO	0.101563
0628	F	23/05/95	0495	0546	GDEWS	BO	0.101563
0638	M	07/07/95	0495	0546	GDEWS	BF	0.101563
0640	M	21/07/95	0495	0546	GDEWS	BO	0.101563
0653	M	07/09/95	0495	0546	GDEWS	BO	0.101563
0654	M	09/09/95	0495	0546	GDEWS	BO	0.101563
4332	M	28/12/95	0536	0553	IAA	WILD	0.106873
5239	F	15/05/95	0570	0577	BO	WILD	0.106873
5240	F	17/05/95	0570	0577	BO	BO	0.106873
0420	M	03/11/89	0410	0408	GDEWS	BF	0.117188
0404	U	08/08/88	0368	0383	GDEWS	BF	0.125000
0451	M	12/03/90	1984	1983	JERSEY	BF	0.125977
0416	M	18/01/89	0378	0401	BF	WILD	0.128906
0399	M	21/01/88	0381	0383	GDEWS	BF	0.132813
0401	F	14/03/88	0381	0383	GDEWS	BF	0.132813
4338	M	03/02/96	4282	4300	IAA	WILD	0.148987
4405	U	04/02/98	4282	4300	IAA	WILD	0.148987
4417	U	11/08/98	4282	4300	IAA	WILD	0.148987
4340	U	11/05/96	0567	4312	IAA	WILD	0.155884
4348	U	14/06/96	0567	4312	IAA	WILD	0.155884
4352	F	26/11/96	0567	4312	IAA	WILD	0.155884
4354	U	16/07/96	0567	4312	IAA	WILD	0.155884
4382	U	13/10/97	0567	4312	IAA	WILD	0.155884
4392	U	12/12/97	0567	4312	IAA	WILD	0.155884
4401	U	09/01/98	0567	4312	IAA	WILD	0.155884
0396	F	22/07/87	0384	0139	GDEWS	BF	0.164063
0397	F	12/08/87	0384	0139	GDEWS	BF	0.164063
0398	F	24/08/87	0384	0139	GDEWS	BF	0.164063
0403	F	16/07/88	0384	0139	GDEWS	BF	0.164063

LSBN	Sex	Hatch date	Sire LSBN	Dam LSBN	Where bred	Where released	Inbreeding coefficient
0405	U	20/09/88	0384	0139	GDEWS	BF	0.164063
0409	U	31/10/88	0384	0139	GDEWS	BF	0.164063
4324	U	15/10/95	4302	4279	IAA	WILD	0.172119
4342	U	16/05/96	4302	4279	IAA	WILD	0.172119
4356	U	16/08/96	4302	4279	IAA	WILD	0.172119
4362	M	22/11/96	4302	4279	IAA	WILD	0.172119
4364	U	14/08/96	4302	4279	IAA	WILD	0.172119
4375	U	13/07/97	4351	4330	IAA	WILD	0.174973
4385	U	20/10/97	4351	4330	IAA	WILD	0.174973
4389	U	26/11/97	4351	4330	IAA	WILD	0.174973
4406	U	12/02/98	4351	4330	IAA	WILD	0.174973
4418	U	07/09/98	4351	4330	IAA	WILD	0.174973
0450	F	21/11/89	0172	1986	JERSEY	BF	0.195313
2089	U	04/11/93	0449	0478	BF	WILD	0.250000
2107	M	22/01/94	0449	0478	BF	WILD	0.250000
2374	U	23/05/96	0449	0478	BF	WILD	0.250000
4285	U	05/01/95	0541	0550	IAA	IAA	0.250000
4297	U	30/01/95	0541	0550	IAA	WILD	0.250000
0485	F	14/08/92	0455	0452	GDEWS	BF	0.261719
4339	U	14/02/96	4303	4313	IAA	WILD	0.269653
4344	U	17/05/96	4303	4313	IAA	WILD	0.269653
4345	U	18/05/96	4303	4313	IAA	WILD	0.269653
4358	F	19/09/96	4303	4313	IAA	WILD	0.269653
4399	U	30/12/97	4303	4313	IAA	WILD	0.269653
4404	U	02/02/98	4303	4313	IAA	WILD	0.269653
4306	U	21/04/95	0551	0553	IAA	WILD	0.270996
5194	U	20/08/96	0608	5245	BO	WILD	0.281250
5245	F	28/07/95	0584	0598	BO	BO	0.281250
4284	F	31/12/94	0536	0532	IAA	IAA	0.297974
4300	F	01/01/95	0536	0532	IAA	IAA	0.297974
4346	U	17/05/96	0557	4284	IAA	WILD	0.297974
0479	F	01/07/92	0453	0452	GDEWS	BF	0.375000

(b) Mean inbreeding coefficients (F) of fledged birds. Inbreeding coefficients were known for all captive-bred released birds.

	Brise Fer	Bel Ombre	Ile aux Aigrettes
Number of captive-bred released birds with known F	102	88	42
Number of wild-bred birds with known F	18	16	104
Number of wild-bred birds with F unknown	112	47	32
Number of birds with known F excluded from analyses	5	0	4
% of all birds with known F used in survival analyses	52	69	82
% of wild-bred birds with known F	14	25	77
Mean F of all birds used in survival analyses (± SD)	0.0416 ± 0.07	0.0391 ± 0.05	0.0715 ± 0.08
Mean F of captive-reared released birds (± SD)	0.0358 ± 0.07	0.0263 ± 0.04	0.0387 ± 0.07
Mean F of wild-bred birds (± SD)	0.0747 ± 0.09	0.0954 ± 0.08	0.0881 ± 0.08

Appendix 5 Kinship coefficients of pairings in released sub-populations used in the analysis of nest success and inbreeding, 1993-98. Site: BF = Brise Fer, BO = Bel Ombre, IAA = Ile aux Aigrettes. LSBN = local studbook number.

Site	Male LSBN	Female LSBN	Kinship coefficient
BF	0447	0470	0.000000
BF	0447	0480	0.000000
BF	0456	0470	0.000000
BF	0465	0478	0.000000
BF	0473	0476	0.000000
BF	0666	0470	0.000000
BO	0590	0627	0.000000
BO	0683	0706	0.000000
BO	0696	0706	0.000000
BO	0714	0718	0.000000
BO	0683	0719	0.000000
IAA	0517	0539	0.000000
IAA	0535	0532	0.000000
IAA	0544	0537	0.000000
IAA	0544	0528	0.000000
IAA	0544	0566	0.000000
IAA	0562	0537	0.000000
IAA	0569	0537	0.000000
IAA	4338	0540	0.008697
BO	5474	0732	0.009033
BO	0696	0747	0.015625
BO	5482	0802	0.022797
IAA	0503	0543	0.023193
BO	0594	0631	0.023315
BF	0646	0680	0.023437
BF	0679	0652	0.023437
IAA	4362	0736	0.024277
BO	0584	0628	0.025391
BO	0597	5240	0.028717
BO	0708	0729	0.029663
IAA	0542	4323	0.031250
IAA	0562	4305	0.031250
BO	0657	0702	0.031921
BF	0674	2368	0.034668
BO	0708	0717	0.035767
BF	0649	5240	0.036224
IAA	0740	4312	0.037537
BO	0597	0588	0.037903
BF	0441	0479	0.038086
BF	0472	1725	0.038818
IAA	0506	0514	0.040527
IAA	0561	0540	0.040771
BO	0572	0552	0.040772
IAA	0738	4357	0.042175
IAA	4361	0735	0.042175
BF	0638	0643	0.043457
BO	0556	0574	0.046875
BO	0572	0574	0.046875
BO	0572	0605	0.046875
IAA	0519	0553	0.046875
IAA	0535	0553	0.046875
IAA	0549	0563	0.046875
BF	0435	0474	0.048828
IAA	4302	4312	0.049149
BO	0615	0628	0.050018
BO	0556	0669	0.051636
IAA	0739	4358	0.052429
IAA	0740	4336	0.054047
IAA	0734	4352	0.054230
BO	0684	0687	0.056641
BO	0570	0591	0.057617
BF	0664	0673	0.060608
BO	0684	0706	0.060608
BF	0447	0652	0.062500
BO	0608	0627	0.062500
BO	0699	0713	0.062500
BO	0720	0731	0.062500
IAA	0488	0524	0.062500
IAA	0488	0553	0.062500
BF	0399	0485	0.071289
BO	0596	0631	0.071533
BF	0465	0480	0.072266
IAA	0567	4299	0.076874
BF	0621	0637	0.078125
BF	0621	0692	0.078125
BF	0622	0633	0.078125
BO	0613	0605	0.078125
IAA	0534	4279	0.078125
IAA	0538	4318	0.078125
BO	5250	0667	0.078369
BF	0636	0618	0.078735
BF	0416	1725	0.079285
BF	0434	1735	0.079285
IAA	4307	4298	0.080292
BO	0594	0605	0.082031
IAA	0567	4298	0.084686
IAA	0519	0523	0.093750
IAA	0534	0524	0.095703
IAA	0488	4336	0.101563
IAA	0536	0553	0.106872
BO	0593	0631	0.121460
IAA	0536	4279	0.148987
IAA	4282	4300	0.148987
IAA	4351	4330	0.154785
IAA	0567	4312	0.155884
IAA	0534	0554	0.156250
IAA	4302	4279	0.172119
IAA	4280	4300	0.207550
BF	0447	0469	0.250000
BF	0449	0478	0.250000
BF	0490	0491	0.250000
IAA	0541	0550	0.250000
IAA	4282	0537	0.266113
IAA	4303	4313	0.269653
IAA	4303	4331	0.269653
IAA	0551	0553	0.270996

Appendix 5 (continued). Kinship coefficients of pairings in released sub-populations used in the analysis of nest success and inbreeding, 1993-98. Site: BF = Brise Fer, BO = Bel Ombre, IAA = Ile aux Aigrettes. LSBN = local studbook number.

Site	Male LSBN	Female LSBN	Kinship coefficient
BO	0608	0574	0.281250
BO	0608	5245	0.281250
IAA	0517	0528	0.297974
IAA	0536	0532	0.297974
IAA	0536	0566	0.297974
IAA	0536	0566	0.297974
IAA	0557	4284	0.297974
BO	0593	0588	0.310791
BF	0416	0401	0.347656

Appendix 6 Inbreeding coefficients of squabs hatched on Ile aux Aigrettes, 1994-98. LSBN = local studbook number.

Pairing ID		Number of squabs hatched	Inbreeding coefficient of squabs
Sire LSBN	Dam LSBN		
0544	0537	3	0.000000
0535	0532	16	0.000000
0517	0539	7	0.000000
0562	0537	5	0.000000
0569	0532	2	0.000000
0569	0537	15	0.000000
4338	0540	14	0.008697
0503	0543	22	0.023193
0562	4305	2	0.031250
0542	4323	1	0.031250
0740	4312	4	0.037537
0506	0514	3	0.040527
0561	0540	3	0.040771
4361	0735	8	0.042175
0738	4357	2	0.042175
0519	0533	1	0.046875
0549	0563	3	0.046875
0519	0553	1	0.046875
4302	4312	1	0.049149
0739	4358	1	0.052429
0740	4336	6	0.054047
0734	4352	11	0.054047
0488	0553	1	0.062500
0567	4299	3	0.076874
0538	4318	1	0.078125
4307	4298	22	0.080292
0567	4298	2	0.084686
0519	0523	9	0.093750
0534	0524	2	0.095703
0488	4336	8	0.101563
0536	0553	3	0.106872
4282	4300	7	0.148987
4351	4330	13	0.154785
0467	4312	11	0.155884
0534	0554	1	0.156250
4302	4279	8	0.172119
4280	4300	1	0.207550
0541	0550	7	0.250000
4282	0537	1	0.266113
4303	4313	16	0.269653
0551	0553	6	0.270996
0536	0532	2	0.297974
0557	4284	6	0.297974