

On the intrinsic capacity for increase of Australian flying-foxes (*Pteropus spp.*, *Megachiroptera*)

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ABSTRACT

In the reproductive biology of organisms, a continuum exists from “highly reproductive species” at one end to “survivor species” at the other end. Among other factors, the position of a species along this continuum affects its sensitivity to human exploitation and its vulnerability to extinction. Flying foxes are long-lived, seasonal breeders, with a rigid, well-defined breeding season that is largely or wholly genetically determined. Unlike opportunistic, highly reproductive species, such as rabbits or mice, female flying foxes are unable to produce viable young before their second or third year of life, and are then capable of producing just one young per year. Such a breeding strategy will be successful only if flying-foxes are long-lived and suffer naturally low mortality rates. In this paper, we assess the vulnerability of flying foxes to extinction, using basic parameters of reproduction observed in the wild, and in captive breeding colonies of *P. poliocephalus*, *P. alecto* and *P. scapulatus*, and survival rates that are likely to apply to Australian conditions. Our models show explicitly that flying-fox populations have a very low capacity for increase, even under the most ideal conditions. The implications of our models are discussed in reference to the long-term management and conservation needs of Australian flying foxes. We conclude that current death-rates of flying-foxes in NSW and Queensland fruit orchards are putting state populations at serious risk.

Key words: Flying-foxes, reproduction, culling, population decline, migration, endangered species

Introduction

There is considerable diversity among the life histories of mammals, and differences in fecundity and survival can have a remarkable effect on populations (Harvey *et al.* 1989). These differences may be arranged along a ‘fast – slow continuum’ with small, short-lived, rapidly reproducing species at one end, and large, long-lived, slow developing species at the other end. Mammals with long gestation periods relative to their size, tend to produce one or two relatively large neonates that often require substantial parental care and investment (Promislow and Harvey 1990). The low reproductive potential of such species is usually off-set by naturally high survival rates, and long reproductive life spans (Harvey *et al.* 1989).

The importance of age-specific mortality rates in shaping the evolution of life-history strategies is well-recognised (Cole 1954; Williams 1966). Species with high mortality rates relative to their body size tend to have a suite of life history characteristics associated with the fast end of the continuum: i.e. short gestation lengths; early age at weaning; large litters (Promislow and Harvey 1990). On the other hand, species with high natural survival rates tend to experience long life expectancies, delayed sexual maturity, long gestation lengths, slow developmental rates and small litter sizes (Saether *et al.* 1996). As we shall demonstrate, Australian flying-foxes of the genus *Pteropus* fall into this category.

The aims of this paper are:

- to estimate the potential for increase in wild populations of flying foxes under various assumptions of fecundity and survivorship;
- to assess the sensitivity of flying-fox populations to changes in fecundity and survivorship;
- to predict the impact of current culling practices on flying-fox populations.

Absence of adequate field-based data

A problem with assessing the vulnerability of *Pteropus* spp. in the wild is that we do not have sufficient data to construct adequate *life-tables*. In particular we do not have adequate methods to accurately determine the age of adult females (Vardon and Tidemann 1998; Tidemann 1999). Since no data are available on the age structure of wild populations, we cannot determine *age-specific fecundity*, or *age-specific death-rates*. This prevents us from estimating the *innate capacity for increase* in wild populations (Andrewartha and Birch 1954), or the *instantaneous rates of increase or decrease*. In any case, it is unlikely that populations exist under *steady-state* conditions where such “precise” calculations are meaningful. However, by using established information on flying-fox reproduction, it is possible to model population growth parameters using estimates of *age-specific fecundity*, longevity, and juvenile and adult mortality based on observations made in captive breeding colonies and in the wild. This has been done in the present paper. In the following sections we review the information on which we base the parameter values used in our population modelling.

Reproductive biology and life expectancy of flying foxes

Seasonality of reproduction

It is generally accepted that Australian flying-foxes are seasonal breeders, in that births occur in the same season each year (Ratcliffe 1931; Baker and Baker 1936; Pierson and Rainey 1992; O'Brien 1993). Pregnancy lasts six months, lactation 3-4, and only one offspring is produced per year (Martin *et al.* 1996). From data obtained by carer groups who raise flying-fox orphan young, it is evident that captive Grey-headed Flying-foxes *P. poliocephalus* and Black Flying-foxes *P. alecto* breed in synchrony with their corresponding wild populations in south-east Queensland, north and central NSW (Martin 1997). These data also show that there is no significant difference in seasonality of free-living *P. poliocephalus* between southeast QLD, northern

NSW and Sydney, and that the vast majority of births occur between October and December.

Further analysis of the data for *P. poliocephalus* (Martin and McIlwee 2002) showed no significant year-to-year differences in birthing seasonality; ie, the *distribution* of births in any given season. Thus *P. poliocephalus* has a rigidly defined breeding season that does not change from year to year or from place to place in NSW. We emphasize this because Tidemann (1999) has claimed that “*Pteropus poliocephalus usually produces a single young in the southern spring... But...is capable of breeding opportunistically to counter unusual phenology events (own data)*”. To breed “opportunistically” implies that flying foxes are capable of initiating breeding if environmental conditions suddenly become favourable. It is not clear how flexibility, in the initiation of breeding, would benefit a species like the grey-headed flying-fox. In particular, one might question the viability of a breeding strategy that commits animals to a 6-month pregnancy and 3-4 months lactation on the basis of sudden, possibly transient, flushes of food. Another argument against opportunist breeding is that LM's (the second author's) well fed captive grey-headed flying foxes bred in synchrony with wild locals year after year, good seasons and bad. Rare twins apart (2 in 173 captive births), females only ever produced one young per season - they did not increase the rate at which they did so, nor did they increase litter size. Twins, as well as being rare, are unlikely to survive in the wild, and are therefore ignored in the calculations described below.

It is generally accepted that Spectacled Flying-fox *P. conspicillatus* is also an obligate seasonal breeder with a tightly defined season that does not change significantly from year to year, with peak births occurring in October to December (MacLean, personal observation, 2001; Richards, personal communication, 2001). The Little Red Flying-fox *P. scapulatus*, which breeds approximately 6 months out of phase with the two previous species, also appears to have a “fixed” breeding season with births occurring in May-June (Martin *et al.* 1966) across its range in Eastern Australia (Ratcliffe 1931; Baker and Baker 1936; O'Brien 1993; Martin 1999; MacLean, personal observation, 2001). *P. scapulatus* was difficult to maintain in captivity and captive breeding was poor, although the animals maintained the strict seasonality that is observed in the wild (O'Brien 1993; O'Brien *et al.*, 1993; Martin 1999; Maclean, personal observation, 2001). As with the other species, females bear a single young after a gestation of about six months.

The only Australian flying-fox which appears to exhibit seasonal plasticity in breeding is *P. alecto*. In southeast Queensland and Northern NSW, its breeding season is closely aligned to that of *P. poliocephalus*, with peak births in October-November (Martin 1997), but the birth season becomes progressively earlier in more northerly populations, albeit by a few weeks only (Martin 1997). However, in the northern territory, most births are in January-March, but some occur, unusually, in November (Vardon and Tidemann 1998). Vardon and Tidemann suggest that November births could result from previous January-March low birth-rate combined with high infant mortality, following which, females “were able to conceive before the usual season”. If such births are the result of a failure to raise young in the previous season, this would not increase the fecundity rate of the population, since the average number of offspring produced per female per year remains at one (or less).

Flying-foxes are prone to abortion under stress (Dukelow *et al.* 1990). Since females may still conceive after the “normal” mating season has finished (Martin *et al.* 1996; Martin and Bernard 2000), those that have undergone abortions early during pregnancy may still produce “late” young. However, it is not clear if females can conceive immediately after a near-term abortion, particularly since their reproductive system has been exposed to high levels of circulating female sex-hormones over preceding weeks (Towers and Martin 1995; Martin and Bernard 2000). Neither laboratory studies (O’Brien 1993; Martin *et al.* 1996) or birth-distribution data (Martin 1997; Martin and McIlwee 2002) provide any evidence that *P. poliocephalus* is able to advance the timing of reproduction, or otherwise accelerate its reproductive rate in response to a “good” season.

Females separated from males during the breeding season may also conceive “late” young. In LM’s captive colony, females placed with males in July conceived almost immediately (Martin *et al.* 1996; Martin and Bernard 2000). This led to the mothers lactating throughout the following mating season. However, each delivered their next young at the usual time. Collins (personal communication, 2001) tells a similar story for an injured female placed with males in October. Such late conceptions presumably account for “late births” and the longish trailing edge of the frequency distribution of births (Martin 1997; Martin and McIlwee 2002).

The possibility of conception after “loss of pups” has recently been raised by Tidemann and Vardon (2001) under the title “flexible reproduction”. They state that “For *P. poliocephalus*, births are recorded from nearly every month of the year and around 100 non-volant young (4-6 weeks old) were observed at Maclean in April 1999 about six months after the usual peak of parturition of September-October (Tidemann, unpublished)... If, as seems possible, females can conceive again after losing pups, this may offer two chances to raise young within a year. As such, high mortality at one time of the year may be offset by recruitment six months later”.

The non-volant young, described by Tidemann as “4-6 weeks old... in April”, would have been conceived in the previous August, well before the birth season, at a time when adult females were late pregnant - and prone to stress-induced abortion. Thus the mothers involved would not have delivered young, lost them and then conceived - as implied by, “after losing pups”. Although females might conceive after a late abortion, there is then a very limited time frame in which they could “be recruited”. Furthermore, if there is no progeny in the year of the abortion and two the following year, there is no gain in reproductive rate, the average still remains at one young/year. This would apply to *P. alecto* births in the NT. As for the statement that “*P. poliocephalus*, births are recorded from nearly every month of the year”, we refer readers to figure 1 of Martin and McIlwee (2002) which shows that the vast majority of young are born from October to December. It is also worth noting that Eby (1999) found no advancement of the birth season of *P. poliocephalus* following a “bad” year in which few females raised young.

Fecundity of adult females

In the wild, most adult grey-headed flying foxes conceive (Nelson 1965; Towers and Martin 1985; 1995) but females are prone to abort (Dukelow *et al.* 1990) and mass abortions and premature births are known to occur in the wild in response to environmental stress (Hall, *et al.* 1991; Collins 1999; Hall and Richards 2000). Thus, it is not clear what proportion of pregnancies, on average, go to term, or produce viable young. For grey-headed flying foxes, the best data are those of Eby (1999) who counted numbers of females with young at the end of December - when the birth season is effectively complete and young have not yet started to leave their mother - and compared camps affected and unaffected by food shortages.

In unaffected camps the proportion of females with young ranged from 72-94% compared with a range of 8-52% in affected camps. Of 28 females born in LM's colony which were allowed to reach their third year of life, 20 were seen to become pregnant [71.4%], 18 weaned young [64.3%], 1 aborted and 1 dropped its neonate [7.1%]. Thus under favourable environmental conditions, we believe an effective fecundity rate of 70% is not unreasonable.

A total of 56 wild-caught and captive-bred females were maintained in LM's breeding colonies beyond three years of age, for periods varying from 1-10 years. This population had a total of 200 possible pregnancies. Confirmed pregnancies totalled 179 [89.5%] with 25 abortions or dropped neonates [12.5%] and 154 young successfully weaned [77%]. The majority of births came from a subset of females who successfully reared young to weaning year after year, for periods up to 10 years and with only an occasional missed pregnancy, abortion or dropped neonate. In such animals there was no indication of any diminution in fecundity with age up to 12-13 years.

Vardon and Tidemann (1998) provide some evidence that the fecundity rates of wild populations may be significantly less than those of captive animals. In a sample of 237 adult sized (forearm >171mm) female *P. alecto*, they found that around 30% were non-breeding.

On the basis of the above data we have modelled constant fecundity rates for adults (3 years of age and above) up to an age 15 years, when all remaining animals die (see mortality assumptions below). We argue that this is representative of wild situations as there is likely to be a strong correlation between fecundity across all age classes for any environmental condition. Under favourable conditions, high fecundity rates may be expected across all classes. Similarly, stressful conditions are likely to reduce the fecundity of all age classes equally. To assess the importance of fecundity in determining population trends, we use a range of fecundity rates from an unrealistic upper limit case where 100% of females deliver live young each year, to more realistic female breeding rates of 90% - 70% (Vardon and Tidemann 1998).

Age of sexual maturation and fecundity in young animals

There is no evidence that flying foxes can become pregnant and carry to term in their first year, but there is little doubt that a proportion of females successfully carry to term in their second year. The

Brisbane carers group ONARR [Orphan Native Animals Rear and Release, personal communication, 2001] report that a few *P. alecto* identified by subcutaneous micro-chips returned to carers as two year olds with babies. Vardon and Tidemann (1998) report that a two year old orphaned *P. alecto* female, released in the Darwin area was noticed suckling young. Likewise, J. Maclean (personal communication, 2001) describes occasional orphaned, human-reared *P. conspicillatus* in Queensland delivering young when only 2 years old, but believes only a minority of two-year-olds do so. Several carers also make the point that many two-year old flying-fox mothers drop their young, and do not rear them to independence (Helen Luckhoff, Linda Collins, Jenny Maclean, personal communications 2001).

Vardon and Tidemann (1998) argue, on the basis of forearm length (FAL), that some female *P. alecto* are capable of conceiving 12 months after birth (FAL <160mm). However, this estimate should be treated with caution as the authors define individuals as less-than-one-year-old if the FAL is <160mm and more-than-one-year-old if FAL is >160mm respectively, despite the large variability in individual FALs (shown by the SD bars in the graph of these data), and the extremely low slope of the regression line relating FAL to age, over the age range 8-14 months.

Nelson (1963) presented FAL, body weight (BW) and pregnancy rates for 147 female *P. poliocephalus* shot "between May and October during 1959-1960". He did not relate FAL or BW directly to age but maintained that, "Since the 500 to 550 grams body weight class... contains no pregnant females, and since the 600 to 650 class contains only pregnant females, maturity occurs at 575 ± 25 grams body weight, and at a forearm length of 145 ± 7 millimetres. The females at maturity are 17 months old. The females in the 550 to 600 group are first year adults. The 65% pregnancy obtained in this group when compared with the 100% pregnancy in all other adult groups...". Nelson (1965), presenting the same data, stated that "Maturity.. occurs at.. 18 months".

However Nelson's data confound individual variations, seasonal changes in BW, and changes in pregnancy rate and BW as breeding season advances. Furthermore, in the graph of these data, the upper standard deviation (SD) bar of the 575g BW-class mean FAL [=152mm] almost overlaps the mean FAL of the 675g BW-class [mean \pm SD = 153 \pm 6mm] and much of the lower range of FALs of the 725g BW-class [mean \pm SD

= 154±6mm]. Thus many animals estimated to be 17-18 month old were probably 29-30 months old. In support of this view, Brisbane flying-fox carers record that female grey-head flying-foxes in good condition, and estimated to be 3 years or older on the basis of tooth wear, come into care with body weights in the range 500-600g. We suggest that Nelson's 65% pregnancy rate in 17-18 month animals is an overestimate.

Of 46 female *P. poliocephalus* and *P. alecto* born in LM's breeding colony, none delivered young in their first year. Of 36 females born in the colony and allowed to continue into their second year of life, 9 were seen to become pregnant [25%], 4 weaned young [11%], 4 aborted or dropped their neonates [11%] and one, euthanased for experimental purposes in late pregnancy, had an apparently healthy, normal, near-term foetus. Thus a birth rate of about 20% is not unreasonable for two-year-old animals.

The sex-ratio in new-born flying-foxes

The data for 1984-1993, from LM's captive colonies and from QLD and NSW carers' records of new-born orphans coming into care are: *P. poliocephalus*, 518 females, 513 males; *P. alecto*, 216 females, 221 males. Given that there is no *a priori* reason for the neonatal sex-ratio to differ from 1.00, we have assumed this value in our modelling.

Mortality of new born and juvenile animals

Mortality rates are generally highest for juvenile bats (Tuttle and Stevenson, 1982) and range in the wild from an estimated 43-80% in *P. alecto* (Vardon and Tidemann, 2000) to 20-40% in smaller, closely related pteropodids (Heidemann and Heaney, 1989). Vardon and Tidemann (2000) estimated that 43% of female *P. alecto* died each year in the first two years of life and that only, "one in three females born.... reproduces".

Mortality rates of flying-foxes in the wild

In general we do not have accurate data for the mortality of flying-foxes in the wild. In discussing death-rates with flying fox researchers and carers, most accept that a 10% per annum "natural" death-rate of adults is not unreasonable. However, all qualify their acceptance by placing it at the low end of the scale. In addition, flying foxes must contend with natural catastrophic events such as droughts and cyclones that have the potential to cause large increases in mortality, particularly among juveniles (Collins, personal communication 2001; Parry-Jones 2000). For example, Parry-Jones (2000) reports that 100% of juvenile *P. poliocephalus* ($n = 7240$) died in the

Gordon colony, NSW, during a 1994 heat wave. Hall (personal communication 2000) has also observed mass abortions and high juvenile mortality in camps of *P. poliocephalus* and *P. alecto* in SE Queensland in 1978 and 1983. In the Atherton Tablelands, North Queensland, an on-going 5-10% death-rate in *P. conspicillatus* is due to tick infestations that cause subsequent paralysis (McClean, personal communication 2000).

Factors underlying the natural mortalities of flying foxes are not well understood. Ratcliffe (1932) identified two mechanisms by which flying-fox populations may be kept in a state of balance. These include food shortages associated with fluctuations in the availability of resources, as well as mass deaths due to heat stress associated with high temperatures. Such mass deaths of adult and juvenile *P. alecto* and *P. poliocephalus* occurred in Northern NSW on 12 January 2002, when day-time temperatures reached 43°C (N. Markus, J. Maisie, personal communications 2002)

Longevity of flying-foxes in captivity and in the wild

There is much evidence to suggest that flying-foxes are naturally long-lived. A captive male grey-headed flying-fox taken into care at the age of 6 months, died recently in his 23rd year (Pritchard 2001). In LM's captive breeding colonies of *P. poliocephalus*, *P. alecto*, individuals in both sexes survived for well over a decade. Similar life-spans have been recorded in captive *P. conspicillatus* in North Queensland (Spencer, personal communication 2001).

Pierson and Rainey (1992), in their review of flying-fox biology, state "flying foxes have relatively few predators other than man" and that, "Though information on age structure and estimates of age-specific mortality rates for *Pteropus* are lacking, the long life span and low reproductive rate clearly indicate animals with an evolutionary history involving low levels of natural mortality".

A maximum natural longevity of 15-20 years, slow sexual maturation and small litter size reflects the environment in which flying-foxes have evolved, one in which they could afford a low reproductive rate. However, as we shall later demonstrate, such a life history strategy can only be biologically successful if the low birth rate is accompanied by a low mortality.

Based on the longevity of captive animals, their strict breeding season and single young per year,

we suggest that Australian flying foxes have evolved in conditions where individuals experience low levels of natural mortality and long survival times in the wild, probably upwards of 15 years. However, since European settlement flying-foxes have been faced, suddenly in evolutionary terms, with a vastly increased mortality due to habitat destruction, persecution and culling. It is therefore important for their conservation that we understand the potential rates of population increase (or decrease) under various mortality regimes.

Assumptions made in examining factors that determine rates of population change in *Pteropus*

In simplest terms, population change is governed by the birth-rate and the death-rate: fecundity versus mortality. When births exceed deaths, the population grows. When deaths exceed births, the population declines. Thus the viability of a flying-fox population is influenced by the size and productivity (fecundity) of the female population. This will depend on the number of young a female can bear per year, how soon a female matures sexually, and how long a female is likely to live (life expectancy). Since a polygamous (male-with-harem) system is the rule rather than the exception in Australian *Pteropus*, the ratio of adult males to adult females is unlikely to have a major effect on female productivity unless the proportion of males in a population becomes excessively low. For example, the ratio of males to females in LM's successful captive breeding colonies of *P. poliocephalus* and *P. alecto* was about 1:5. In the calculations which follow, therefore, we have not examined the effects of changing sex-ratio in adult populations.

We have assumed that the most offspring a female can deliver per year is one. However, since only females contribute to the next generation, and the sex-ratio at birth is one, the birth of one young per year is equivalent to one half of a female per year. We therefore define the age-specific fecundity, m_x , (where x is the age of the female in years) as the number of viable female neonates delivered per adult female per year. We use the figure 0.5 to designate the **maximum** fecundity of females. In the calculations that follow, we deal only with numbers of females.

Changes in the size of natural populations are influenced by the addition of individuals through both birth and immigration, and by the removal of individuals through death and emigration. In this paper, all models are based on closed populations. This is equivalent to looking at changes in the total population of a species, which is unaffected by immigration and emigration.

We base our calculations on flying foxes being strict seasonal breeders, with females effectively giving birth around the time of their own birthday. In formal terms this is a birth-pulse model, with all births occurring at discrete time intervals. For the models, we assume that females give birth to offspring on the day they enter a new age class, and that deaths occur continuously throughout the year that follows.

We have assumed that: $m_x = 0$ for the first year of life of a female; that in the second year of life, some surviving females are capable of delivering a viable young around the time of their second birthday; that all females are capable of doing so around the time of their third birthday. In the light of pregnancy rates observed in the wild, and in LM's captive colonies, we have assumed that after a female attains the age of three years, her potential productivity remains constant over the rest of her lifetime (ie. it is age-independent). Nevertheless, the proportion of females in a population that **actually** deliver young (breeding success), will vary with environmental conditions. We have therefore modelled the effects of different degrees of breeding success. For example, if, on average, only 90%, 80% or 70% of adult females deliver young, the corresponding fecundities are, respectively, 0.45, 0.4 and 0.35.

We have assumed that no female survives beyond her 15th year. In the simplest calculations we have assumed that a constant proportion of females die each year from the time of birth (time zero) until the 16th year, when all surviving females die (death rate is age-independent). A cut-off at 15 years is not incompatible with the species' longevity in captivity, or with Tidemann's (1999) estimate for *P. poliocephalus* and, apart from the 100% survival case, the postulated death-rates lead to a relatively small proportion of animals surviving to 15 years. We have also examined the effects of high death-rates in the first and second years of life, ie. among new-born and juveniles.

Methods

Intrinsic capacity for increase (r_m)

We have first used the “life-table” approach described in Andrewartha and Birch (1954), using various hypothetical death rates to calculate the proportion of females surviving (l_x = survivorship) to a given age (x). We have tabulated our basic calculations at some length, together with the underlying equations, in order that our methodology is relatively transparent to those who are not specialists in population ecology. Since the animals are seasonal breeders, and births effectively occur close to each maternal birthday, the values of x refer to end of each year of a cohort’s life (the birth-pulse model described above). The *net reproduction rate* (effectively the number of viable female young that one adult female can deliver in her lifetime) R_0 is calculated as

$$\sum l_x m_x$$

and is the capacity of the species to multiply in one generation time.

In unvarying environmental conditions in which a population of animals can breed without restraint, and birth-rate exceeds death-rate, the population will increase exponentially at a constant (exponential) rate as

$$N_t = N_0 e^{r_m t}$$

where N_0 is the number of animals at time 0, N_t the number of animals at time t , and r_m is the “rate constant” - the *intrinsic (or “innate”) capacity for increase in numbers*. It should be noted here that, if death-rate exceeds birth-rate, all other factors remaining constant, population numbers will decline at a constant exponential rate, and r_m is negative. In an exponentially growing or diminishing population:

$$R_0 = e^{r_m T}$$

where T is the mean duration of a generation (the *duration of a generation* is defined as “the mean period elapsing from birth of parents to birth of offspring”). Thus, T may be calculated as:

$$\sum l_x m_x x / \sum l_x m_x$$

and r_m from

$$r_m = \log_e R_0 / T$$

Lotka (1925) showed that the distribution of ages in an exponentially increasing (or decreasing) population, in which birth-rates and death-rates for each age group remain constant, will quickly converge on a stable age distribution regardless of its initial age structure (see below). As a population approaches this distribution, so too

does the value for r_m . Andrewartha and Birch (1954) point out that the method of calculating r_m described above does not take account of the stable age structure of a population, and thus gives only approximate values of r_m - though usually within 10% of the true value (Stearns 1992).

Age structure

Describing a population in terms of its age structure requires a shift from using ages to age-classes. Age-structured demographic population models classify members of a population according to their age-class, and keep track of the number of individuals in each age-class over time. In order to do this, one needs to keep a vector of numbers, one for zero-year-olds (by convention we classify newborns as age zero (not age one)), one for one-year-olds, one for two-year-olds etc. An example of an animal that lives to four years is:

$$N = \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \end{bmatrix}$$

This vector is known as the age distribution of the population. For most age-classes, the number of x -year-olds is the proportion of $(x-1)$ -year-olds who survived the intervening twelve months. The number of zero-year-olds is the sum of the offspring produced by individuals of all reproductive ages.

Leslie Matrices

Leslie matrices offer a convenient way of modelling age-structured populations (Leslie 1945). A Leslie matrix consists of a matrix with the fecundities of each age-class along the top row and their survivals along the subdiagonal. If there are k age-classes, the Leslie matrix is a $k \times k$ square matrix. A simple example with four age classes would be:

$$L = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix}$$

The entries in the matrix reflect the probabilities that members in one age class (each column) have of contributing to another age-class in the next year, either by reproduction into the zero-age-class (F), or surviving through to the following age-class (S). The yearly updating of the abundance vector amounts to using matrix algebra to multiply the age-distribution vector by the Leslie matrix.

$$\text{Thus } N_{(t+1)} = LN_{(t)}$$

The top element of the age distribution (N_0), which represents the abundances of zero-year-

olds, is the product of the top row of the Leslie matrix and the age distribution. The remaining elements are the products of the survival rates multiplied by their corresponding elements from the age distribution. For a fixed Leslie matrix, there are three possible long-term population trends: It may grow exponentially, decline to extinction, or remain balanced at equilibrium.

Stable age distributions

Repeated multiplication of an age-distribution by a fixed Leslie matrix will cause the distribution to converge on the configuration known as the stable age-distribution. In this configuration, the proportion of individuals within each age-class remains the same, irrespective of the population's size. At this point, multiplying the age-distribution by the Leslie Matrix is the same as multiplying it by a scalar number (λ), also known as the finite rate of increase.

$$N_{(t+1)} = LN_{(t)} = \lambda N_{(t)}$$

Once the stable age distribution has been reached, the population continues to grow (or decline) exponentially, with λ as the rate of increase (or decrease).

The general solution for the equation after t years is:
 $N_t = \lambda^t N_0$ (where $\lambda = e^{rm}$)

Stable age distributions may be used in modelling populations whose actual age structure is unknown, as we know that irrespective of the initial age structure, the population will converge on a stable distribution that can be calculated for any given fecundity and survival schedule.

The DOS-based computer program RAMAS/age (Ferson and Akcakaya 1990) was used to calculate the vital statistics and changes in flying-fox population sizes described in this paper.

Results

Survivorship and fecundity of females under ideal and natural conditions

Figure 1 provides examples of basic life-table calculations for hypothetical flying-fox populations. The proportion of females surviving to a given age (x) is (l_x). The number of females born per surviving female per year is (m_x) and maximum is 0.5. We have assumed that; $m_x = 0$ for age 1 year, 0.1 for age 2 years, and remains constant thereafter,

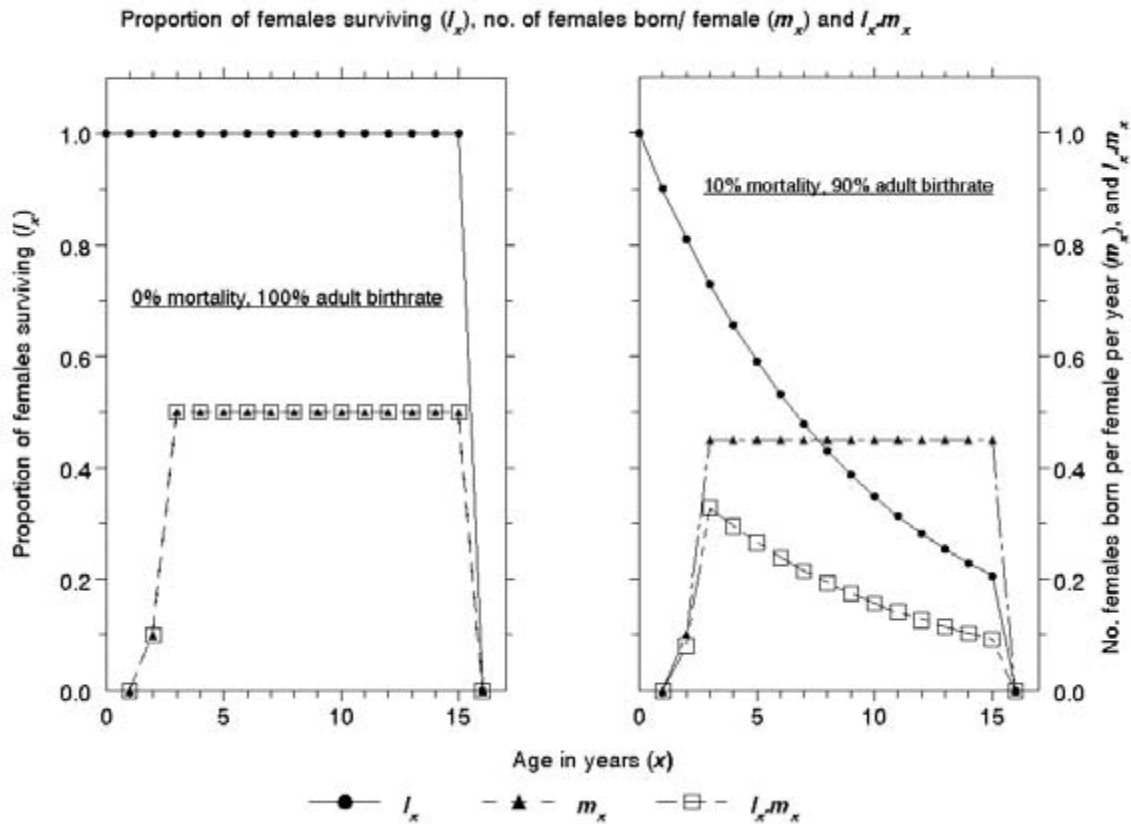


Figure 1. Survival, breeding success and lifetime productivity in female flying foxes.

The graph on the left illustrates the upper limit case where no female dies before age 16, 100% of adult females (≥ 3 years) bear young each year, and 20% of females bear young in their second year.

In the graph on the right, 10% of surviving females die each year, 90% of adult females (≥ 3 years) bear young each year, and 20% of females bear young in their second year.

at values ranging from 0.5 - 0.35 (respectively 100% - 70% of females deliver 1 young each year). It is assumed that all surviving females die on completing year 15. Since the animals are seasonal breeders, and births occur close to each maternal birthday, the values of x refer to the end of each successive year of life.

The left hand graph shows the theoretical, upper-limit case - a set of circumstances that could never happen in the wild. Females are born at time zero; none survive beyond year 15, but none die before year 16 - annual mortality is zero. We have assumed that all adult females deliver 0.5 females once a year (100% reproductive success), every year including their 15th year.

Since no females die until the 16th year, the proportion surviving (l_x) remains at 1 for 15 years, Adding up (\sum) the proportion surviving each year gives the life expectancy - 16 years ($\sum l_x = 16$). The scale of the right axis shows female fecundity as the number of female young/per female/per year (m_x), equal, in the left-hand graph, to the theoretical maximum of 0.5. The right axis scale also shows the number

of female young per surviving female per year - obtained by multiplying the proportion of females surviving each year by the number of females born per female per year ($l_x m_x$). Adding up the number of females per surviving female per year gives the total females produced per female life-time ($\sum l_x m_x = R_0$). For the left hand graph, this equals 6.6 females. From such data we can calculate the time that it takes for a population to double or halve. In this case the doubling time (T_d) is 3.1 years. If all two-year-olds deliver young, the total born per female lifetime is 7.0 and T_d is reduced correspondingly. We argue that flying-fox populations cannot increase any faster than this, and that maximum rates in the wild are much less.

The left hand graph of **Figure 1** illustrates a more realistic maximum rate of increase in the wild. Here, the population suffers a moderate mortality, in that 10% of females die each year, and the proportion surviving declines progressively. Here, life expectancy is 8.2 years. Nevertheless, even with the relatively low, and not unrealistic annual death rate of 10%, only

Survival (l_x), age-specific fecundity (m_x) and $l_x m_x$ in flying foxes
15, 20, 25 or 30% die each yr; 10% 2 year olds & 90% adults deliver one viable young/ yr

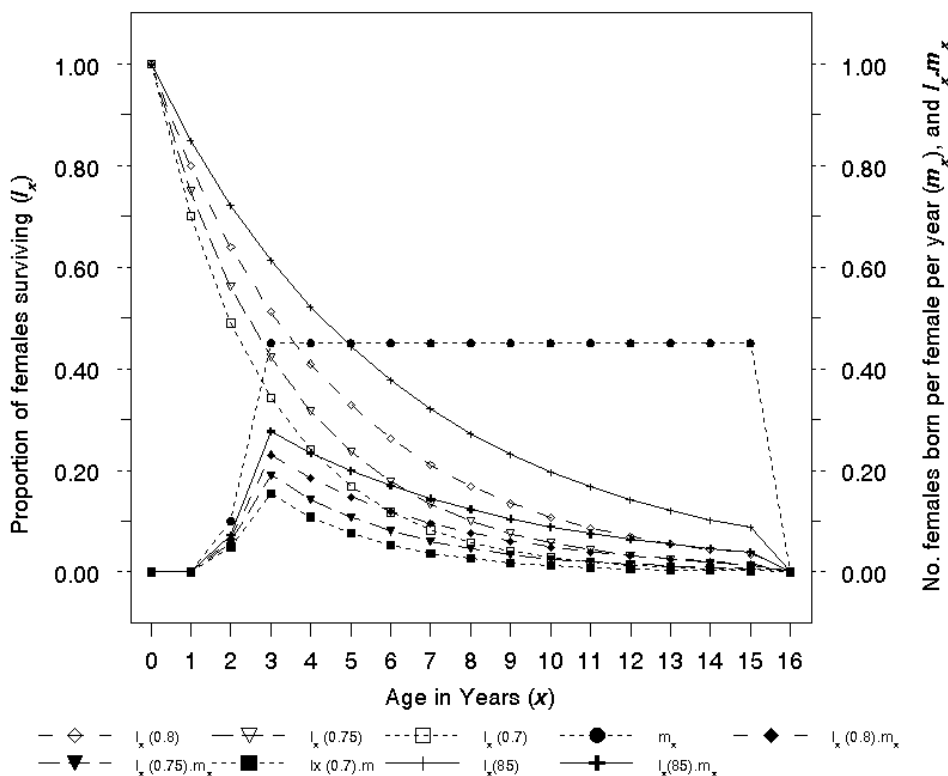


Figure 2. Survival, breeding success and lifetime productivity in female flying foxes.

The graph illustrates four populations experiencing differing annual mortalities of 15, 20, 25 and 30%. In all cases 20% of females deliver one young in their second year and 90% of adult females (≥ 3 years) bear one young each year.

0.59 of a cohort of animals born at time 0 remain alive by year 5, and the proportion drops to 0.35 and 0.20 by years 10 & 15 respectively.

We assume, again, that 20% of two-year-olds deliver half a female. Here, the vast majority (90%) of surviving adult females produce half a female per year, throughout their life, to age 15, and the total females produced per female lifetime (R_0) is 2.5. The population increases, but T_d is 5.7 years. If all two-year-olds deliver young, $R_0 = 2.8$ and the doubling time is reduced correspondingly.

Figure 2 shows similar plots for populations in which adult females have a breeding success of 90%, and 15, 20, 25 or 30% of animals die each year. With annual death rates of 20, 25 and 30% per year, the proportions of females alive by year 5 are, 0.33, 0.24 and 0.17 respectively, and the

R_0 s are 1.2, 0.8 and 0.6 respectively. If R_0 is < 1 – then the population is in decline. From these calculations we argue that, irrespective of female fecundity, flying fox populations cannot sustain average mortality rates greater than 20% per year.

Intrinsic capacity for increase (r_m) in flying fox populations.

The relationship, $r_m = \log_e R_0 / T$, describes the instantaneous rate at which a population increases or decreases. r_m values for four of the populations illustrated in figures 1 and 2, each with 90 percent breeding success, but with annual mortalities of 10, 20, 25 and 30% are respectively, +0.1255, +0.0237, -0.0417 and -0.1183. The corresponding “precise” r_m s calculated by the Leslie matrix method for populations with a stable age-distribution are, +0.1213, +0.0206, -0.0344 and -0.0931

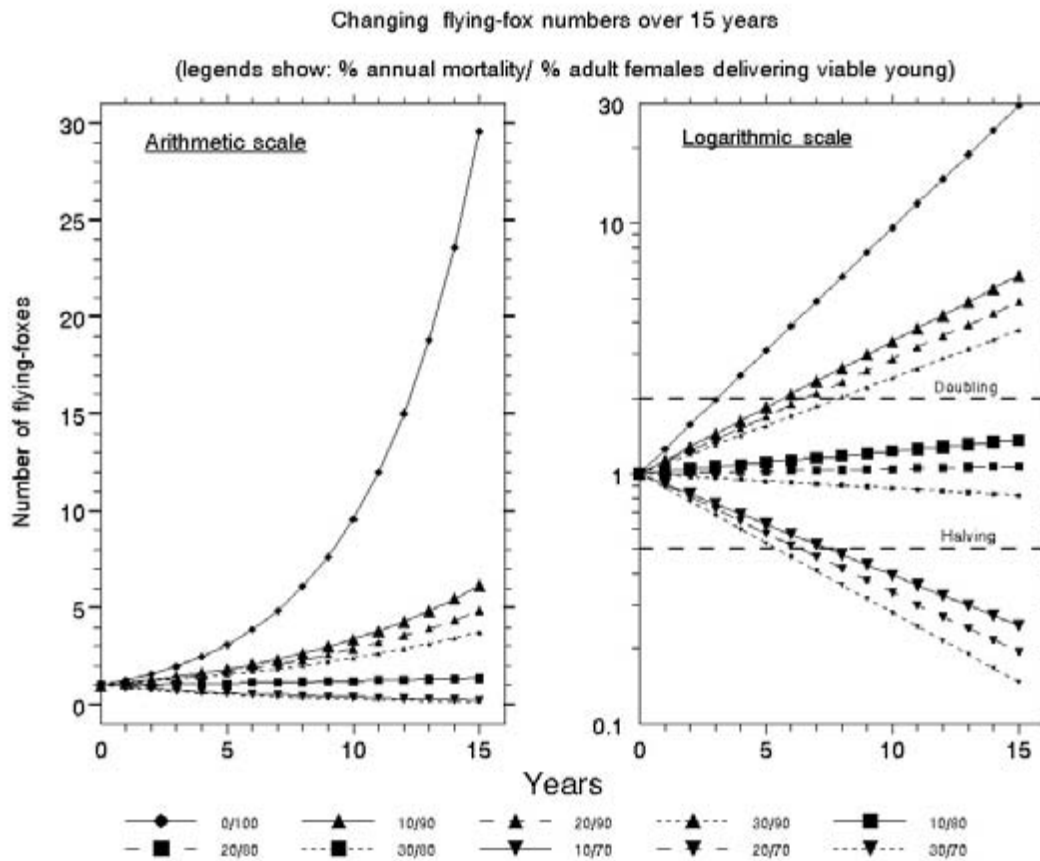


Figure 3. The effect of differing mortality and fecundity on flying fox population dynamics.

It is assumed that conditions remain constant over the period shown and that populations increase or decrease according to the relationship $N_t = N_0 e^{r_m t}$, where N_0 is the number of animals at time 0, N_t is the number of animals at time t , e is the base of natural logarithms, and r_m is the “rate constant” - the intrinsic capacity for increase in numbers. In the left hand graph, r_m is the “instantaneous rate of increase” in numbers. In the right hand graph, r_m is the slope of the line. All populations suffer age-independent mortalities (i.e. they remain constant from time zero to the 16th year; when all surviving animals die) The four mortalities illustrated are 0, 10, 20 and 30% per annum - the first number in each figure legend. 20% of females bear one young in their second year of life. Thereafter, female productivity is age-independent (i.e. remains constant to the end of life) with three rates of reproductive success illustrated, 90, 80 and 70% - the second number in each figure legend.

respectively. This means that populations of flying foxes under the last two scenarios will decline at constant exponential rates, with half lives of 20 and 7.5 years respectively. A summary of flying-fox population statistics obtained by the Leslie matrix method are listed in Appendix 1.

The expansion and decline of grey-headed flying-fox populations under various conditions

Figure 3 shows, how population numbers change over time for various death and birth rates, using r_m s calculated by the Leslie matrix method, and assuming that 20% of two-year-olds deliver a viable young.

On the left, in an arithmetical plot, the top line shows that, under zero mortality and 100% reproductive success, the population numbers increase to give a line with an ever increasing upwards slope - characteristic of exponential increase. Here, r_m describes the instantaneous rate at which a population increases (or decreases). Population size starts at 1 in year 0,

doubling every 3.1 years, to increase almost 32-fold by year 15. As stated previously, this is an unrealistic maximum rate that would never occur in the wild. When 10% of bats die annually and only 90% of surviving females rear young to independence each year, the doubling time extends to about 6 years. In this graph, all of the other cases are crowded below and difficult to distinguish

On the right, the same numbers have been graphed on a log scale [the scale is geometric] to produce straight lines which show declining populations to better effect. Here r_m describes the slope of the line. Horizontal drawn lines enable one to read off doubling and halving times. The top line again shows population growth where animals have 100% survival and breeding success. Below, three groups of lines correspond respectively to age-independent mortality rates of 10, 20 and 30%. Within each group of lines, successively lower lines represent, respectively, 90, 80 and 70% breeding success. The figure shows that flying-fox populations with an average annual

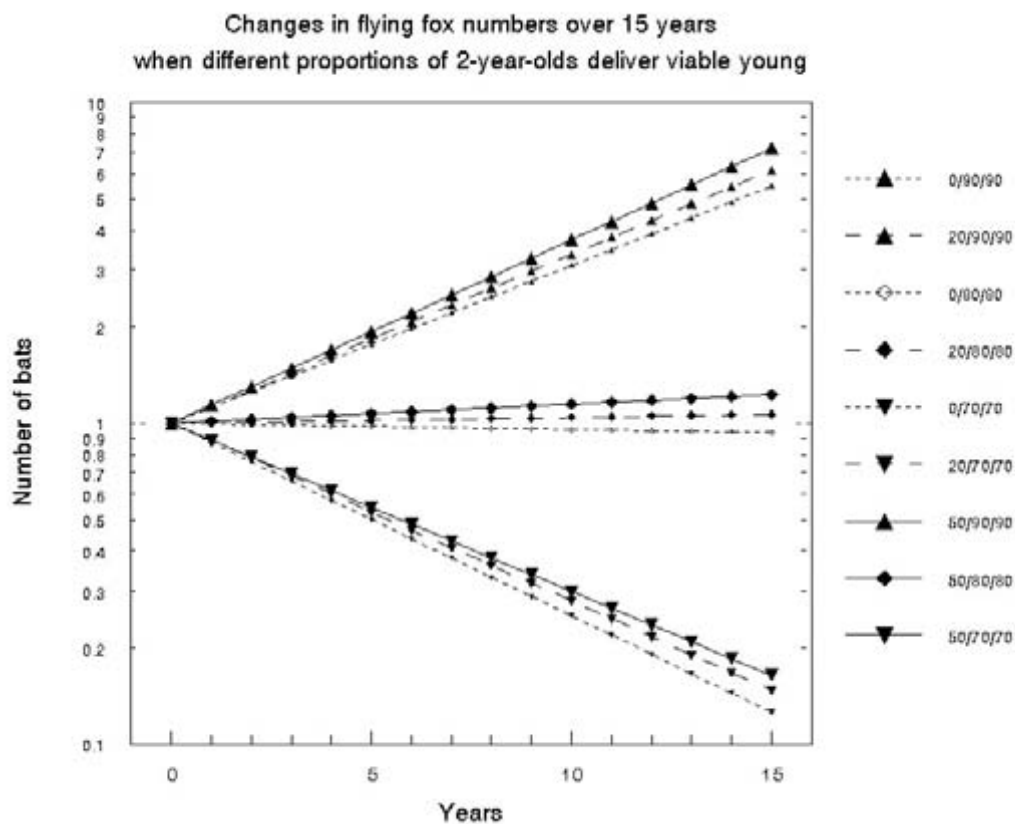


Figure 4. The effect of early breeding success on flying fox population dynamics.

The assumptions are as for figure 3. All populations suffer age-independent mortalities - the final number in each figure legend. The breeding success of 2-year old females is assumed to be 0, 20%, or 50% of the adult rate - the first number in each figure legend - the adult breeding success - the second number in each figure legend - remains constant to the end of life

breeding success of 80%, and a 20% annual mortality rate across all age classes, results in a near-stable population.

Clearly it is the mortality of females that has the greatest influence on the dynamics of flying-fox populations, in the sense that a 10% increase in mortality has a much greater effect than a 10% decline in breeding success. However, these differences are predicated on the assumption that only 20% of two-year olds are capable of delivering a viable young.

The effects of early breeding success on population growth

Figure 4 shows how differing degree of breeding success in 2-year-olds (0-50% of adult values) affect rates of change of flying-fox populations. Increased breeding success of 2-year-olds produces pro-rata changes in rates of population change, but these are small relative to those associated with differences in adult mortality rate. It is also worth noting (although we have not modelled it) that there is evidence that young born to 2-year olds have a lower chance of surviving than young born to adults.

The effects of neonatal and juvenile mortality on population growth

For simplicity, all previous examples have been based on death-rates which remain constant over the life of the bat. However, mortality rates are generally highest for juvenile bats (Tuttle and Stevenson, 1982) and range in the wild from 43-80% in *P. alecto* (Vardon and Tidemann, 2000) to 20-40% in smaller, closely related pteropodids (Heidemann and Heaney, 1989). Figure 5 shows the survivorship in populations in which about 40% per annum of young die in their first year, or first and second years. Figure 6 shows how such early mortalities have major effects in reducing the rate of population increase, or increasing the rate of decline.

Stable age distributions of flying-foxes

If environmental conditions, and l_x and m_x , remain constant, then a population will reach the characteristic stable age-distributions associated with its particular mortality and fecundity rate. Figure 7, graph 1, shows the stable age-distributions for the range of population mortalities and fecundities listed in table 1. When age-independent mortality and fecundity both change there is effectively no change in the age-distribution (Graph 2).

Changing mortality while fecundity remains constant, produces minor changes (Graph 3) as does changing fecundity, as mortality remains constant (Graph 4). Only where there is relatively high infant mortality (40% in year 1), is there any marked increase in the proportion of older animals (Graph 4, 60/90/90, etc.).

When the four superimposed distributions of graph 2 are plotted on a logarithmic scale, all follow a straight line - effectively each follows a negative exponential. This, perhaps surprisingly, includes the upper limit case where all females have 100% breeding success, and none die before the fifteenth year. Clearly, in this case, the progressively smaller proportion of older females in the population is not due to progressively older females dying, but to dilution of the population with young, and the young of young etc. We note, however, that random samples taken from any of these populations could well lead un-informed researchers to conclude that the animals had a relatively short life-span.

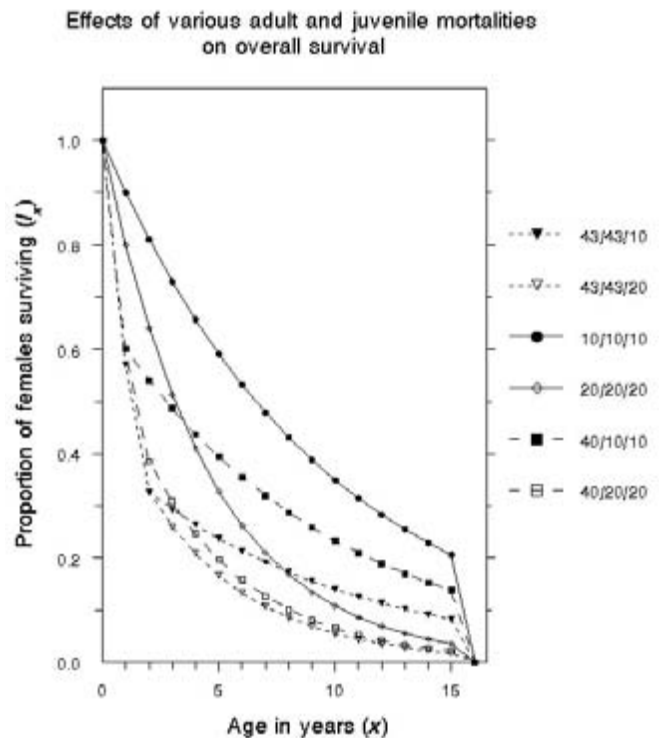


Figure 5. Effects of juvenile mortality rates on survival of females over a period of 15 years.

The numbers in the figure legends show the % annual mortalities for the first, second and subsequent years of life. For example, 43/43/10 indicates that 43% of females die each year in their first and second years of life, and 10% die each year thereafter until year 16 when all remaining females die.

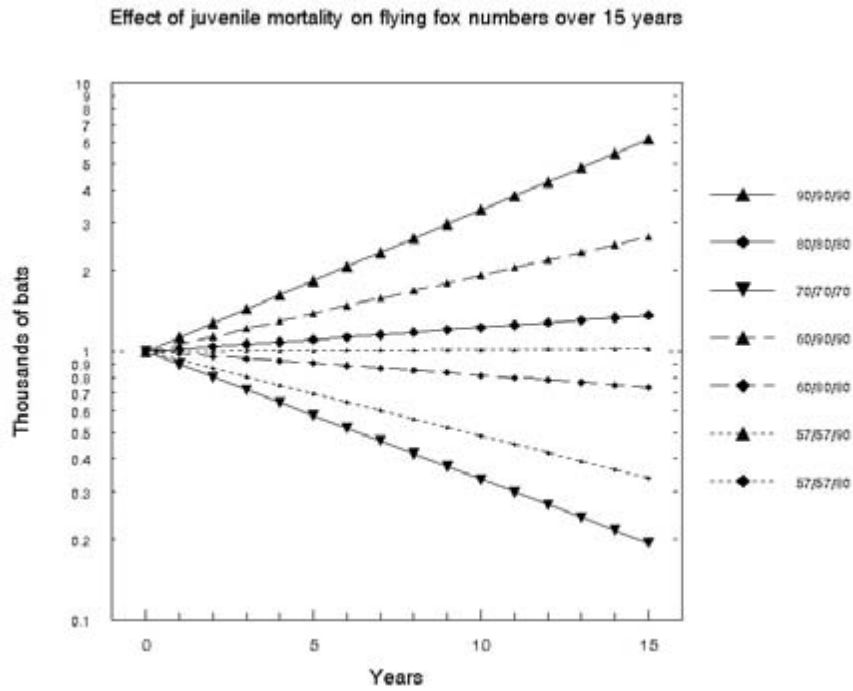


Figure 6. Effects of juvenile mortality on flying fox numbers over 15 years. The assumptions are as for figure 3. All populations have an adult breeding success of 90%, and 20% of 2-year olds deliver young. Successive figures in the legends show survivorship for year 1, year 2, and years 3-15.

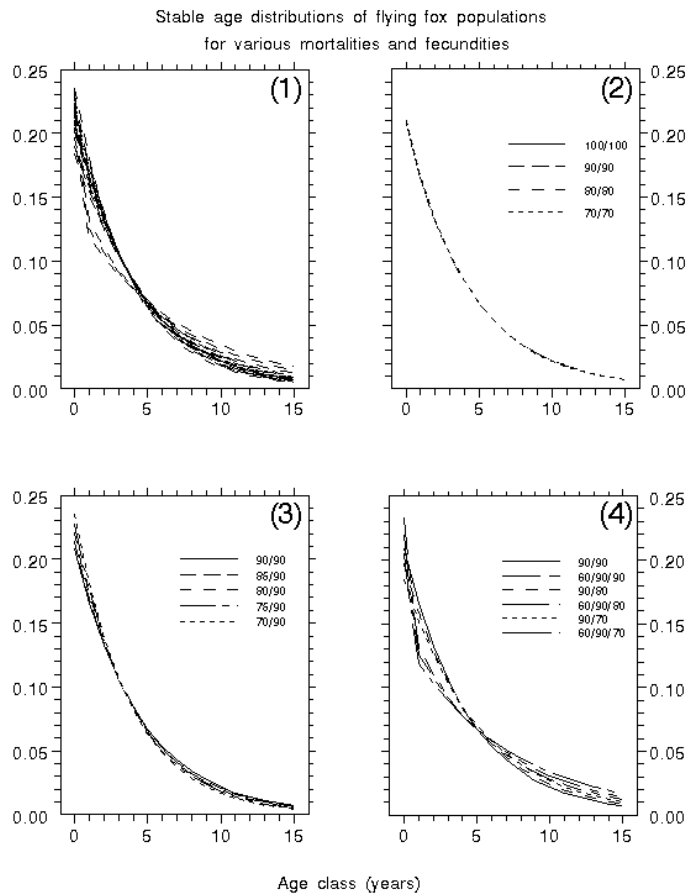


Figure 7. Stable age distributions of flying fox populations. The ordinate of each graph is the proportion of the population in each age class. Graph 1 shows the range of distributions for the various combinations of mortality and fecundity examined in Table 1. Graph 2 shows the distributions when age-independent mortality and fecundity change together. Graph 3 shows the effects of changing age-independent mortality, against a constant fecundity. Graph 4 shows: the effects of a high year 1 infant mortality, and the effects of changing fecundity, as mortality remains constant.

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Discussion

Other estimates of population dynamics of Australian flying-foxes

Ratcliffe (1931) speculated as follows: "Assuming... the numbers of the two sexes are equal and that every female produces a young one yearly..., we get a figure of 50 per cent. for the annual increase... Allowing for the "natural" death-rate..., and the fact that females do not appear to breed until their second year, a potential annual increase rather less than this is arrived at. (As a flying fox has been kept in captivity for seventeen years..., it seems safe to allow each female, under natural conditions, an average potential breeding life of ten years. On this basis, the potential annual rate of increase of a flying fox population is approximately 40 per cent... Except for relatively slow changes in the size of the... population, the numbers from year to year are presumably approximately the same†. This means that some natural check occurs which neutralizes this potential increase, and accounts for some 40 per cent. of the animals each year". This last later became, "...for about 30 per cent. of the population each year", (Ratcliffe 1932).

Following these "calculations", there appear to be no later attempts to quantify the population dynamics of Australian flying-foxes. Vardon and Tidemann (2000) state that, for *P. alecto*, "the maximum reproductive potential of the species... is likely to be around 0.4 as calculated for *P. giganteus* (Dolbeer et al 1988)", and that, "Dolbeer et al. (1988) calculated that *P. giganteus* had a maximum (or intrinsic) rate of growth [sic] of 0.40. Simply put, this means that populations of this species can theoretically increase in size by 40% each year". Vardon and Tidemann (2000) appear to have confused the instantaneous rate of increase (r_m) with the finite rate of increase (λ), since an r_m of 0.4 would lead to a population doubling time of 1.73 years, which is clearly nonsense.

We have examined Dolbeer et al. (1988), and their description of reproduction in the Maldivian subspecies of *P. giganteus* agrees with that of Marshall's (1948) description of the mainland population. It appears that, while Dolbeer et al. (1988) do list an r_m of 0.4, their calculations, as they mistakenly include the number of female offspring delivered per adult female per year as 1, rather than 0.5 (Dolbeer personal communication 2001) involve an arithmetical error of 2.

Marshall (1948) examined *P. giganteus* material sampled monthly from the wild over three years at 7 °N. He described the breeding season as "sharply defined", noting that all conceptions occurred in December/ January, and parturition "in late May and perhaps early June". He observed a tight distribution of foetal weights in March/ April/ May and stated that, "The gestation period is thus about six months, and the number of young was invariably one". This equates to the annual cycle of reproduction in Australian *Pteropus*, in which the maximal possible r_m is 0.2558 and the shortest possible doubling time 2.72 years, and then only if no animals die before age 15 years, and 100% of females, including 2-year olds, deliver a viable young.

In reality, the likely statistics for Australian *Pteropus* in the wild, are those arising from the equivalent of 10-20% mortality per annum, 20-30% of 2-year olds delivering a viable young, and 70-90% breeding success for adult females. Thus r_m s will range from +0.1213 to -0.0133, giving populations rates of change ranging from a potential doubling time of 5.7 years to a halving time of 6.3 years.

Flying-foxes: survival species or opportunistic species?

This paper arose from a recent proposal to cull Grey-headed flying-foxes *P. poliocephalus* roosting in the Royal Melbourne Botanic Gardens (RMBG). In this case, the proponents of the culling had little or no understanding of the reproductive potential of flying-foxes. It was stated that the RMBG population had increased from 3000 to 8000 in eighteen months, and implied that this was due to reproductive increase alone. Other cull-proponents such as NSW and Queensland fruit growers, often refer to similar "population explosions", implying that flying-foxes are opportunistic breeders, capable of increasing to plague proportions within a short period of time. As can be seen from our population models, this is far from the truth. Flying-foxes are clearly "survivor species" that possess a very low natural capacity for increase. To emphasise this, we compare the population dynamics of flying foxes, with those of the vole (*Microtus agrestis*), a small opportunistic breeding, northern hemisphere rodent.

In laboratory studies of populations in optimal breeding conditions (Leslie and Ranson 1940), the vole begins to breed at 3 weeks and the "natural" death-rate is such that most adults are dead by 72 weeks ($l_x@72w = 0.025$). Young

mature females raise litters of 5-6; the net reproduction rate $R_0 = 5.9$ and the generation time $T = 24.4$ weeks. Using these statistics, one can calculate the per annum r_m as 3.7946. Using the equation $N_t = N_0 e^{r_m t}$, with $N_0 = 1$ (one female vole) and $t =$ years, $N_t = 45$ in year 1, 1,977 in year 2, 87,886 in year 3 and 3,907,467 in year 4. Another, perhaps intuitively simpler, way to do the calculation is to raise the net reproduction rate to the power of the number of generations per year (2.137) multiplied by the number of years eg., $5.90424^{(2.137 \times 4)} = 3,907,598$. The slight difference between methods is due to rounding-off errors. This is indeed the type of population dynamics associated with mouse plagues in Australia - but not with flying-foxes.

Density dependent factors and the regulation of flying-fox populations

During discussion of an oral presentation of Martin and McIlwee (2002), a fruit grower noting that an age-independent mortality of 20% per annum and female breeding success of 80% produced a near-stable population (see figure 3), wondered if cessation of orchard culling might lead to increases in the grey-headed flying-fox population. LM could not provide a definitive answer. This is because the mechanisms which regulate population growth in flying-foxes are not well understood. If a population can grow exponentially, why does it not eventually take over the continent? The reason populations cannot grow indefinitely has been a subject of debate for many years in ecology (Andrewartha and Birch 1954; Hassell 1986). There are two schools of thought as to how flying-fox populations may have been kept in balance prior to European settlement. The first emphasises the role of density-dependent factors, where limiting resources or predators regulate population growth. The second considers that populations do not grow for very long before the environment changes and they begin to decrease. Climatic fluctuations such as droughts, extreme temperatures and other random events such as episodic food shortages can cause changes in population growth rates.

Predators probably have a relatively minor effect on flying-fox populations, and there are no reports of massive deaths associated with disease. However, flying-foxes experience natural catastrophic events, such as droughts and heat waves, which were cited by Ratcliffe (1931). These have the potential to cause heavy mortality, particularly among juveniles. In the late 1990s, in maternity roosts in Queensland

and NSW, very high day-time temperatures and smoke caused death from dehydration and heat-shock of large numbers of *P. poliocephalus* and *P. alecto* of all ages, but particularly juveniles. Hall (personal communication 2000) observed mass abortions in camps of these species in SE Queensland; 2,000 out of 12,000 females aborted near-term foetuses in Beenleigh in 1978; large numbers of aborted foetuses were observed in the Indooroopilly camp in 1983; numerous bats were found dead and foetuses were aborted during a winter failure of blossom in 1990 (Hall *et al.* 1991) and there are other more recent examples.

Most of the observed "natural" causes of flying-fox mortality appear not to be related to, or dependent on, the size or density of the population. We include the massive deaths and abortions caused by starvation, since these events appear to arise from massive, widespread failures of blossom, rather than an exhaustion of the food source by the animals. Thus most causes appear to be "density independent".

This is not to say that "density-dependent" factors do not also limit population growth under certain conditions, only that such a linkage has yet to be demonstrated. While the operation of a putative density-dependent factor is relatively easy to demonstrate in laboratory experiments, it is extremely difficult to do so in the field. It is therefore disconcerting to find Vardon and Tidemann (2000) stating that, "There is evidence of density-dependent factors affecting reproduction in *P. alecto* (Vardon and Tidemann, 1998)". Alas, the "evidence" comprises no more than a statement (referring to 30% of adult females being rated as non-breeding), that, "this large non-breeding female population could be an indication of density-dependent mechanisms that reduce female reproductive success". This statement makes no sense, as the large non-breeding population could just as well result from any of a range of density-independent environmental stresses. With such data, there is no way to distinguish between density-dependent and density-independent effects!

The subject of density-dependent factors is not trivial. Were such factors operating to regulate flying-fox populations, then culling, by reducing population density, would release the population from the constraints imposed by the density dependent factors, and allow it to recover towards its previous level. Thus, one could argue, that orchard culling would not have a permanent

detrimental effect on the flying-fox population. However, we maintain that there is no evidence that density-dependent factors presently have any significant effect on flying-fox populations. In addition, the limited reproductive potential of the animals would not allow any rapid recovery of the population.

Implications of seasonal breeding for the vulnerability of *Pteropus* spp

The fixed seasonality of *P. poliocephalus*, *P. conspicillatus* and *P. scapulatus* indicates a strongly established evolutionary adaptation to the climatic and blossom/fruitlet cycles in Australia prior to the 19th century. The subsequent massive clearance of feeding and roosting habitat would therefore have had much greater effects on these species than on opportunistic breeders that could, as it were, "flow" with the changing environment. It is worth noting, therefore, that *P. alecto*, which exhibits some plasticity in breeding season, has, in recent years, expanded its range southwards, apparently at the expense of *P. poliocephalus* (Vardon and Tidemann 1998; Hall 2000).

A seasonal breeder with a rigidly (genetically) defined breeding season is also much more at the mercy of large climate fluctuations than an opportunistic breeder. This is true, whether fluctuations be relatively long-term (eg. global warming), or short-term, like the several months of winter drought in 2000. The plight of a seasonal breeder is greatly exacerbated if it has a lengthy gestation, like *Pteropus*. In the 2000 drought in northern NSW and south-east QLD, there were many reports of deaths of adult *P. poliocephalus*, together with aborted young, low birth weights and birth defects, just as in a previous (1990) episode of adult flying-fox deaths (Hall, *et al.* 1991). In the Brisbane area, the Orphan Native Animals Rear and Release group (ONARR), reported more than 2000 adult *P. poliocephalus* found dead over a 3-week period in August- September 2000, numerous abortions and a drop in survival rate of neonates taken into care from >90% to ~ 20% (Luckhoff, personal communication 2001). Seasonality also has major implications in the culling of flying-foxes by fruit growers, as discussed below.

The relative importance of mortality and fecundity on population dynamics of flying-foxes

In relation to the importance of fecundity and survival, our results show that the relative contribution of fecundity rates on population

growth rate is minor in comparison to adult survival rates. Such contributions may be compared directly through elasticity analysis, which quantifies the proportional changes in population growth rate (λ) resulting from changes in life history parameters (De Kroon *et al.* 2000). This provides a means of assessing the relative impact of comparable changes in fecundity and survival on the growth rate of a population. Because elasticities measure the relative importance of life history stages to population growth, it is inferred that management should focus on protecting stages with the largest elasticities. Here, a clear distinction can be made between highly reproductive species and survivor species, as mammals that mature early, produce large litters and have short live spans, possess large fertility elasticities and relatively small survival elasticities (Heppell *et al.* 2000). This means that populations of highly reproductive species are less affected by changes in survivorship, but more influenced by changes in breeding success, relative to long-lived species.

There is much evidence in long-lived species of birds (Saether and Bakke 2000) and mammals (Heppell *et al.* 2000), that survivorship elasticities are significantly larger than fecundity elasticities, with the greatest differences found in long-lived species that produce few offspring. So too for flying-foxes. This means that conservation efforts to reduce adult mortality in flying-foxes will have the greatest effect in halting population decline.

Hypothetical versus real death rates: calculating the effects of culling

From the data presented above, we argue that any stable population of flying foxes would be experiencing an average per annum mortality in the region of 20%. Present day "natural" mortality experienced by *Pteropus* spp. is likely to be significantly higher than that experienced prior to European settlement as a result of habitat destruction, reduced food sources and roost sites. Such "natural" mortality is likely to go unnoticed. In addition, flying-fox populations suffer a significant level of intentional, human-imposed mortality via electrocution, shooting, poisoning, maternity-roost disturbance/ destruction. Such human-imposed mortality is likely to be age-independent. Thus, the age-independent death-rates, used to compute the population changes in this paper, can effectively be equated to "harvesting" or "culling" rates.

In relation to actual death-rates, any **perceived** "human-imposed" mortality would have an additive effect on the **unperceived** "natural" mortality. This means that a perceived, imposed death-rate of 10% per annum by intentional electrocution, or other form of culling, adding to an unperceived natural death-rate of 10%, will produce a **total** death-rate of 20%, and given an adult fecundity of 90%, a population in stasis. At this fecundity, any imposed death-rate greater than 12% will cause population decline. With adult fecundities below 90%, and "natural" death-rates higher than 10%, any imposed-mortality leads to greater and greater rate of population declines. So, under a "natural" death rate of 20% and adult fecundity of 80%, an imposed mortality of 10% will lead to a halving of the population in well under a decade (see Table 1). From these relationships, one can calculate the effects of a known harvesting rate on a population of any given size.

Although the effects of harvesting depend on the size of the population at risk, it is often difficult to provide scientifically valid estimates of population size that are acceptable to all researchers. For this reason, it is perhaps more practicable to use realistic estimates of natural mortality and fecundity, and work "back" from **known** culling rates to calculate the size of population that would be put into rapid decline by such culling.

A case study: electrocution deaths of *P. conspicillatus* in a Queensland Orchard

Recently there has been concern over deaths by electrocution of *P. conspicillatus* in lychee orchards in north Queensland. In Australia, the main population of this species is restricted to the high rainfall forests of the Wet Tropics, with a small isolated population found in the Iron Range area of Cape York. A separate population occurs in New Guinea (Hall and Richards 2000). We use this species as a case study to highlight the current vulnerability of flying-foxes to decline and extinction by assessing the effects of culling on local populations of *P. conspicillatus* throughout the Wet Tropics.

The calculations below use the same bases as before, namely: all females are dead/infertile after year 15; there is a "natural", age-independent mortality; a constant age-independent adult fecundity, with 20% breeding success in 2-year-olds; "imposed" deaths are age-independent and additive with the "natural"; processes associated with "imposed" deaths do not affect fecundity. In calculating what size of female population will go into serious decline with a given electrocution rate, we have used three "natural" death and fecundity rates, namely: 10% annual natural mortality with 90% breeding success; 20% annual natural mortality and 80% breeding success; 27% annual natural mortality and 70% breeding success.

Table 1. The relationship between "natural" mortality and fecundity of a flying-fox population, and the size of population that is put into rapid decline by an imposed mortality - in this case, electrocution in a single orchard.

The table shows the sizes of population that are put at risk by various kill rates; figures in brackets are the times, in years, to halve each population. It should be noted that the population sizes given are for females only. If the male: female sex ratio in the overall population is 1:1, then the size of the total population put into decline is doubled.

Column 1 lists three possible "natural" baseline mortalities and fecundities. It is assumed that, in all populations, breeding success of 2-year-olds is 20%.

No. adult females killed are the estimated number of adult female *P. conspicillatus* killed in one season in one orchard, based on counts of adult bats found dead on the electrocution grid. Columns 2 & 3, respectively assume 50 and 70% of counted dead are female; columns 4 & 5, are as for columns 2 & 3, but assume that the counts of dead bats on the grid underestimate actual deaths by 10%.

No. adult females killed	Size of female population put at risk (halving time in years)			
	50%=10,584	70%=14,818	55%=11,642	77%=16,299
"Natural" state of target population				
Mortality 10%;fecundity 90%	52,920 (7.5)	74,090 (7.5)	58,210 (7.5)	81,495 (7.5)
Mortality 20%;fecundity 80%	105,840 (6.3)	148,180 (6.3)	116,420 (6.3)	162,990 (6.3)
Mortality 23%;fecundity 70%	529,200 (5.4)	740,900 (5.4)	582,100 (5.4)	814,950 (5.4)

In November-December 2000, four once-nightly counts of newly-killed bats on one orchard's electrocution grid, made over a two week period (409, 499, 305, 297; Booth, personal communication 2001) gave a mean \pm standard deviation of 378 ± 96 bats killed per night (95% confidence limits of 226-530; i.e. there is 95% probability that the mean lies within these limits). On the basis of an 8-week, 7-nights-a-week electrocution season we calculate that, in this orchard alone, some 21,168 bats were killed. This number might seem excessively large, but should be viewed in the context of a grid system of 6.4 km in an orchard of 60 hectares containing 10,000 trees - a kill rate of 2 bats per tree per season. We also note that the grid had been in operation for some time before the first counts were made, and that many bats were still being killed a fortnight later, indicating that the grid had no measurable deterrent effect on the flying-fox population.

However, the counts do not allow for deaths of severely injured animals away from the grid, or for bodies that fell from the grid. A 10% adjustment upwards to 23, 284 to account for **actual deaths** is not unrealistic. Since this kill occurred at the peak of the birth and lactation season, it is likely that the population entering the orchard comprised more than 50% females. We have therefore assumed at least 50%, and possibly 70% of animals killed were adult females. Thus there are 4 likely values for total adult-female-kills of: 10,584; 14,817; 11,642; and 16,298. The size of the population that is put at risk is then calculated as follows: taking the deaths by electrocution to be, for example, 10,584 per season, from Appendix 1 one sees that the mortality rate for a fixed fecundity rate of 90% ($m_x = 0.45$) that produces a halving time of close to 7.4 is 30%. Thus, if electrocutions are responsible for increasing the mortality rate from 10% to 30%, then 10,584 amounts to 20% of the female population, whence the total **female** population is $5 \times 10,584 = 52,920$, as recorded in Table 1.

Table 1 demonstrates the sizes of populations of female flying-foxes of differing "natural" mortality and fecundity that would be put into rapid decline (halving time of 7.5 years or less) by the year 2000 season's electrocution of adult female *P. conspicillatus* in this one orchard. It can be seen that the current killing rate will cause rapid declines in *P. conspicillatus* populations of 52,920 to 814,950 females. The first figure is best-case scenario, the last figure the worst. Given likely natural mortality and fecundity, the most probable estimate is in the range 100,000 to

200,000 females. However, the table does not take into account deaths of young resulting from maternal deaths or injuries, with consequent failure of lactation, rejection of young, etc. Add in this "unperceived" kill of neonates, and the size of population driven into rapid decline by electrocution goes up accordingly. Thus we should be concerned about a decline in a population of more than 200,000 flying foxes. If the population of *P. conspicillatus* within range of this orchard is less than this number, then the culling rates will contribute to the rapid decline and possible extinction of the population. In terms of the conservation of *P. conspicillatus* as a species, the kill rates from this one orchard should not be taken in isolation, and there is a need to assess the effect of culling by orchards over the entire Wet Tropics.

The status of *P. conspicillatus* populations in North Queensland

In reviewing the status of *P. conspicillatus*, Whybird *et al.* (2000) quote a loss throughout the Wet Tropics of "15 permanent camps with a total population of 610,000 bats in the last 15 years... This indicates an approximate 78% population decline in just 15 years." According to the report, *P. conspicillatus* populations have declined from an estimated 820,000 in 1985, to 80,000 in November 2000 (Whybird, personal communication, 2001). Treating these values as indicative of the rate of population decline of *P. conspicillatus*, we used Leslie Matrix projections to determine the death-rates required to reduce starting populations, ranging from 400,000 to 1,000,000, to 80,000 in 15 years. We used three sizes for the starting population, because of likely errors in estimating the actual size of the 1985 population. Figure 8 shows that with a fecundity rate of 90%, mortality rates of 30-35% cause such starting populations to decline over 15 years to the year 2000 population size.

If an estimated mortality of 10-20% is attributable to "natural" causes (as outlined above), this leaves 10-25% as the human-imposed rate. Thus, it can be seen that the effect of culling a starting population of 800,000 *P. conspicillatus* is the death of 80,000 - 200,000 animals per year. For a starting population of 80,000, the number killed is 8,000 to 20,000 flying-foxes per year. Given that the cull rate of one lychee orchard exceeds the estimated harvest rate for the entire Wet Tropics, it is likely that the *per capita* mortality of *P. conspicillatus* is increasing yearly as the population declines. It is not known if an imposed-mortality like culling

Matrix projections of decline of *P. conspicillatus* over a 15 year period, with 90% adult fecundity rate and mortality rates of 30-34% for all age classes

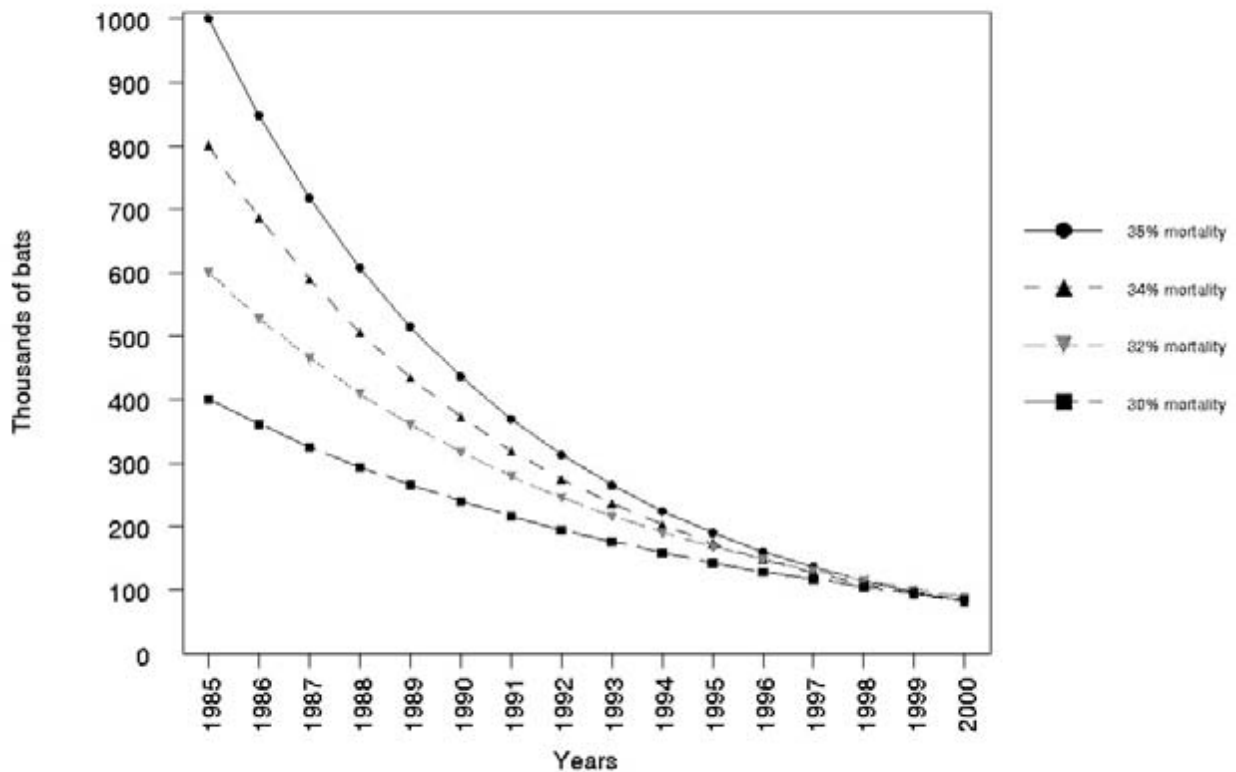


Figure 8. Possible rates of decline in *P. conspicillatus* populations since 1985. The graph shows how, with 90% fecundity, different mortality rates would cause various sized populations to decline to the present estimated size, over 15 years. It is assumed that conditions remain constant throughout.

acts in a density dependent manner - such that a constant proportion of a population, but smaller absolute number, is lost each year, or whether it has the more destructive potential of killing similar absolute numbers each year (and thus an increasing *per capita* mortality as the population declines) until a population becomes extinct.

Unlike ground-dwelling mammals whose populations are isolated and restricted by geographical barriers, flying-foxes have the potential to travel large distances in search of food (Pierson and Rainey 1992). This means that animals attacking a given orchard cannot be regarded as a separate population. While there are benefits in the movement of animals between populations (i.e. a decline in one population may be offset by immigration from others), there is the danger that a population being culled can become a perpetual vacuum or “pteropucidal black hole” that continually draws in animals from far afield. Such “sink” populations are capable of sustaining artificially high mortality rates that would otherwise drive a local population to extinction. The high cull rate by one orchard, in the absence of any *known* large

populations that could sustain such high rates of mortality (ie >200,000 animals), suggests this may be happening. Thus, this one lychee orchard may have the potential to exterminate a very large proportion of the estimated 80,000 *P. conspicillatus* remaining in the Wet Tropics. We also argue that culling on this orchard is likely to fail to protect crops long term, unless the entire population of flying-foxes is destroyed.

We have, therefore, (Table 2) estimated the numbers of *P. conspicillatus* that may have been “harvested” annually over the past 15 years from putative starting populations of 400,000, 600,000 and 800,000, with “natural” baseline fecundity/mortality schedules of 90%/10%, 80%/20% or 75%/25%, and no reproduction in year 2. It can be seen that harvesting rates over the past 15 years could have averaged: 6,800 – 22,500 animals per year under the 75/25 schedule; 20,300 – 46,000 animals per year under the 80/20; and 50,500 – 103,000 animals per year under the 90/10 (Table 3). Note that: the larger the starting population, the larger the estimate of animals harvested. Note also that, the higher the “natural” mortality, the smaller the estimate animals

Table 2. Estimated numbers of *P. conspicillatus* killed each year by direct human-imposed mortality. Estimates are based on declines in population size from 400,000, 600,000 or 800,000 in 1985, to 80,000 in 2000. For each starting population, estimates were made for three baseline "natural" schedules of fecundity/ mortality, namely: 90%/10%; 80%/20%; 75%/25%, with corresponding r_m values of 0.1133, -0.0045 and -0.0691, respectively. It is assumed that these values remained constant from 1985 to 2000.

Year	90/10 Baseline		80/20 Baseline		75/25 Baseline	
	Harvest Rate	Population size	Harvest Rate	Population size	Harvest Rate	Population size
1985	103,000	800,000	46,000	800,000	22,500	800,000
1986	103,000	780,590	46,000	750,601	22,500	725,621
1987	103,000	758,852	46,000	701,425	22,500	656,204
1988	103,000	734,507	46,000	652,470	22,500	591,420
1989	103,000	707,242	46,000	603,736	22,500	530,958
1990	103,000	676,708	46,000	555,222	22,500	474,530
1991	103,000	642,511	46,000	506,926	22,500	421,868
1992	103,000	604,214	46,000	458,848	22,500	372,720
1993	103,000	561,323	46,000	410,987	22,500	326,851
1994	103,000	513,289	46,000	363,342	22,500	284,043
1995	103,000	459,494	46,000	315,911	22,500	244,091
1996	103,000	399,248	46,000	268,694	22,500	206,805
1997	103,000	331,776	46,000	221,691	22,500	172,008
1998	103,000	256,213	46,000	174,899	22,500	139,531
1999	103,000	171,588	46,000	128,317	22,500	109,222
2000	103,000	76,813	46,000	81,946	22,500	80,936
1985	76,700	600,000	33,200	600,000	14,700	600,000
1986	76,700	586,058	33,200	564,245	14,700	546,245
1987	76,700	570,445	33,200	528,651	14,700	496,077
1988	76,700	552,958	33,200	493,217	14,700	449,257
1989	76,700	533,375	33,200	457,944	14,700	405,561
1990	76,700	511,443	33,200	422,829	14,700	364,780
1991	76,700	486,881	33,200	387,872	14,700	326,721
1992	76,700	459,373	33,200	353,074	14,700	291,201
1993	76,700	428,567	33,200	318,432	14,700	258,051
1994	76,700	394,065	33,200	283,946	14,700	227,113
1995	76,700	355,426	33,200	249,615	14,700	198,240
1996	76,700	312,153	33,200	215,440	14,700	171,293
1997	76,700	263,691	33,200	181,418	14,700	146,144
1998	76,700	209,416	33,200	147,550	14,700	122,673
1999	76,700	148,633	33,200	113,835	14,700	100,769
2000	76,700	80,560	33,200	80,271	14,700	80,326
1985	50,500	400,000	20,300	400,000	6,800	400,000
1986	50,500	391,415	20,300	377,988	6,800	366,963
1987	50,500	381,800	20,300	356,076	6,800	336,131
1988	50,500	371,032	20,300	334,262	6,800	307,356
1989	50,500	358,973	20,300	312,547	6,800	280,501
1990	50,500	345,468	20,300	290,929	6,800	255,438
1991	50,500	330,342	20,300	269,409	6,800	232,048
1992	50,500	313,403	20,300	247,986	6,800	210,218
1993	50,500	294,433	20,300	226,660	6,800	189,844
1994	50,500	273,187	20,300	205,430	6,800	170,831
1995	50,500	249,394	20,300	184,295	6,800	153,086
1996	50,500	222,747	20,300	163,256	6,800	136,524
1997	50,500	192,904	20,300	142,311	6,800	121,068
1998	50,500	159,482	20,300	121,461	6,800	106,644
1999	50,500	122,052	20,300	100,705	6,800	93,182
2000	50,550	80,133	20,300	80,043	6,800	80,618

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harvested. In other words, to account for any given population decline, the higher the “natural” mortality, the lower the cull mortality. Under the harvest rates estimated in Table 3, and assuming a genuine population decline as described by Whybird *et al.* (2000), we suggest that *P. conspicillatus* currently faces severe threats from human-imposed mortality, the magnitude of which has not been reported before. Indeed, based on the numbers legally taken by fruit farmers under Damage Mitigation Permits, issued by the Queensland Parks and Wildlife Service, Garnett *et al.* (1999) state, “declared figures would suggest that mortalities from shooting and electrocution exceed 2000 animals, or 1.3% per year”. In light of these figures, which may underestimate average cull rates across the Wet Tropics by as much as 50 fold, we suggest that a review of culling practices in North Queensland is urgently required.

The status of *P. poliocephalus* populations in Victoria, NSW and southern Queensland

Grey-headed flying-foxes are found in coastal south-eastern Australia, from Victoria to south-east Queensland (Hall and Richards 2000) and are vulnerable to loss of habitat, and culling by humans. A recent census in NSW by Eby *et al.* (1999) and in Queensland by Birt (unpublished data), estimate the total population of *P. poliocephalus* to be 360,000 - 400,000. These figures represent a decline of 35% over the past decade, when compared to a 1989 count of 566,000 from 15 of 23 known camps (Parry-Jones 2000b).

Using the same methods and fecundity/mortality schedules as for *P. conspicillatus*, we calculated the likely number of *P. poliocephalus* culled from the population each year from 1989 to 1998, using 560,000 as the likely population size in 1989. Table 4 shows that, on average, between 0 - 72,000 *P. poliocephalus* could have been culled from the population each year. It should be noted that both the 75/75 and 80/80 baseline models represent naturally declining populations, (the reason why putative cull rates under these conditions are significantly lower than the 90/90 baseline model). If the *P. poliocephalus* population were experiencing a natural mortality and fecundity that would lead to positive growth under natural conditions, the actual number culled could range from 20,000 - 72,000. With 90% fecundity, the minimum rate of decline experienced by *P. poliocephalus* equates to a total (“natural” plus imposed) mortality rate of 25% across all age classes. This is just 3%

higher than the minimum rate that allows a stable population to be sustained (as outlined in Appendix 1), yet this mortality is sufficient to reduce the total population size of *P. poliocephalus* by 35% over 10 years.

While our calculated cull-rates of *P. poliocephalus* are based on a minimum rate of population decline, our results are consistent with the mortality rates estimated from other studies. Culling rates by NSW growers were estimated by Richards (2000) to be as high as 10% of the population, but this estimate (i.e. 30,000 bats per annum) was based on only 7% (of a total of 1500 orchards) shooting 10 bats per night for 30 days of the fruit-harvesting season. The actual kill could be much higher. Our results also support the findings of Tidemann *et al.* (1999) who state that as many as 100,000 bats are killed annually.

Conclusions

This paper has explored how flying fox populations respond to changes in mortality and reproduction. From this assessment, we argue that the life history of flying-foxes has evolved to match a much higher longevity and reproductive success than is presently possible in many regions of Australia, due to current threats. High levels of mortality, either natural or unnatural, will lead to species decline. Of the four species of flying-fox in Australia, we calculate that two, *P. poliocephalus* and *P. conspicillatus*, are in imminent danger of extinction if current threats persist.

We found that the mean longevity of females contributes most to the growth and decline of populations. Due to a range of threats, the survival rates of populations are likely to be highly variable, both spatially and temporally. Source/sink dynamics are likely to play an important role in maintaining local populations from decline. However, under a vacuum effect, this has the potential to cause many (if not all) populations within a region to fall into decline. We argue that this has occurred for *P. conspicillatus* and *P. poliocephalus*, and may explain the contraction of the latter from the northern part of its range, which has allowed *P. alecto* to move in.

Though little information is publicly available on culling rates of flying-foxes by NSW and Queensland fruit-growers, our models suggest that current death rates exceed all previous estimates for *P. conspicillatus*, and are within the range of estimates published for *P. poliocephalus*.

Table 3. Estimated numbers of *P. poliocephalus* killed each year by human-imposed mortality. Estimates are based on a likely decline from a population of 560,000 in 1989 to one of 360,000 in 1998, for three baseline "natural" schedules of fecundity/ mortality, namely: 90%/10%; 80%/20%; 75%/25%, with corresponding r_m values of 0.1133, -0.0045 and -0.0691 respectively. It is assumed that these values remain constant throughout.

Year	90/10 Baseline		80/20 Baseline		75/25 Baseline	
	Harvest Rate	Population size	Harvest Rate	Population size	Harvest Rate	Population size
1989	72,000	560,000	20,100	560,000	0	560,000
1990	72,000	546,525	20,100	537,466	0	522,633
1991	72,000	531,434	20,100	515,034	0	487,760
1992	72,000	514,533	20,100	492,703	0	455,214
1993	72,000	495,605	20,100	470,472	0	424,839
1994	72,000	474,407	20,100	448,342	0	396,491
1995	72,000	450,667	20,100	426,311	0	370,035
1996	72,000	424,079	20,100	404,380	0	345,344
1997	72,000	394,304	20,100	382,548	0	322,301
1998	72,000	360,957	20,100	360,814	0	300,795
1999	72,000	323,611	20,100	339,178	0	280,724

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Appendix 1. A summary of flying-fox population vital statistics calculated by the Leslie matrix method. Juvenile and adult fecundity rates are shown in the first column, in that order: Year 1, year 2 and adult (age-independent) mortality rates are shown in that order; in the second column. In all save six cases, the maximum life-span is 15 years. In the final four cases (mortalities superscripted 10) the maximum life-span is 10 years. m_x is the number of females delivered per female per year; l_x is the proportion surviving each year; λ is the finite rate of increase per year; the figures after the decimal point giving the percentage increase per annum; r_m is the intrinsic rate of increase; R_0 is the net reproduction rate - the number of female young delivered per female-lifetime; T is the generation time; $T_{d/h}$, when positive, is the population doubling time, and when negative is the population halving time.

APPENDIX

m_x for years 2/3-15	l_x for years 1/2/3-15	λ	r_m	R_0	T	Life Expectancy	$T_{d/h}$
0/0.5	1.0/1.0/1.0	1.24	0.2186	6.5	8.6	16.0	+3.18
0.1/0.5	1.0/1.0/1.0	1.25	0.2258	6.6	8.4	16.0	+3.08
0.5/0.5	1.0/1.0/1.0	1.29	0.2558	7.0	7.6	16.0	+2.72
0/0.45	0.90/0.90/0.90	1.12	0.1133	2.4	7.9	8.1	+6.12
0.1/0.45	0.90/0.90/0.90	1.13	0.1213	2.5	7.6	8.1	+5.71
0.22/0.45	0.90/0.90/0.90	1.14	0.1315	2.6	7.4	8.1	+5.3
0.45/0.45	0.90/0.90/0.90	1.16	0.1504	2.8	6.9	8.1	+4.61
0/0.45	0.80/0.80/0.80	1.01	0.0118	1.1	7.2	4.9	+63.0
0.1/0.45	0.80/0.80/0.80	1.02	0.0206	1.2	6.9	4.9	+33.6
0.1/0.45	0.79/0.79/0.79	1.01	0.0098	1.1	6.8	4.7	+70.7
0.1/0.45	0.78/0.78/0.78	1.00	-0.0010	1.0	6.8	4.7	-693
0.1/0.45	0.77/0.77/0.77	0.99	-0.0120	0.9	6.7	4.7	-57.8
0.1/0.45	0.76/0.76/0.76	0.98	-0.0232	0.9	6.6	4.7	-29.9
0/0.45	0.75/0.75/0.75	0.96	-0.0436	0.74	6.9	4.0	-15.9
0.1/0.45	0.75/0.75/0.75	0.97	-0.0344	0.80	6.6	4.0	-20.1
0/0.45	0.70/0.70/0.70	0.90	-0.1028	0.51	6.6	3.3	-6.74
0.1/0.45	0.70/0.70/0.70	0.91	-0.0931	0.56	6.3	3.3	-7.45
0/0.40	0.90/0.90/0.90	1.10	0.0973	2.17	8.0	8.1	+7.12
0.1/0.40	0.90/0.90/0.90	1.11	0.1055	2.26	7.7	8.1	+6.57
0/0.40	0.80/0.80/0.80	1.00	-0.0045	0.97	7.3	4.9	-154
0.1/0.40	0.80/0.80/0.80	1.00	0.0045	1.03	7.0	4.9	+154
0.2/0.4	0.80/0.80/0.80	1.01	0.0137	1.10	6.7	4.9	+50.6
0/0.40	0.75/0.75/0.75	0.94	-0.0601	0.66	6.9	4.0	-11.5
0.1/0.40	0.75/0.75/0.75	0.95	-0.0507	0.72	6.6	4.0	-13.7
0/0.40	0.70/0.70/0.70	0.89	-0.1195	0.45	6.6	3.3	-5.80
0.1/0.40	0.70/0.70/0.70	0.90	-0.1095	0.50	6.3	3.3	-6.33
0/0.35	0.90/0.90/0.90	1.08	0.0796	1.90	8.1	8.1	+8.71
0.1/0.35	0.90/0.90/0.90	1.09	0.0880	1.98	7.8	8.1	+7.88
0/0.35	0.80/0.80/0.80	0.98	-0.0226	0.85	7.4	4.9	-30.7
0.1/0.35	0.80/0.80/0.80	0.99	-0.0133	0.91	7.0	4.9	-52.1
0/0.35	0.75/0.75/0.75	0.92	-0.0785	0.58	7.0	4.0	-8.83
0.1/0.35	0.75/0.75/0.75	0.93	-0.0687	0.63	6.7	4.0	-10.1
0/0.35	0.70/0.70/0.70	0.87	-0.1380	0.40	6.7	3.3	-5.02
0.1/0.35	0.70/0.70/0.70	0.88	-0.1277	0.45	6.3	3.3	-5.43
0.17/0.35	0.70/0.70/0.70	0.89	-0.1204	0.48	6.1	3.3	-5.76
0/0.45	0.60/0.90/0.90	1.06	0.0596	1.63	8.2	5.8	+11.6
0.1/0.45	0.60/0.90/0.90	1.07	0.0655	1.69	8.0	5.8	+10.6
0/0.45	0.60/0.80/0.80	0.97	-0.0275	0.82	7.4	3.9	-25.2
0.1/0.45	0.60/0.80/0.80	0.98	-0.0205	0.86	7.1	3.9	-33.8
0/0.45	0.57/0.57/0.90	1.00	-0.0022	0.98	8.6	4.1	-316
0.1/0.45	0.57/0.57/0.90	1.00	0.0016	1.01	8.4	4.1	+433
0/0.45	0.57/0.57/0.80	0.93	-0.0776	0.55	7.6	3.1	-8.93
0.1/0.45	0.57/0.57/0.80	0.93	-0.0724	0.59	7.4	3.1	-9.57
0/0.5	1.0/1.0/1.0 ¹⁰	1.22	0.1983	4.00	7.0	11.0	+3.50
0.1/0.5	1.0/1.0/1.0 ¹⁰	1.23	0.2069	4.10	6.8	11.0	+3.35
0/0.45	0.90/0.90/0.90 ¹⁰	1.10	0.0930	1.87	6.7	6.9	+7.45
0.1/0.45	0.90/0.90/0.90 ¹⁰	1.11	0.1024	1.95	6.5	6.9	+6.77