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"Demographic analyses of free-living endangered species"

Demographic analyses of free-living endangered species.

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Introduction.

A recent survey of extinctions in North American fish species provides data that quantify causes of extinction in natural populations (Miller, Williams and Williams, 1989). This survey illustrates two important features: (1) rates of species extinction are increasing at an exponential rate and (2) human interference, through habitat alteration, pollution or overexploitation, is a major contributory factor to extinction rates (Figure 1). In most cases more than one factor contributed to the extirpation of a species and in many cases the species disappeared before it could be classified as endangered. The harsh data presented in these figures are not unique; similar patterns of declining abundance and extinctions have been reported recently for birds (Terborgh 1989) and amphibians (Blaustein & Wake, 1990). All the studies emphasize the need to set more comprehensive guidelines for determining endangered status (Group Report, this volume; Mace & Lande, 1991).

Because elephants are not beetles (Poole and Thomsen 1989), and endangered species are not test-tube colonies of *Drosophila*, viability assessment for potentially endangered vertebrates requires the use of different techniques than might be applicable under more controlled conditions. Traditional attempts to undertake species viability analyses are usually restricted to linear life-table analyses. However, non-linear density-dependent effects often have significant effects on the dynamics

of free-living populations. In particular, resource acquisition and social organization often influence population dynamics in a very non-linear fashion. Because these aspects of a species biology are often highly susceptible to human interference, quantifying the links between behavioral ecology and demography remains both a formidable academic challenge (Hassell & May 1986) and a major management problem in conservation biology (Dobson & Lyles 1989).

The ability to manage a population efficiently depends upon an understanding of its population dynamics. For endangered species the data available on which to make decisions changes quantitatively and qualitatively as we move from captive populations in zoos and wildlife parks to free-living populations. Almost universally the data collated for free-living populations contains limited information about the genetic and age-dependent vital rates of the population, but instead emphasize changes in abundance and geographical distribution. Although some of the analytical techniques developed for captive populations will apply to intensely studied wild populations, a variety of alternative analytical tools are required to assess the relative health of free-living populations. Fundamental to these techniques is the quantification of rates of birth, mortality and dispersal in the population. This information is only of limited value unless supplemented by identification of the key density-dependent and density-independent factors

influencing the magnitude and variation of these demographic parameters.

This chapter presents a number of techniques for examining the demography of free-living populations of endangered or protected species. Obviously it is impossible to provide a comprehensive survey of techniques in so limited a space. Instead I have concentrated on a few classic long term studies of bird populations, some general models that apply to less intensely studied mammal populations and a review which illustrates how little we know about most other species.

Long-term population studies of birds.

The seminal work of Lack, 'The Natural Regulation of Animal Numbers', stimulated the initiation of a number of intensive long-term studies on British birds (Lack 1954). In general, these studies monitor the demography of one population within some fairly well defined area. Newton's work on Sparrowhawk (Accipiter gentilis) (Newton 1986) and Southern's work on Tawny Owls (Strix aluco) (Southern 1970) contain a wealth of data on two species that are protected in Great Britain. Sufficient numbers of sparrowhawk and tawny owl nestlings have been banded (or ringed) and subsequently recovered that excellent survival data are available for these species.

It is possible to fit Siler survival functions to these data (Siler 1974, Dobson 1985); for both species a simple three parameter function is sufficient to describe the change in mortality rate with age (Figure 2). However, as age-dependent biases in the recovery rates of banded birds may distort the estimates of age-dependent mortality rates obtained for any particular species (Lakhani & Newton, 1982), the survival estimates obtained from free-living populations are not fully comparable with those obtained from captive populations (Barlow & Gage, this volume). Nevertheless, it is possible to use these techniques to generate a constantly updated 'null-model' of survival for banding data which might then be used as a basis for more broad-scale population monitoring (Dobson 1990). Significant differences between observed and expected banding returns, or consistent trends away from a previous norm in the fitted function, might provide important information about the welfare of a range of free-living bird populations. For example, comparison of fitted functions for periods of high and reduced pesticide use illustrate the significant impact of pesticides on sparrowhawk survival (Figure 2). Similarly, given the current speculations about long term climate change, bird banding data could provide invaluable information on a range of bird species at comparatively negligible cost, particularly in countries where long term banding schemes are already in operation (Dobson & Hudson 1991).

Habitat choice and population recruitment.

The data on Sparrowhawks and Tawny Owls also allow examination of the mechanisms regulating the size of each population. The Tawny Owl population studied by Southern (1970) was monitored as it recovered from the severe British winter of 1947 (figure 3a). As the total population increased in size, both the clutch size and fledgling success of breeding birds declined (Figure 3b). A re-analysis of Southern's data suggests that habitat quality may have been important in mediating this effect; at the initiation of the study, the majority of the birds lived in the Marley and Radbrook Common sections of the study site (Figure 4). As the population grew the numbers of birds living in these areas remained more or less constant. In contrast, population densities increased in adjacent areas of habitat (Great Wood and Park areas) due to colonization by younger birds born in the primary areas, and by immigrants from outside the population. This colonization of marginal, less productive areas is largely responsible for the observed decline in mean clutch size and fledging success. Choice and availability of suitable breeding habitat thus operated to determine rates of recruitment, which in turn determined net changes in population size.

Similar effects operate in the two populations of sparrowhawks studied by Newton and Marquiss (1986). In one study area (Eskdale) the population remained relatively constant, while in a neighbouring area (Annandale) the population has declined

throughout the duration of the study (Figure 5a). In the Eskdale population mortality of pre-breeding birds increased in years when the breeding population was large, this density dependent increase in mortality was complemented by increases in the numbers of recruits to the population when numbers were low (Figure 5b). The majority of these recruits were birds that had not been born in the main study area. In Annandale there was no density dependent increase in recruitment as the population declined. Newton & Marquiss (1986) conclude that competition for home ranges in prime habitat is the functional mechanism producing the observed changes in recruitment in the healthy population. When population density is low most individuals breed in heavily wooded territories; as population density increases lower quality territories in sparsely wooded areas are used. Inability to capture enough prey in the marginal habitats, rather than overt competition for resources, thus leads to increased mortality in high density years. In the Annandale area tree-felling and agricultural changes have reduced nesting and hunting habitat, this considerably reduces rates of recruitment to the population and ultimately causes it to decline.

In both of these long-term population studies variations in habitat quality were critical in determining the way that per capita recruitment to the adult population varied with the size of the breeding population. The majority of endangered woodland and forest species are threatened by changes in their habitat

from selected logging, habitat fragmentation and clear-cutting. An understanding of how habitat choice effects breeding success and recruitment is crucial in determining how habitat modification will effect the viability of populations living in forested areas.

A major problem that conservation biologists have yet to address is how population regulation is affected by habitat destruction and fragmentation. When managing a potentially endangered population it is of prime importance to understand how habitat alteration interacts with the behavioral and physiological mechanisms which ultimately determine territory acquisition, mate choice and breeding success. This involves understanding a range of subtle behavioral and ecological mechanisms that have non-linear effects on recruitment and survival (Dobson & Lyles, 1989; Lande 1987, 1988). For example, wildlife managers often attempt to quantify the habitat qualities that determine prime breeding habitat for endangered vertebrate species. Indices of habitat quality are then used as the basis of population management and even to estimate the number of individuals an area can support (see papers in Verner, Morrison & Ralph, 1986). If individuals are only attracted to potential breeding sites when conspecifics are present, then prime breeding areas may go unused and remain unoccupied in years following local extinctions (Stamp 1988, Warner 1990).

Fitting density-dependent functions to long-term data sets.

The behavioral mechanisms that determine rates of birth, death and migration often affect the dynamics of a population in a complex non-linear way (May 1976). A variety of functions have been developed by ecologists and fisheries biologists to model the phenomena (Ricker 1954; Hassell, May & Lawton 1974; Maynard-Smith & Slatkin 1974; Bellows 1980). A suitably general function with highly tractable analytical properties has been suggested by Sheperd (1982). The function describes the relationship between per capita recruitment and population size;

$$f(N_t) = 1 / (1 + aN_t^b) \quad (1).$$

The two parameters of the function, a and b respectively determine the size of the population at which resources become limiting and the intensity with which they become limiting. Thus if 'b < 1', there is a gradual decline in 'per capita' resource availability, while if 'b >> 1', there is a rapid decrease in 'per capita' resource availability as population density exceeds 1/a. These functions may be readily fitted to data for long-term population studies. Their application will be demonstrated by an analysis of the two sets of data described above and for data on two populations of Avocets (Recurvirostra avosetta).

Hill (1988) has reconstructed the demographic history of two populations of Avocets from records kept by the Royal Society for

Protection of Birds. This species is one of the rarest breeding birds in Great Britain; both populations studied by Hill have only established in the last forty years and both breed exclusively in loose colonies on two nature reserves in Eastern England (Fig 6). The species has been a classic "flagship" species for conservation efforts throughout Britain.

Analyses of long term sets of this type of data may be given considerable focus if a simple population model is used as a basis for understanding the dynamics of the population. A model suitable for most bird species would take the general form

$$N_{t+1} = sN_t + s^a N_{t-a+1} E f(N_{t-a+1}) \quad (2).$$

Here N_i is the population size in year 'i', s is the survival of adult birds, E is the number of eggs laid per season, a is the age of first reproduction and $f(N_{t-a+1})$ is a recruitment function such as Eqn 1. If independent estimates are available for adult survival and clutch size, equation 2 can be rearranged to give an expression which allows a linear estimate to be made of the two parameters in the recruitment function. In the simplest case where birds reproduce for the first time at age one, per capita recruitment, R_t , is given by

$$\log(R_t) = \log\left(\frac{ESN_t}{N_{t+1} - sN_t} - 1\right) = b \log N_t + b \log a \quad (3).$$

Thus estimates of "a" and "b" may be obtained from a linear regression of $\log R_t$ on $\log N_t$. The parameter estimates obtained in this way can then be used to plot the recruitment functions for four of the bird populations discussed above (Figure 7).

This exercise reveals a number of important points about detecting relationships between population size and recruitment. In all the studies, increases in population size lead to decreases in recruitment. However, the avocet populations provide a clearer relationship between population size and recruitment than the sparrowhawk and tawny owl data. This is primarily because the data for the avocets have been collected over a wide range of population densities. In contrast, the sparrowhawk and tawny owl populations are relatively constant, but small stochastic variations, due to climatic variations between years, have a detrimental effect on parameter estimation (see the original papers for detailed analyses of the effects of weather on demography). This is an example of a problem that occurs widely in fisheries management; although the main goal of management is to maintain stock, and hence yield, at a constant density, the best information about how to do this comes from examining recruitment to the population at a range of densities! Similar problems arise in other ecological studies where many standard tests fail to detect population regulation by either examining a population over too narrow a range of densities, or over too short a time span. A recent review by Hassell, Latto &

May (1989) comprehensively demonstrates that the probability of detecting density dependent regulation increases rapidly with the number of generations over which the population is studied. Although the ultimate goal of many population analysis is to unravel the role that behavioural mechanisms and resource limitation play in determining rates of recruitment, when considering population viability, it is also important to examine the role that climate and environmental changes play in determining density independent rates of survival and fecundity.

Allee effects in metapopulation and social structure models.

In populations that have been reduced to low densities it is also possible that individuals have increasing difficulty in locating potential mates. Similar effects occur in many colonial bird species, where hormone levels may be tied to a threshold population size (Collias & Collias, 1984). These effects will give rise to inverse density-dependence or "depensatory recruitment" (Allee 1931, Lande 1987, Dobson & Lyles 1989). African elephant (*Loxodonta africana*) populations provide a classic example of this type of effect; because of differences in the age of sexual maturity of male and female elephants, the sex-ratio of breeding adults in any population is skewed towards females (Moss 1983). In heavily poached populations, the resultant decline in survival leads to significant disparities in the operational sex ratio (Table 1). The skewed sex-ratio may be further exasperated by poachers tending to favor the more

solitary, larger tusked males (Pilgrim & Western 1986). The reductions in life expectancy also lead to younger, less experienced males and females attempting to breed. The rutting or 'musth' periods of young male elephants are short and sporadic, while those of a forty year, and older, males are regular and prolonged (Poole 1987). Female elephants are much more receptive to mature musth bulls, but tend to either run or struggle when approached or mounted by an immature musth male (Moss 1983, Poole 1989). In heavily poached populations this could lead to a considerable reduction in the number of times a female is successfully mated (Poole and Dobson, in prep).

The population dynamic consequences of the variety of behavioral mechanisms that lead to reductions in female fertility as populations decline may be examined using models originally derived for parasitic helminths (May 1977) and sperm whales (May & Beddington (1980). These functions have the opposite effect to those described above (Eqn 1); at low population densities, the probability of finding a mate approaches zero, and as population size increases the function approaches unity (Figure 8). A simple function that incorporates the sex-ratio of a population, m , the average level of male promiscuity, p , and the duration of female receptiveness, τ , takes the form;

$$f(N) = \left(1 - e^{-\left(\frac{N}{T} \left(\frac{\rho m}{1 + \rho m} \right) \right)^\tau} \right) \quad (4)$$

The function assumes promiscuous matings within groups of a population that is sub-divided into groups of random size. As population size declines, or as the population is fragmented into smaller groups, a smaller proportion of females are mated. More complicated functions may be used where the species exhibits either monogamy or more aggregated or regular social group sizes (Anderson 1982; Dobson & Lyles 1989; May 1980). Inclusion of compensatory functions in simple demographic models produces a deterministic threshold or breakpoint below which the population will collapse to extinction.

Table 2 illustrates how variations in different social behaviors effect the magnitude of these thresholds. An analysis of these models suggests that populations of species with monogamous, solitary habits will tend to collapse at higher population densities than more promiscuous gregarious species. Lande (1987) has derived similar functions for territorial species which show similar breakpoints between positive and negative population growth. The presence of these thresholds is important for a number of reasons in conservation studies: not only do they determine the size at which a fragmented or over-exploited population will collapse to extinction, they also determine the minimum size of a population for potential reintroductions.

All of these factors are likely to be important in elephant populations (Poole and Dobson, in prep). The social system of elephants is also dependent upon the presence of older matriarchal females and their collective 'cultural' knowledge of where water and food resources may be found in times of drought. This 'pool of knowledge' is considerably reduced in poached populations of elephants where life expectancy, and thus acquired knowledge, may be considerably reduced. Inclusion of subtle social behaviors into models for viable population analyses presents a further challenge to both wildlife managers and conservation biologists.

Non-vertebrate populations and plants.

The majority of population viability analyses undertaken to date have tended to emphasize large vertebrate species (see Soule 1987). The main scientific justification for this approach argues that larger species require larger areas and by protecting these species we preserve sufficient habitat for the multitudes of species with more restricted area requirements. Nevertheless, it is important that population viability analyses be developed for both invertebrates and plants, particularly as these organisms may be "keystone species" crucial to the viability of the whole ecosystem. An excellent example of this type of analysis comes from the work of Southwood and his colleagues (Southwood, Hassell & Reader 1989) on the dynamics of three populations of *Viburnum* white fly (*Aleurotrachelus jelineckii*) on

isolated bushes at the edge of the species natural range. Hutching (1988) has performed similar viability analyses on an endangered species of British orchid. The techniques used in both these analyses are analogous to those described above for Sparrowhawk, Tawny Owl and Avocet. Unfortunately, there are very few other long term studies of rare invertebrates and endangered plant species; for most of these species we have little or no data. In part this reflects both the diversity of these groups of organisms and the relatively low intensity with which they are studied relative to the vertebrates. An analysis of the relative research effort into different taxa suggests that the intensity of research effort declines rapidly as we move from the charismatic mega-vertebrates to the spiny or squirmy invertebrates (Table 3).

Taxonomic variation in demographic rates.

How then might we assess the viability of populations of potentially endangered species for which we have only limited information? One approach is to review data for related species and attempt to quantify systematic trends in the way that key life history variables change with more readily quantifiable characteristics such as body size. Harvey & Pagel (1988, 1990) recently reviewed and generalized comparative methods that can be used to unravel the ways that quantitative phenotypic traits respond to potential selective forces. These techniques might be used to provide 'null estimates' of demographic parameters for

species for which we only have basic morphometric data. For example, nested analysis of variance may be used to examine how different life history traits vary at different taxonomic levels (Harvey & Clutton-Brock, 1984). Figure 9 illustrates the result of such an analysis using data for primates (Clutton-Brock & Harvey, 1986) and carnivores (Gittleman, 1986). The analysis suggests that variability in age at first reproduction, inter-birth interval, litter size and life expectancy is low between closely related species of primates, significant variation only appears at the subfamily level. In carnivores, more variation is present at lower taxonomic levels, but most variation still occurs between higher taxonomic units.

Simple models and management guidelines.

Further examination of the systematic variation in life history attributes between members of the same taxon indicate alternative time scales on which to collect data or undertake demographic analyses. For example, age at first reproduction seems to vary remarkably uniformly with inter-birth interval for most primate sub-families (Fig 10). This suggests that demographic analyses for primate species for which only limited data are available might be rescaled to a time scale determined by the inter-birth interval of the species (Dobson & Lyles 1989). This demographic simplification allows simple rules to be established for ascertaining the relative health of a population. In the primate case, models based on general assumptions about

age at first reproduction and inter-birth interval suggest that primate populations will collapse when adult survival is less than approximately 70% per inter-birth-interval (Dobson & Lyles 1989). In situations where the population has had time to attain a stable age distribution this is roughly equivalent to a population in which 50 percent of the population is immature. This figure corresponds closely to that observed in Harcourt et al's (1981) analysis of Gorilla demography, here declining populations were characterized by ratios of immatures to adults of less than unity.

Conclusions.

Significant differences occur in the type of management and monitoring techniques that are employed as we move from captive to free-living populations of endangered species. In wild populations, birth rates and juvenile mortality are often a function of density and prevailing climate conditions, in captive populations they are primarily a function of husbandry. Viability analyses should move from an emphasis on genetics, nutrition and husbandry in small captive populations, to a greater emphasis on demography and community interactions in free-living populations. When data are severely restricted, as is often the case for endangered species, it may be possible to make sensible extrapolations from studies of related species.

It is particularly important to bear in mind that non-linear effects, due to interactions between resource availability, foraging activity and social behavior, will often have profound effects on the dynamics of animal populations. As most human interference involves either reducing habitat or changing resource distributions, a fuller understanding of how resource distributions affect social behavior, and thus recruitment and demography in different species, is fundamental to an assessment of the viability of any animal or plant species. The mandate of any species management plan should not be restricted to conservation of the habitat used by the species, but should also aim to increase the quantity and quality of information with which to manage the species efficiently. Ultimately, management strategies and population viability analyses for endangered and threatened species have to be based upon sound ecological techniques.

More specifically, as viability models are developed for free-living populations, it will become increasingly important to attempt to find a balance between deterministic non-linear models which include information on the interaction between the species habitat and its social system (May & Beddington, 1970; Lande 1988; Dobson & Lyles 1989), and stochastic linear models, which assume time to extinction is largely a function of population size and the observed vital rates (Goodman 1987; Mode & Jacobson 1987a,b; Lande & Orzack 1988). Because all population models

that include some aspects of the social system have the propensity to collapse to extinction, genetic models for population viability should also begin to consider the deterministic effects of social organization on rates of gene loss. The threshold effects that cause populations to collapse when social systems are disrupted are also likely to cause non-linearly accelerating rates of loss of rare alleles particularly in fragmented populations.

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TABLE 1.

Population	Female (%)	Male (%)
<u>Relatively unpoached</u>		
Amboseli (Kenya)	77.9	22.1
<u>Poached</u>		
Tsavo East (Kenya)	95.0	5.0
Tsavo West (Kenya)	96.2	3.8
Mikumi (Tanzania)	99.6	0.4
Queen Elizabeth (Uganda)	98.7	1.3

Table 1. The sex-ratio of breeding adult elephants (taken as females ≥ 10 and males ≥ 25 years old) in one relatively unpoached and several poached populations (Poole & Thomsen, 1989).

TABLE 2.

Demographic parameters affected by perturbation	s	i	F	a	T	δ	k	b	K	N ⁺	N _r
Habitat destruction	?	?	?	?	?	?	?	?	-	--	??
Habitat fragmentation	?	?	?	?	+	+	?	?	-	--	++
Inclement weather	-	-	-	+	0	+	0	?	?	??	++
Reduction in food supply	-	-	-	+	?	0	?	+	-	--	++
Increased aggression	-	-	-	+	+	?	+	+	0	--	++
Loss of shelter	-	-	-	+	+	?	+	+	0	--	++
Increase in predators	-	-	-	?	-	?	-	?	?	-?	-?
Infectious diseases	-	-	-	?	?	?	+	?	?	-?	+?
Human disturbance & encroachment	-	-	-	?	?	?	?	?	-	-	??

Table 2. This table lists the qualitative effects of different classes of perturbation on the linear and non-linear demographic parameters (after Dobson & Lyles 1989).

TABLE 3.

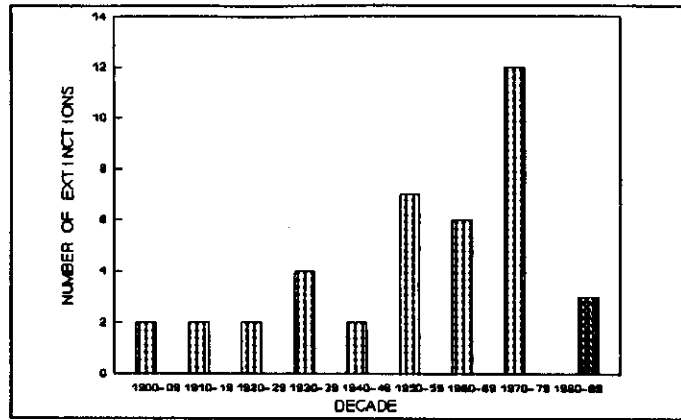
Phylum Subphylum Class Order	Average number of papers per year.	Approx. number of recorded species.	Papers per species / year.
Protozoa	3,900 (10)	70,000	0.05
Porifera	190 (22)	10,000	0.02
Coelentera	740 (12)	10,000	0.07
Echinodermata	710 (15)	6,000	0.12
Nematoda	1,900 (1)	1,000,000	0.002
Annelida	840 (9)	15,000	0.06
Brachiopoda	220 (14)	350	0.63
Bryozoa	160 (15)	4,000	0.04
Entoprocta	7 (53)	150	0.04
Mollusca	4,200 (8)	50,000	0.08
Arthropoda			
Crustacea	3,300 (9)	39,000	0.09
Chelicerata			
Arachnida	2,000 (6)	63,000	0.03
Uniramia			

Insecta	17,000 (7)	1,000,000	0.02
Coleoptera	2,900 (6)	300,000	0.01
Diptera	3,200 (7)	85,000	0.04
Lepidoptera	3,500 (9)	110,000	0.03
Hymenoptera	2,200 (9)	110,000	0.02
Hemiptera	1,700 (7)	40,000	0.04
Chordata			
Vertebrata			
Pisces	7,000 (13)	19,000	0.37
Amphibia	1,300 (12)	2,800	0.47
Reptilia	2,400 (7)	6,000	0.41
Aves	9,000 (10)	9,000	1.00
Mammalia	8,100 (12)	4,500	1.80
<u>Mammalian Orders</u>			
Monotremata	20	3	6.8
Marsupialia	269	266	1.0
Insectivora	270	345	0.8
Dermoptera	2.2	2	1.1
Chiroptera	402	951	0.4

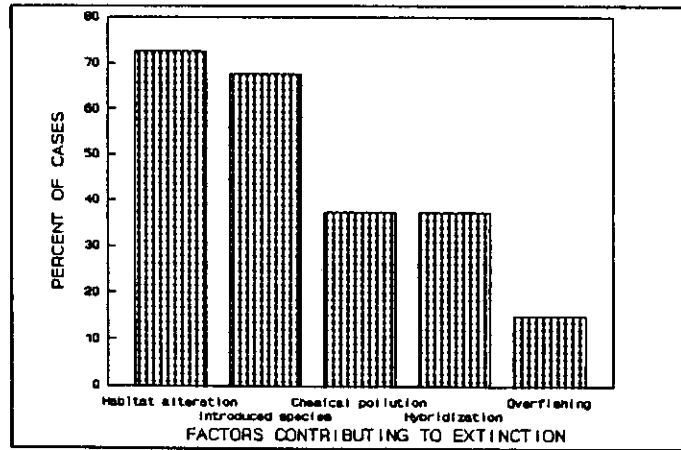
Primates	956	181	5.3
Edentata	38	29	1.3
Pholidota	5	7	0.7
Lagomorpha	173	58	3.0
Rodentia	1,538	1,702	0.9
Cetacea	360	76	4.8
Carnivora	1,157	231	5.0
Tubulidentata	2.7	1	2.7
Proboscidea	94	2	47.0
Hyracoidea	12	11	1.0
Sirenia	43	4	10.8
Perissodactyla	142	16	8.9
Artiodactyla	1,124	187	6.0
Pinnipedia	218	33	6.6

Table 3. A rough indication of the relative research effort devoted to animals from different taxonomic groups. The data are provided by the average number of papers listed in the Zoological Record, 1978 through 1987 (after Dobson, Lyles and Merenlender in May, 1988).

FIGURES FOR FRONT ROYAL MANUSCRIPT.

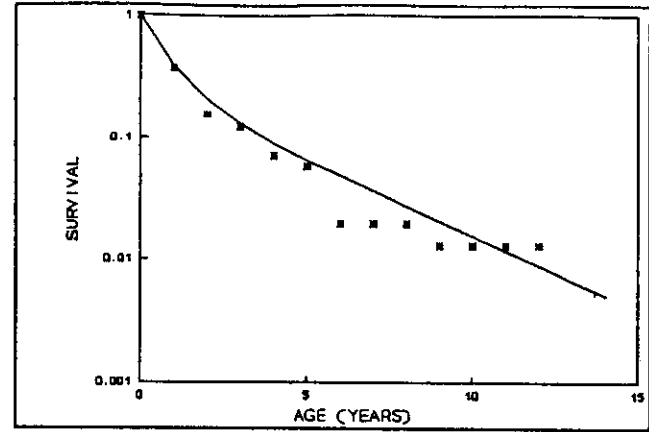


(a)

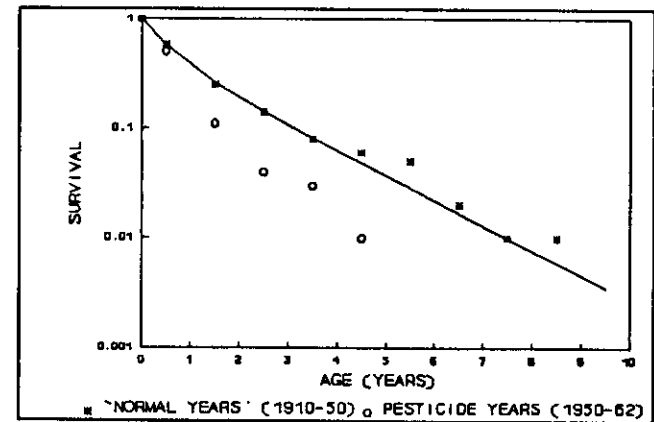


(b)

Figure 1. (a) The numbers of extinctions occurring in the North American fish fauna in the different decades of this century. The data for 1980-89 are provisional. (b) Different factors which contributed significantly to each of the above extinctions. The histogram totals sum to more than the total number of extinctions as in many cases more than one factor contributed to a species extinction (Miller, Williams & Williams, 1989).

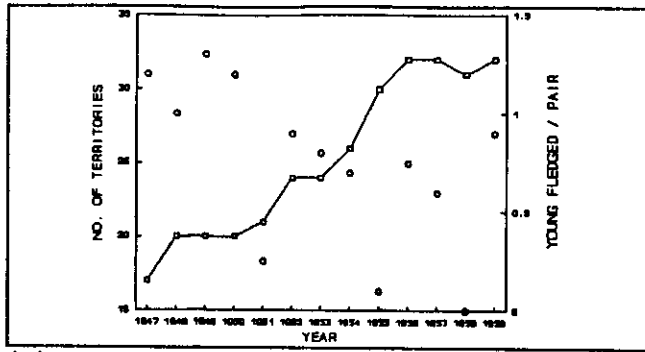


(a)

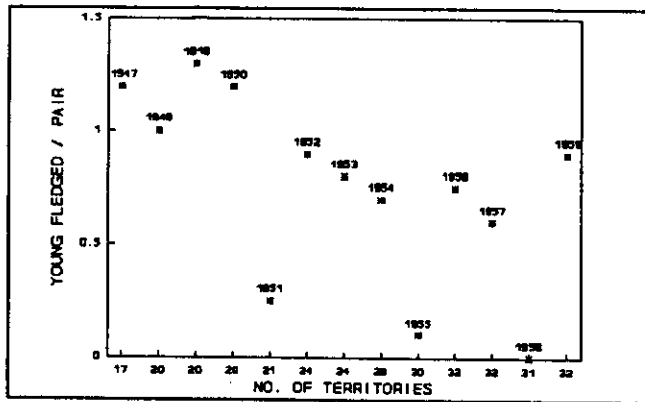


(b)

Figure 2. Siler functions fitted to the ringing (or banding) data collected from Tawny Owls and Sparrowhawks ringed as nestlings and recovered as dead birds (after Dobson 1982, 1985). In both cases a mortality function of the form $\mu(t) = a \exp(-bt) + c$ has been fitted to the instantaneous mortality rate data. Parameter estimates for (a) Tawny Owl are $a=0.91$, $b=0.66$ and $c=0.28$; for (b) Sparrowhawk $a=0.77$, $b=1.1$ and $c=0.52$. The survival curve illustrated is given by function $N(t) = N(0) \exp(a/b (\exp(-bt) - 1) - ct)$. The data in the sparrowhawk curves in the lower figure compare the observed data for the years 1910-50 with the data for 1951-62, a period when organochloride pesticides were widely used.



(a)



(b)

Figure 3. (a) The population size of Tawny Owls in Wytham Wood, Oxford (solid line) and the number of chicks fledged per territory in each year (open circles). (b) The relationship between population size and per capita fledging success in each year of the study (after Southern 1970).

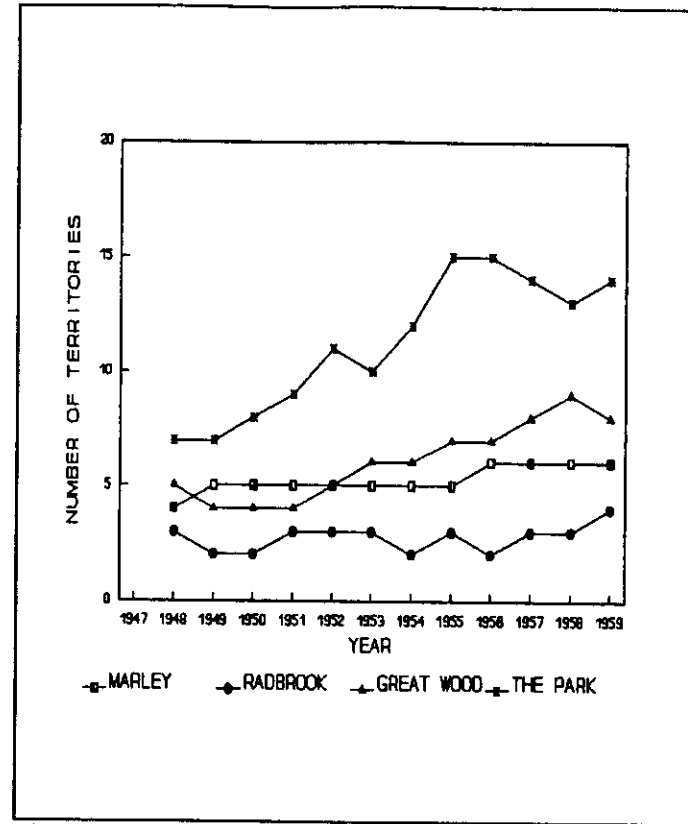
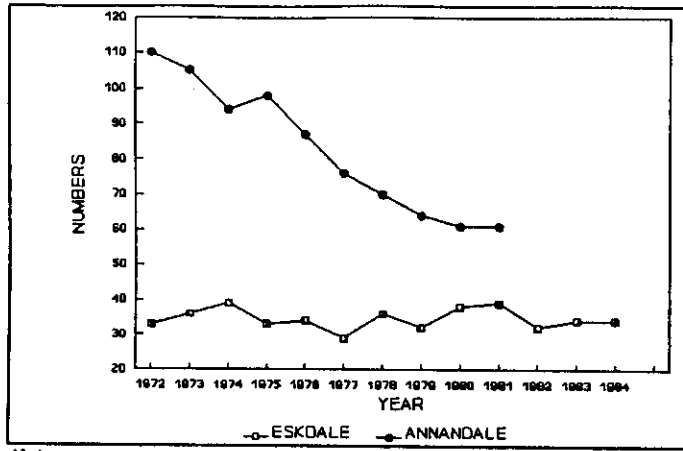
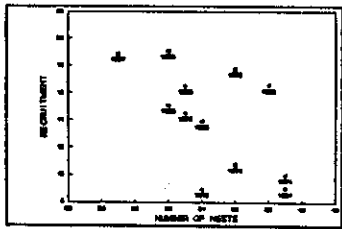


Figure 3.

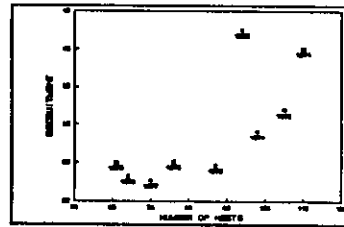
Figure 4. The numbers of of Tawny owls breeding in different sections of Wytham wood (after Southern 1970).



(b)

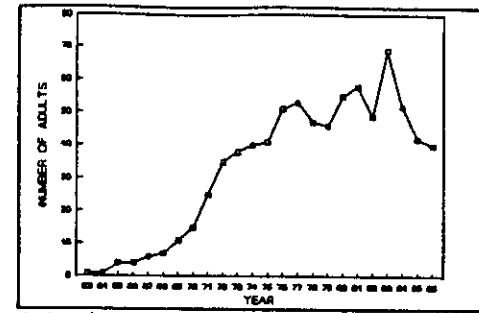


(b)

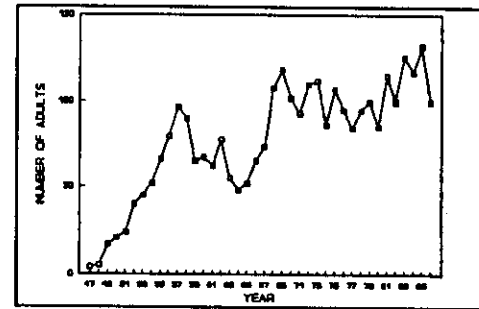


(c)

Figure 5. (a) The numbers of Sparrowhawks breeding in the Eskdale and Annandale study areas of Southern Scotland. The relationship between population size and immigration recruitment into the population for each study site (b) Eskdale, (c) Annandale (after Newton & Marquiss, 1986).



(a) Minsmere



(b) Havergate Island

Figure 6. The size of the Avocet populations at the Minsmere and Havergate Island nature reserves in Suffolk, England. Both colonies have been monitored since their establishment and managed by the Royal Society for Protection of Birds to improve habitat and reduce the impact of predators (after Hill, 1988). The impact of predators is particularly noticeable at Havergate Island where the numbers of gulls increased between 1957 and 1965; they were then culled and the Avocet population recovered.

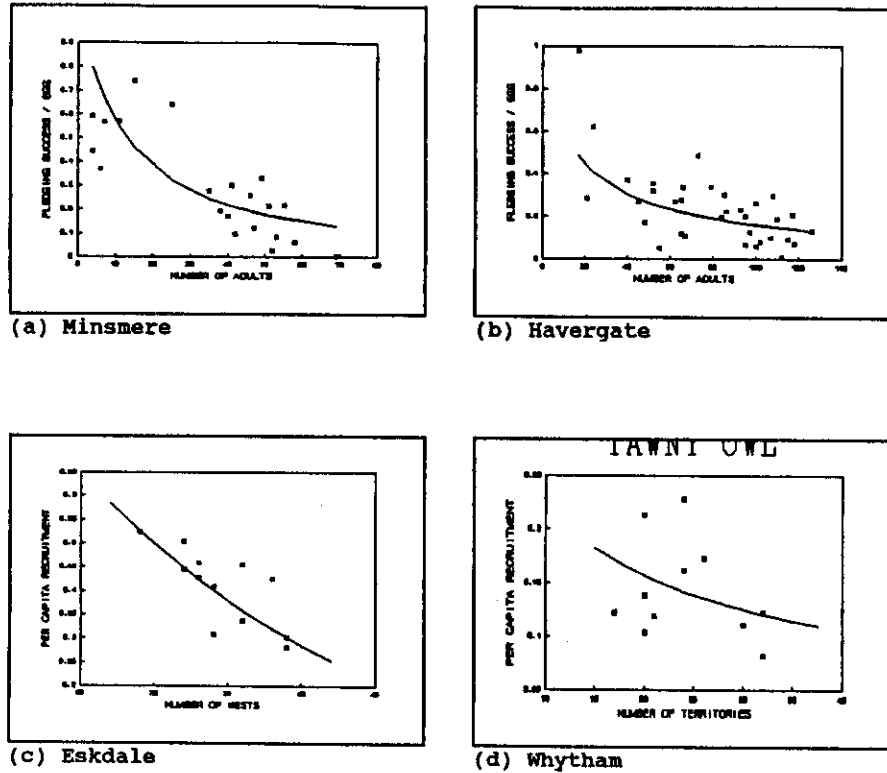


Figure 7. The relationship between recruitment and population size for (a,b) Hill's (1988) study of the Avocets (c) Newton & Marquiss's (1986) study of the Sparrowhawks and Southern's (1970) Tawny Owl study. In all cases the solid squares are observed numbers of adults entering the breeding population ($N_t - sN_{t-1}$), the dashed line is the best fit to Sheperd's recruitment function (Eqn 1). In the Avocet case $a = 1/13$ and $b = 1.2$ for Minsmere and $a = 1/16$ and $b = 0.9$ for Havergate; the data for years of high predator density (1957-65) were excluded in analyzing the Havergate data. In the Eskdale Sparrowhawks $a = 1/30$ and $b = 3.2$; no model was fitted to the data for Annandale as changes in habitat quality violate the assumptions of the model. Parameter values for the Tawny Owls in Whytham wood are $a = 1/1.5$ and $b = 0.65$.

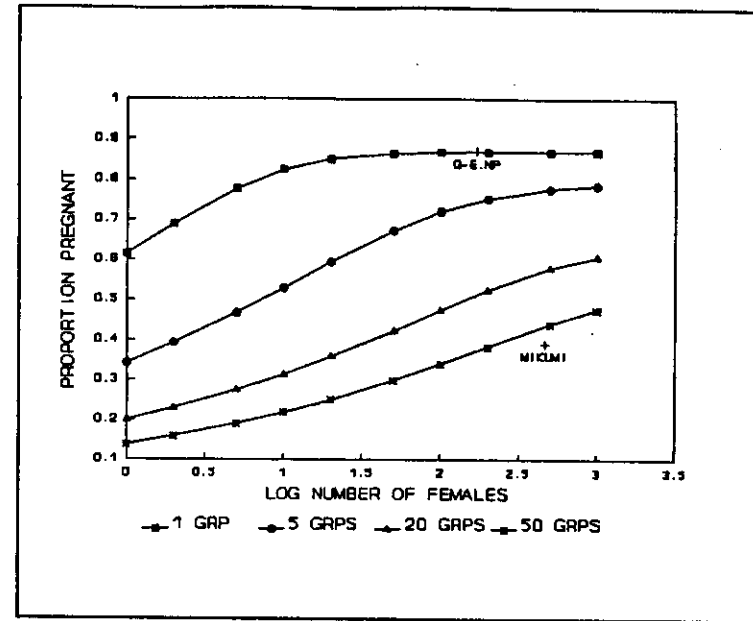
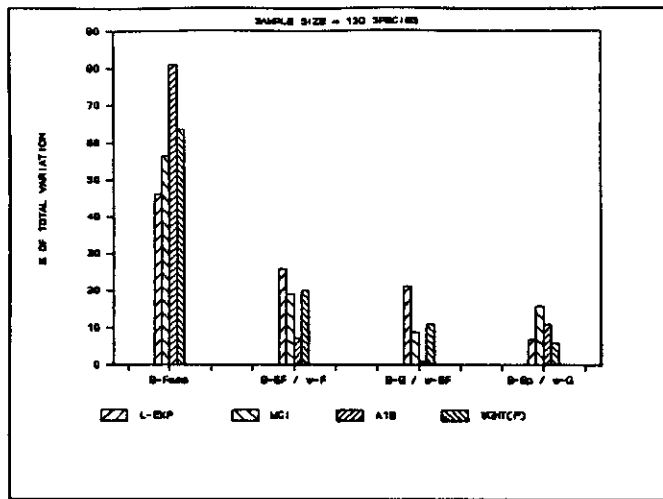
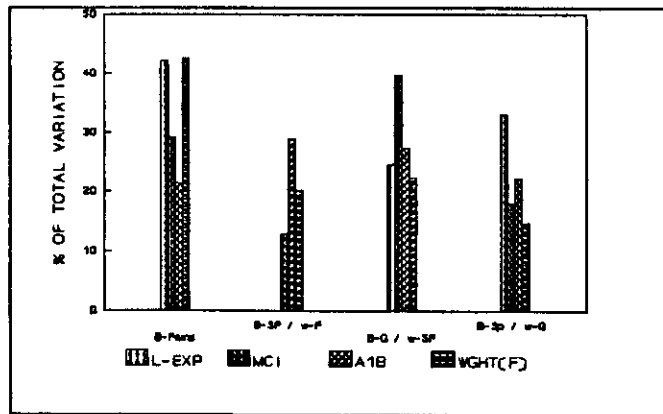


Figure 8. The influence of population size and group fragmentation on the mating probability for female elephants living in 2,5,10 and 50 groups. The model roughly conforms to data for elephant populations (after Poole & Dobson, in prep). It assumes that only five males are present in the population and that each male guards a female for 2 days during her period of peak oestrous. The females come into oestrous five times per inter-birth interval. The observed data for Queen Elizabeth Park, Uganda and Mikumi National Park, Tanzania are included for comparison (Poole 1989).



(A) PRIMATES



(B) CARNIVORES

Figure 9. Taxonomic variation in life history attributes of fundamental demographic importance for (a) 112 primates (after Clutton-Brock & Harvey, 1986) and (b) 130 carnivores (after Gittleman, 1986). In each case nested analysis of variance were performed on data collated in large surveys of these orders. The analysis partitions the variance in each order into that occurring between species within the same genera, between genera within subfamilies, between sub-families within families and between families.

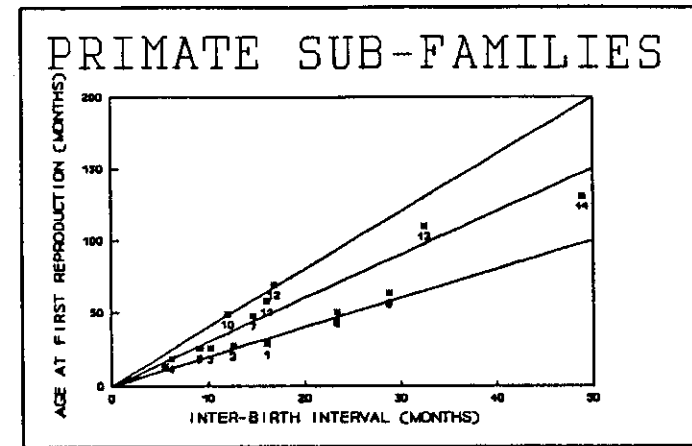


Figure 10. The relationship between age at first reproduction and inter-birth interval for primate sub-families (after Lyles and Dobson, 1988). The lines have slopes 2,3, and 4; the middle line (slope 3) is indistinguishable from the best fit major axis regression constrained to pass through zero.