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Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms

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We argue that a relationship between life history variation and population processes may form the foundation for developing a theory for variation in population growth rate. An examination of the distribution of 104 European bird species in relation to their clutch size and adult survival rate showed three different clusters. First, there is a large group of species which lay a large number of eggs and have low adult survival rate. The second cluster consists of species with very high survival rates and a clutch size of only one egg. The third group is characterized by species with high survival rates but still a relatively large clutch size. From these clusters of life history characteristics we argue that the species can be classified according to the quality of their survival and breeding habitats, respectively. *The high-reproductive species* live in favourable breeding habitats, but poor survival habitat. In contrast, the survival habitat of *the survivorship species* are very good, but the breeding habitats are poor. *The bet-hedging species* live in favourable breeding and survival habitats, but the annual variation in the quality of the breeding habitats is very large, favouring the evolution of a larger clutch size than in the survivorship species.

In order to examine the effects of these patterns of covariation between life history traits on population dynamics we calculated the sensitivity and elasticity of population growth rate to a change in age-specific fecundity or mortality rates for one species from each of the three life history types. These analyses showed that population growth rates of high-reproductive species were more sensitive and elastic to changes in the fecundity among the younger age-classes, compared to the species from the two other groups. Furthermore, elasticity to variation in mortality rates was higher than to variation in fecundity rates in all three species.

To provide a further link between life history variation and population dynamics the results from key-factor analyses of population fluctuations in birds and mammals were reviewed. In most altricial birds, the key-factor appears during the non-breeding season. In contrast, in precocial birds key-factors from the breeding season explained a higher proportion of the variance in the total losses than the losses during the non-breeding season. In the majority of the cases density-dependence was found in the losses during the non-breeding season.

According to the Allee-effect, we would expect that the population growth rate should decrease with density at low population sizes. No evidence was found for the presence of an Allee-effect in the studies of 11 bird species which were reduced to very low population levels during the study period. We suggest however that such an Allee-effect still may be important due to a reduction in the defence efficiency among predators or parasites, reduction in mating efficiency, or reduction in the foraging efficiency at low population densities.

These results may have some important implications for overall priorities in the development of strategies for conserving species diversity. In particular, we focus on the securing of survival habitats for especially longlived species outside the breeding season.

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Conservation biology became established as a scientific discipline in the 1970's with the publication of papers by e.g. Frankel (1974), Diamond (1975) and Wilson and Willis (1975) and books by Soulé and Wilcox (1980) and Frankel and Soulé (1981). It rapidly became popular as it was soon evident that it provided general baseline principles for the conservation of biodiversity. One such principle, the "50/500 rule" stated that a minimum of 50 effective individuals are necessary for securing short-term survival, and that a population size of 500 will prevent a reduction in the amount of heritable variation in the population. This principle was easily grasped by managers and was soon included into several management plans (Simberloff 1988). However, some of these initial principles were later greatly revised. For instance, Lande (1995) argued forcefully that the effective population size should be 5000 rather than 500 individuals in order to maintain the adaptive potential in quantitative characters in balance between mutation and random genetic drift.

Although they can often be very controversial, successful scientific contributions to the solution of the biodiversity crisis are likely to depend on the ability of conservation biologists to further present such general principles. Such principles can be used by decision-makers to put money and effort into management rules which will make the greatest contributions toward conserving biodiversity. In this paper, we assume that successful conservation of biodiversity will depend on the ability of politicians and managers to make the correct overall priorities at a very high level. More specifically, we argue that a broader understanding of the relationship between life history patterns and population processes may facilitate the development of some more general principles through which managers can direct their efforts.

Recently, Caughley (1994) contrasted two approaches in conservation biology: the small-population and the declining-population paradigms. The small-population paradigm raised in the early 1980's (Soulé and Wilcox 1980, Frankel and Soulé 1981, Shaffer 1981) dealt with the consequences for populations occurring in small numbers. Theoretical analyses were made of factors likely to influence the chances of extinction of a small population (e.g. inbreeding depression, demographic stochasticity). A lucid summary of this early theoretical development is found in Soulé (1987). However, Caughley (1994) argued that a lot of these early theoretical models were based on unrealistic assumptions and parameters which were almost impossible to estimate from field data (see also Simberloff 1988). In contrast, the declining-population paradigm is strongly empirically founded, but lacking a theoretical framework. It focuses on why populations are declining and how to reverse this trend.

Although we agree with Caughley's (1994) general conclusions of the current status of conservation biology, we are sceptical of his emphasis on the difference between the two research traditions. We view the two approaches as complementary rather than contrasting. As pointed out by Lawton (1995), the small-population paradigm can be considered to mainly deal with the proximate causes for populations going extinct even when protected. In contrast, the declining-population paradigm considers ultimate reasons for some species becoming rarer than others at the outset. Obviously, these different focuses are not mutually exclusive; the same factors influencing the degree of rarity of a species may also affect its chances of extinction (cf. Gaston 1994). The integration of the two research traditions has, however, been difficult mainly for two reasons: (1) Theorists have dealt with models which are either based on biologically unrealistic assumptions, or which include parameters that are impossible to estimate with data collected in the field. (2) Empiricists often do not collect (or publish) the relevant data. For instance, in studies of the dynamics of small populations, data on single individuals (and not only population means) are of profound importance. In contrasting the two paradigms, there is a danger that communication and interaction between theorists and empiricists may be made more difficult (cf. Greenwood 1995).

Our aim in this paper is to contribute to the unifying of the two research traditions in conservation biology. We will focus on the development of overall conservation strategies for vertebrates in relation to their life history characteristics. Our emphasis will be on population processes. Theoretical analyses of time to extinction using stochastic population models (Leigh 1981, Goodman 1987, Lande and Orzack 1988, Lande 1993) show that conserving viable populations in the future will depend on both securing a mean population growth rate $\bar{\lambda} \geq 1$ (the declining-population paradigm) as well as having large enough populations to reduce the effects of stochasticity on the risk of extinction (the small-population paradigm). The understanding of the population processes emphasised in the present paper will hopefully provide us with information that can be useful for management actions. As forcefully pointed out by Boyce (1992) and Caughley (1994), we have little knowledge about the actual values of parameters (e.g. demographic and environmental variances) used in stochastic models. Similarly, our knowledge about the most important environmental factors causing variation in the population growth rate λ is limited. We will argue that knowledge of differences in basic population processes, for instance in relation to species-specific life history characteristics, may provide a foundation for a more general theory in conservation biology. Thus, we will try to extend the pioneering approach by Dobson and Lyles (1989) in their development of principles for the management of primates.

One of the main paradigms in behavioural ecology is that individual variation exists, and that this variation may affect the reproductive success and the probability of survival of different individuals. Thus, a central focus of behavioural ecology is to develop models to understand this individual variation. The mechanisms of individual variation are likely to provide a foundation for a causal understanding of why populations are changing, and, in particular, for the variances in demographic parameters.

Life history categories in birds

Comparative studies of vertebrates have documented a strong pattern of covariation in life history variables across species (Sæther 1987, 1988, Harvey et al. 1989, Promislow and Harvey 1990, Shine and Charnov 1992, Charnov 1993). In general, variation in adult survival rate can explain a high proportion of the differences in several reproductive traits, leading to robust, often invariant, relationships between different life history variables. At one extreme of a slow-fast continuum are species that mature early and produce a large number of offspring during a short period of time. On the other end are species with delayed maturity and a low reproductive output, well exemplified by the mammalian megaherbivores (Owen-Smith 1988) and procellariform seabirds (Croxall and Rothery 1991). In this section, we relate these patterns to differences in population processes, relying heavily on patterns derived from bird studies. We suggest that population regulatory mechanisms will differ in relation to life history characteristics.

Due to the enormous work of amateur ornithologists, data are available on many life-history characteristics of a large number of European birds (Sæther 1987, 1989). Consider the distribution of two important life history characteristics (clutch size and adult survival rate p) among 104 of those species. We see from Fig. 1 that many species have either a high survival rate and a small clutch size, or a low adult survival rate and a large clutch size. Nevertheless, some species have a relative large clutch size even though they have a relative high survival rate (e.g. $p > 0.7$).

In order to relate this pattern of life history variation to population dynamics, we compute the sensitivity (s_{ij}) and the elastisticity (e_{ij}) of the eigenvalues of the population projection matrix **A** to small changes in the matrix element a_{ij}. According to de Kroon et al. (1986)

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \qquad (1)$$

and

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} \qquad (2)$$

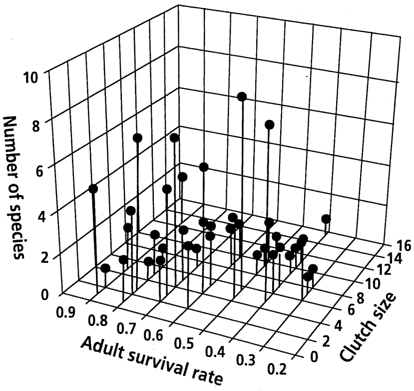

Fig. 1. The distribution of 104 European bird species in relation to adult survival rate and clutch size. The data is taken from Sæther (1987, 1989).

where s_{ij} denotes the effects of a change in the matrix element a_{ij} on the population growth rate λ, and e_{ij} gives the proportional change in λ resulting from a proportional change in a_{ij}. Thus, each e_{ij} gives the relative contribution of its a_{ij} to λ.

In Fig. 2 we present s_{ij} and e_{ij} values for three bird species, which represent the different clusters of life histories identified in Fig. 1. Three points can be made from these graphs: (1) As expected (Caswell 1989: 123), in younger age classes λ is more sensitive to a change in survival than in fecundity (Fig. 2a,b). (2) The sensitivity and elasticity of λ to a change in fecundity in the younger age classes decrease with adult survival rate. (3) The greatest elasticity of λ to a change in adult survival rate is found in the two most long-lived species. In contrast, a similar relative change in survival

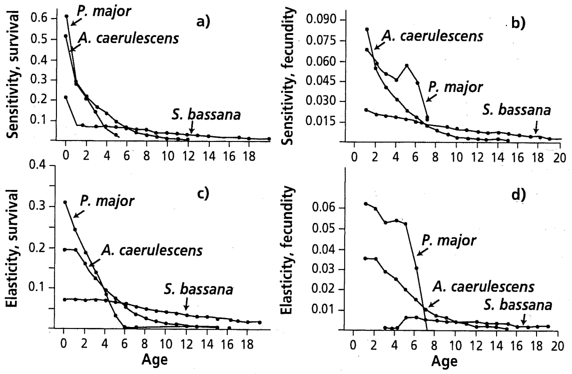

Fig. 2. The sensitivity (a, b) and elasticity (c, d) of the population growth rate λ to variation in age specific survival rate and fecundity rate of the great tit *Parus major* (McCleery and Perrins 1988, with a juvenile survival rate $P_0 = 0.22$ (Bulmer and Perrins 1973)), the lesser snow geese *Anser caerulescens* (from Figs 7.3 and 7.4 in Cooke et al. 1995, with $P_0 = 0.424$ and $P_1 = 0.756$) and the gannet *Sula bassana* (from Table 18 in Nelson 1978).

rate in the youngest age classes has the greatest relative impact on λ in the short-lived great tit *Parus major*.

The patterns in Figs 1 and 2 can be used as a basis for a qualitative characterisation of different life history types. We follow the approach of Sibly and Calow (1985), and classify life histories according to differences in habitat quality at different life cycle stages. Our classification specifies habitat quality for the species as the suitability of habitats for breeding and survival. Thus, this is an elaboration and generalisation of a previous suggestion by Alerstam and Högstedt (1982). The first life history category consists of *high-reproductive species*, which are often small-sized, live in favourable breeding habitats and have a large reproductive output but whose mortality rates, particularly outside the breeding season, are high. We suggest that the population fluctuations are most influenced by annual fluctuations in mortality, particularly among juveniles during the non-breeding season (cf. Fig. 2). Opposite to the highly reproductive species on the slow-fast continuum are species which fall in the *survivorship* life history category. These are species characterised by high adult survival, delayed maturation and a low reproductive capacity, as exemplified by long-lived procellariform seabirds. Other species with high survival rates are those within the *bet-hedging* life history category. The reproductive output of these species is determined by stochastic variation in breeding conditions, such as large annual fluctuations in food resources (e.g. raptors), climate or predation rate. The difference between the later two life history categories, which both have a high adult survival rates, is that low availability or difficult access to resources prevent high reproductive output in the survivorship species. Several studies of long-lived seabirds have indicated that reproductive rate is sensitive to variation in the food provisioning rate (Croxall and Rothery 1991). Thus, even though the mean reproductive output across years may be similar in those two categories, the variance among years in the reproductive success will be larger among the bet-hedgers. They have therefore evolved a strategy with a large number of breeding attempts combined with a larger clutch size than in the survivor.

Two distinct types of life history strategies can further be recognised within the bet-hedgers. One is the capital breeders (Sibly and Calow 1986), i.e. precocial species that invest large amount of body mass in order to raise a large number of offspring as rapidly as possible. Such a strategy has probably evolved in order to minimize offspring predation risk (Erikstad et al. 1993, Tombre and Erikstad 1996). The other life history strategy found among the bet-hedgers is exemplified by waders and gulls, species with a high survival rate but still having a relative large clutch size. The relationship between the different life history categories is schematically presented in Fig. 3.

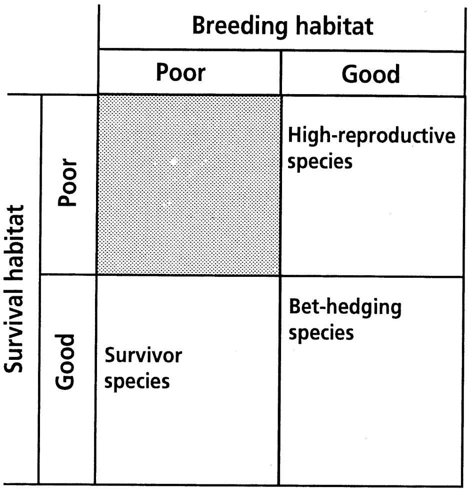

Fig. 3. Proposal for a classification of life history categories based on the quality of the habitats for breeding and survival.

Population processes in relation to life history categories

As pointed out by Green and Hirons (1991), a simple rule-of-thumb for conservation priorities based on results of sensitvity analyses is dangerous because large changes in some demographic parameters may be easier to obtain through management actions than small changes in others. Further, such an approach also ignores the feed-back relationship between demography and population processes. In order to relate these life history categories to differences in population processes we surveyed the literature for studies of key-factor analyses. This is a technique developed by Varley and Gradwell (1960, 1970), primarily for analyses of insect populations. Assuming discrete generations, the method interprets changes in a population as changes in mortality at different stages of the life cycle. The mortality during an interval (the k-factor) is expressed as the $\log_{10}$ of the ratio of the population size before and after the period that the mortality has occurred. The separate submortalities $k_1 \ldots k_n$ sum up to the total mortality, K. When the k-factors are plotted against time, the correlation between each of the k-factors and K identifies which k-factor explains the largest proportion of the variation in K and, then, accordingly, $\log(\bar{\lambda})$. The regression coefficient of the different k-factors on K gives the relative contribution of the submortalities to the total losses (Podoler and Rogers 1975). Furthermore, the relationship between the different k-factors and population density may also indicate at which life cycle stage population regulation (Sinclair 1989) is most likely to take place.

Unfortunately, key-factor analyses have been published for only a small number of vertebrate species. It is therefore not yet possible to relate interspecific differences in population processes as revealed by the results from key-factor analyses to life history type by means of appropriate comparative statistical methods (Harvey and Pagel 1991). However, the small data-set does indicate some patterns. Firstly, there seems to be a difference between precocial and altricial species in which stage of the season the key-factor appears (Fig. 4). In all but one precocial species the population fluctuations are correlated with variation in the losses during one part of the breeding season. The only exception is the willow grouse *Lagopus lagopus* (Podoler and Rogers 1975), where the critical period occurs during autumn when the birds that fail to establish territories disappear (Watson 1971). Also, in this species, variation in breeding success determines a large proportion of the variance in the total loss. In contrast, the opposite pattern is found in altricial birds. In this group, the variation in the total loss is with one exception best explained by differences in the number of individuals that disappear during the non-breeding season. The only exception is the tawny owl *Strix aluco* where the population fluctuations are closely correlated with the failure of the pairs to breed (Southern 1970). However, this factor was negatively correlated with losses in the non-breeding season (Podoler and Rogers 1975). Thus, the non-breeding season is of great importance for the population fluctuations also in this species.

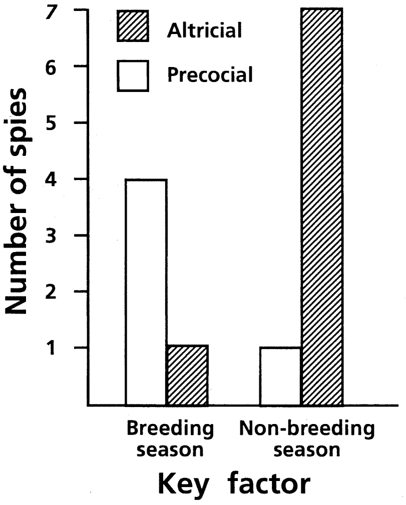

Fig. 4. A summary of the results of key-factor analyses of altricial and precocial bird species. The population fluctuations of a species is assumed to be dependent on conditions in the breeding season if the highest correlation coefficient was obtained between a k-factor from the breeding season and the total loss, *K*. Similarly, if the highest correlation coefficient with *K* was recorded between a k-factor from outside the breeding period, the population fluctuations were assumed to be most influenced by losses in the non-breeding season. The altricial species are: sparrow hawk *Accipiter nisus* (Newton 1988), tawny owl *Strix aluco* (Southern 1970, Podoler and Rogers 1975), little owl *Athene noctua* (Exo 1987), wood pigeon *Columba palumbus* (Dempster 1975, Murton and Westwood 1977), pied flycatcher *Ficedula hypoleuca* (Järvinen 1987), redstart *Phoenicurus phoenicurus* (Järvinen 1987), great tit *Parus major* (Krebs 1970, McCleery and Perrins 1985) and willow tit *Parus montanus* (Ekman 1984). The precocial species are: mallard *Anas platyrhynchos* (Hill 1984), grey partridge *Perdix perdix* (Blank et al. 1967, Podoler and Rogers 1975), willow grouse *Lagopus lagopus* (Watson 1971, Podoler and Rogers 1975), ptarmigan *Lagopus mutus* (Weeden and Theberge 1972) and avocet *Recurvirostra avocetta* (Hill 1988).

The second pattern indicated in this limited data-set of key-factor analyses is that density dependence is indeed present in most bird populations and that it mainly occurs outside the breeding season. In all of the 12 cases from the data-set presented in Fig. 4 where a significant relationship between a k-value and density was found, it occurred during the non-breeding season. In addition, in three species (willow tit *Parus montanus* (Ekman 1984), wood pigeon *Columba palumbus* (Dempster 1975) and grey partridge *Perdix perdix* (Blank et al. 1967)) density dependence was also recorded in losses during the breeding season. Similarly, a great majority (61%) of the bird studies reviewed by Sinclair (1989) showed density-dependence during the non-breeding season.

Few key-factor analyses have been made of mammalian populations. However, there are some evidence that there is a great similarity between the bird and mammalian results. For instance, in the African buffalo *Syncerus caffer* juvenile mortality was the key factor operating in a density-independent way, whereas the losses of adults increased significantly with population density (Sinclair 1977). In the red deer *Cervus elaphus elaphus* (Clutton-Brock et al. 1985), elk *Cervus elaphus canadensis* (Houston 1982) and Soay sheep *Ovis aries* (Clutton-Brock et al. 1991) density-dependent winter-losses were the key-factor. This supports Lack's (1954, 1966) original proposition that population fluctuations are determined by a combination of density-independent variation during the breeding season in fecundity and density-dependent mortality, often related to the amount of food (Sinclair 1989), acting outside the breeding season.

Demographic consequences of small population size: the Allee-effect

Smallness per se has a great influence on the viability of a population. Two factors may influence the risk of extinction of such a population. First, the population growth rate may decline at small densities, i.e. due to an Allee-effect. Second, the fluctuations in size of small populations will depend on the demographic and environmental variances, which are caused respectively by individual and temporal variation in birth and death rates (May 1973, Leigh 1981, Goodman 1987, Lande 1993). As pointed out by Caughley (1994), an evalua-

Table 1. The annual recruitment rate (R), fecundity rate (F) or clutch size (CS) in relation to population size (N) in studies where the minimum density was 15% or less of the maximum density recorded during the study period. The presence of an Allee-effect was tested by fitting a parabolic function $y = c + aN_x - bN_x^2$ to the data. The regression coefficients a and b indicate the shape of the regression curve (see text for details).

Species	Range of variation in N	Number of years	Variable	Parabolic shape			Author
				a	b	r^2	
Pheasant *Phasianus colchicus*	8–1325	6	R	−0.003	2.204	0.728	Einarsen (1945)
			F	−0.005	1.978	0.767	
Bobwhite quail *Colinus virginianus*	39–339	15	R	−0.010	2.115	0.224	Errington (1945)
			F	−0.014	2.139	0.774***	
Great tit *Parus major*[1]	14–172	17	R	−0.034	1.273	0.485*	Lack (1966)
			F	−0.041	1.196	0.603**	
			CS	−0.079	2.247	0.597**	
House sparrow *Passer domesticus*	3–31	15	R	−0.091	9.745	0.395	Kendeigh (1944)
Song sparrow *Melospiza melodia*	3–28	15	R	−0.056	1.865	0.367	Kendeigh (1944)
House wren *Troglodytes aedon*	3–29	26	R	−0.075	0.001	0.537***	Kendeigh (1944)
			F	−0.098	0.002	0.401*	
Blue jay *Cyanocitta cristata*	1–10	14	R	−0.384	0.024	0.038	Kendeigh (1944)
American crow *Corvus brachyrhynchos*	2–20	14	R	−1.024	0.034	0.602*	Kendeigh (1944)
Tufted titmouse *Parus bicolor*	1–14	14	R	−0.674	0.031	0.637*	Kendeigh (1944)
Cardinal *Cardinalis cardinalis*	1–16	14	R	−0.230	0.011	0.230	Kendeigh (1944)
Dark-eyed junco *Junco hymealis*	1–85	14	R	−0.238	0.004	0.109	Kendeigh (1944)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[1] Lack 1966, pp. 60–61.

tion of the effects of stochasticity on population growth at small densities still await methods for empirically estimating the variances. Thus, we will therefore emphasise on summarising the evidence and mechanisms for a reduction in population growth rate at very low densities.

The Allee-effect is defined as a decrease in population growth rate at low population sizes. The concept can be traced back to the early works of Allee (1931, 1938, 1941) and Allee et al. (1949) on the flour beetle *Tribolium condusum*, where some negative effects of undercrowding on the population growth rate were discovered. The Allee-effect has received great attention in conservation biology since it can greatly influence the persistence time of a small population (Lande 1987, Dennis 1989).

Examples on Allee-effects are known from almost all major taxonomic groups of animals (Fowler and Baker 1991). Very few studies have, however, actually provided data on a positive relationship between population density and population growth rate or a demographic variable. In an important contribution, Fowler and Baker (1991) made an attempt to quantitatively assess the effects of a reduction in the size of populations of large mammals on the population growth rate. Only studies in which the minimum recorded population sizes were less than 10% of the maximum historical level, were included in the analyses. By choosing those relative strict criterias, Fowler and Baker (1991) were able to include only a few studies, mainly due to the fact that the population size of large mammals does usually not fluctuate over such a great range. No effects were found either for an Allee-effect or a hyper-compensation (i.e. an increase in the population growth rate at low population densities, which implies that the second derivative of the population growth rate becomes positive with decreasing population size) were found in this data-set.

In order to examine the generality of these results, we extended the approach of Fowler and Baker (1991) to birds. In a review of the literature we were able to find 11 studies where the population size was reduced to less than 15% of the maximum recorded and where there was a linear decrease either in the mean clutch size in year x (CS_x), the recruitment rate ($R_x = (N_{x+1} - N_x)/N_x$, where N_x is the population density in year x) or in the fecundity rate ($F_X = (N_{X\ \mathrm{autumn}} - N_{X\ \mathrm{spring}})/N_X$, where N_X denotes the population size at different seasons). The Allee-effect was modelled according to Tonkyn (1986) as a simple parabolic function, $y = c + aN_x - bN_x^2$, fitted to the data by means of a multiple regression analysis. In the equation y represents the reproductive traits R, F or CS. A convex regression curve, showing the presence of an Allee-effect, will give $a > 0$ and $b < 0$. However, in all the analyses the regression coefficients were $a < 0$ and $b > 0$ (Table 1), i.e. all the regression curves have a concave shape. Thus, this confirms the pattern found in the large mammal data set (Fowler and Baker 1991) that the presence of an Allee-effect is difficult to document by such analyses.

Recently Myer et al. (1995) investigated 128 exploited fish stocks for depensatory effects at low population levels. Only three stocks showed a significant depensation, and estimates of the statistical power of the tests strengthen the conclusions that no Allee-effect was apparent for fish populations at the population levels studied.

One major hindrance to why a quantitative demonstration of the Allee-effect has been difficult, is that small sample sizes make it difficult to provide reliable estimates of the demographic variables. Based on evidence from behavioural ecology, we will try to derive predictions about where the Allee-effect is most likely to appear. We will examine the following hypotheses for a decrease in population growth rate at small densities: (1) the efficiency in the defence against predators or brood parasites will be reduced, (2) a reduction in the mating efficiency, and (3) the foraging efficiency will be decreased. Andrewartha and Birch (1954) provided the first extensive treatment of the two first of those hypotheses.

Reduced defence against predators or brood parasites

The efficiency in defending themselves against predators or brood parasites may be reduced when population size comes under a certain level. This may be due to reduced group defence or difficulty in fending off predators (Birkhead 1977, Clark 1974). It has been shown for many vertebrate species that group defence against predators (Brown et al. 1990, Wiklund and Andersson 1994) or the probability of escaping a predator is related to group or flock size (e.g. Kruuk 1964, Kenward 1978, Møller 1987). The time an individual is scanning for predators is also negatively related to flock size (e.g. Bertram 1980). In such cases, populations or colonies declining to a lower threshold size might experience higher predation rates which are likely to affect the population growth rate negatively (Brown et al. 1990).

For species living in large schools, flocks or groups, the dilution effect of large group size might be reduced in small populations. At a certain low threshold, schools of fish might experience a sudden fall in the antipredator function, since the efficiency of schooling has collapsed (Clark 1974). In these cases each individual fish no longer feels the safety of a large school. The antipredator efficiency of each individual of a large school or flock may in such cases be reduced and each individual will change its behaviour, which again might affect their reproductive success, and reduce population growth rate.

Brood parasites might have similar effects on their hosts. The red-winged blackbird *Agelaius phonicerus* is less affected by parasitism by the brown-headed cowbird *Molothrus ater* when breeding in large dense populations than when breeding in less dense populations (Robertson and Norman 1976, 1977). Similarly, Fretwell (1977, 1983) found that rates of parasitism by the cowbird on the dickcissel *Spiza americana*, decreased with increasing density of nests. Brood parasites are known to reduce the breeding success of their hosts dramatically (Røskaft and Moksnes 1996), and with high rates of parasitism this will affect population growth rate.

Thus, in many gregarious vertebrate species there is now evidence that group size is important for the efficiency of the defence against both predators and parasites. It is likely that these will show an Allee-effect when population level reaches a lower threshold.

Reduced mating efficiency or social interactions

Several authors have hypothesized that individuals at low population levels may have difficulties in finding mates which reduces population birth rate (Andrewartha and Birch 1954, Dennis 1989). However, this effect may be difficult to distinguish from stochastic variation in the sex ratio among the breeding adults.

For species in which the choice of a correct mate (e.g. assortative mating) is of crucial importance for the reproductive success of both sexes, access to limited numbers of potential mates may result in a choice of poor pairings which in turn reduces reproductive success. A female may reduce this effect by being more willing to accept extra-pair copulations, particularly with high-quality males (Lifjeld 1994). Accordingly, rook *Corvus frugilegus* females mated with low-quality males more frequently enganged in extra-pair copulations than females mated with high-quality mates (Røskaft 1983). Thus, reduction in the availability of mates may reduce the possibilty for females to compensate for poor mates through extra-pair copulations and therby create an Allee-effect. We predict that this will occur especially in monogamous, long-lived species where the quality of both mates is important for the reproductive success.

Reduced foraging efficiency

Communal roosts or nesting colonies of birds may serve as information centres, where individuals inform each other about good feeding sites (Ward and Zahavi 1973, Brown 1986). However, at low population levels the probability for all individuals to find good foraging sites might be reduced, which might affect the average foraging efficiency of individuals in the colony (cf. Brown et al. 1990).

Furthermore, group living predators may also be more successful in capturing prey at higher group sizes that at lower ones (Bertram 1978, Major 1978, Berryman et al. 1985, Bednarz 1988, Caro 1994). Thus, if population level decreases there is a certain risk that the low foraging efficiency might affect the reproductive success of individuals, causing an Allee-effect of the population. There is therefore some indirect evidence that in social species that are dependent of cooperation or information to forage efficiently, a reduction in population size to a certain low threshold, may cause an Allee-effect.

Discussion

The comparative analyses presented in the previous sections are a preliminary attempt to predict which part of the life cycle is most likely to influence variation in λ for different types of life histories. By this approach, we suggest a first step on a theoretical foundation for Caughley's (1994) species-decline paradigm. The next step will obviously be to examine how well the predictions from the sensitivity analysis of the population growth rate λ to changes in different demographic parameters can explain population fluctuations. We would predict from the analyses presented in Fig. 2 that in survivor and bet hedging species (Fig. 3), population fluctuations should be more closely correlated with variation in adult survival rates than in high reproductive species.

The theoretical results on the dynamics of small populations have shown that the time to extinction is not only dependent on population growth rate, but also on demographic and environmental variances (May 1973, Leigh 1981, Goodman 1987, Lande and Orzack 1988, Lande 1993). We need methods for jointly estimating those variances, separated from sampling error, especially in age-structured populations. If such data become available for a set of species, we can then examine the two hypotheses summarised by Pimm (1991). (1) Population fluctuations of long-lived species may be most influenced by stochastic variation because of low reproductive potential. In contrast, (2) it can also be argued that long-lived species are less influenced by random variation because they will have several breeding attempts averaging out the stochastic effects. The presence of such a relationship may obviously have great implications for land use strategies which focus on conserving biodiversity because they will strongly affect the minimum population sizes that is necessary for securing viable populations.

If there exists a relationship between different life history categories (Fig. 3) and population processes, this may have major implications for the development of overall conservation strategies, for instance at a national level. Several countries have as a consequence of their ratification of the Convention for Biodiversity conducted surveys of the status and threats to biodiversity. Even though great differences exist between the countries in the amount of existing knowledge, a large number of problems affecting biodiversity can easily be identified. Conserving biodiversity often then becomes a matter of prioritisation, a fact that is often forgotten by conservationists and scientists. The patterns presented here may be helpful for such overall higher-level decisions, which often must be based on limited knowledge.

A relationship between life history variation and population processes may have implications for management and conservation strategies in order to conserve species diversity. For instance, survivor species are likely to be strongly affected by human activity influencing adult survival rate. For example, in the southern Atlantic two studies have independently reported a decline in the populations of the wandering albatross *Diomedea exulans* (Weimerskirch and Jouventin 1987, Croxall et al. 1990), which probably can be explained (as predicted by Fig. 3) by a reduction in adult survival rate. One important factor for this decrease in survival is probably an increased mortality due to fishing activity in the bird's foraging areas (Croxall et al. 1990).

One of the great challenges in conservation of biodiversity is to secure sufficient space for a fulfilment of species' requirements. In conservation biology there is a long-standing discussion on the strategies for establishing conservation areas, the so-called SLOSS-debate (some large or several small) (Soulé and Mills 1992). However, another question is often more important for ministries or national protection agencies: given a limited amount of money, which habitat-types shall we prioritise? From the lines of argument presented in the previous sections, we suggest that it will depend on the life history of the species in question. Again we are often faced with a matter of prioritisation. Our summary of the few existing key-factor analyses in birds (Fig. 4) clearly points out how important factors outside the breeding season may be for population fluctuations. It is likely that securing viable populations of especially survivor and bet hedging species, will be dependent on access to good survival habitats. Thus, we suggest that national plans for securing species diversity of vertebrates should focus on securing enough high-quality survival habitats for bird species such as swifts, waders, raptors, and long-lived seabirds and mammals, such as large herbivores and carnivores (cf. Wallis de Vries 1995). We want to emphasise that this is not a question of an "either or" but more where to direct the effort.

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