Life-history strategies associated with local population variability confer regional stability

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A widely held ecological tenet is that, at the local scale, populations of K-selected species (i.e. low fecundity, long lifespan and large body size) will be less variable than populations of r-selected species (i.e. high fecundity, short lifespan and small body size). We examined the relationship between long-term population trends and life-history attributes for 185 bird species in the Czech Republic and found that, at regional spatial scales and over moderate temporal scales (100–120 years), K-selected bird species were more likely to show both large increases and decreases in population size than r-selected species. We conclude that life-history attributes commonly associated with variable populations at the local scale, confer stability at the regional scale.

Keywords: population fluctuations; birds; life history; body size; fecundity; habitat fragmentation

1. INTRODUCTION

Human-related alterations of the natural environment have led to decline and extinction in many taxa (Burney *et al.* 2001) including birds (Brooks *et al.* 1999; Renjifo 1999). Identifying those species most sensitive to anthropogenic stress is a necessary first step in ameliorating the effects of such stress. One promising and well-studied area of conservation research is the search for life-history traits associated with large population declines and/or extinctions (Terborgh 1974; Pimm *et al.* 1988; Gaston & Blackburn 1995; Bennett & Owens 1997, 2002; Owens & Bennett 2000). Surprisingly, less attention has been paid to the relationship between life-history traits and large population increases even though biological-interaction hypotheses (i.e. competition and/or predation) to explain declines can only be explicitly tested if we understand the patterns of increasing as well as decreasing species.

The probability of, and the time to, extinction have been related to life-history variables such as body size, fecundity, age of maturation and lifespan (Gaston & Blackburn 1995), but the relationships between these variables and the probability of extinction have not been consistent (Tracy & George 1992). Some researchers have found positive correlation between body size and the probability of extinction (Fagan *et al.* 2001); others have found no relationship (Brooks *et al.* 1999; Davies *et al.* 2000), while still others have found negative correlation (Hanski 1994). This lack of consistency may have been caused in part by the wide range of spatial and temporal scales, from annual species turnover on small lake islands to global extinctions over the last 100 Myr (Peltonen & Hanski 1991; Johnson 1998) that have been used to assess these relationships.

Differences in spatial scale are a particular source of potential confusion. It is unlikely for most species that local extinction events are simply a small-scale version of global extinctions. A fundamental tenet of metapopulation

theory is that local extirpations of a species may have little or no effect on larger scale population dynamics if they are balanced by colonization events, and thus there is the potential for local and global population trends of a species to be independent. It should come as no surprise then that life-history traits that are correlated with local declines/extinctions are not necessarily correlated with regional or global declines or extinctions. Differences in temporal scale are another potential confounding factor because life-history traits associated with declines or extinctions over evolutionary time may not be those associated with declines or extinctions under present conditions of high anthropogenic stress (Cassey 2001). In a conservation context, the spatial and temporal scales of greatest concern are those involving large geographical regions and recent historic times, respectively.

However, studies of the relationship between bird life-history attributes and conservation status (i.e. threatened or not) consistently find that threatened species are, on average, larger (Gaston & Blackburn 1995; Bennett & Owens 1997; Bennett & Owens 2002) and less fecund (Bennett & Owens 1997; Bennett & Owens 2002) than species that are not threatened. The analyses cited here were not confounded by differences in scale because all of the data used describe the global status of birds.

There has been almost no research on the relationship between life-history traits and large population increases except in the context of introductions. The success of introductions was found to be negatively related to body size (Cassey 2001) and longevity (Forsyth & Duncan 2001); however, introduced species are unlikely to be a representative sub-sample of species that have shown large increases in population size.

We believe that valuable insight can be found in examining the relationship between life-history attributes and the entire gradient of trends, rather than concentrating on only those species that are disappearing or have disappeared. Here, we examine the relationship between body size, fecundity and longevity, and population trends for 185 bird species in the Czech Republic.

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2. METHODS

For this study, we examine the relationship between body size, longevity and fecundity, and bird population trends in the Czech Republic and Slovakia (former Czechoslovakia) between c. 1850 and 1980.

Ornithology in the former Czechoslovakia has a rich history with anecdotal and quantitative data on bird abundance and distribution dating back several centuries. This region is particularly suitable for this study, as it has experienced a considerable deterioration of its natural environment (Moldan 1990; Vavrousek 1990). These changes can be characterized by the fragmentation and disappearance of natural habitats (e.g. hardwood floodplain forest and old mature forest in general) on the one hand, and the associated increase and consolidation of artificial habitats (forests defoliated by industrial emissions of sulphur dioxide) on the other. We examined all species that have been persistent breeders in the region between c. 1850 and 1980. For each species we compiled data on female body mass, fecundity and longevity (Hudec & Cerny 1972, 1977; Cramp & Simmons 1977, 1979, 1983; Hudec 1983; Cramp 1985, 1988; Cramp & Perrins 1993; Dunning 1993) and their long-term population trends (Hudec & Cerny 1972, 1977; Cramp & Simmons 1977, 1979, 1983; Hudec 1983; Cramp 1985, 1988; Stastny *et al.* 1987; Sedlacek 1988; Cramp & Perrins 1993; Stastny & Bejcek 1993). For female body mass, preference was given to data pertaining to the breeding season (May–June). Fecundity was measured as the mean clutch size multiplied by the number of broods per year. Longevity was measured as the maximum recorded lifespan.

Because of the nature of the information we have chosen population trend classes that are very coarse grained, that is, we have not attempted to examine trends at a resolution that the data are unlikely to permit. Species were classified as: (i) rapidly declining, if their population size declined by more than 50% of its original size (16% (5 out of 31) of these are species that have gone extinct between 1850 and 1980); (ii) slightly declining if the decline was less than 50%; (iii) stable, if there was no discernible change in their population size; (iv) slightly increasing, if their population size increased by less than 50% of its original size; and (v) rapidly increasing if the increase was more than 50% (63% (12 out of 19) of these are species that were not found in the Czech Republic in 1850 and were established breeders by 1980). The 'rapid declines' category includes species that went extinct between 1850 and 1980 and the 'rapid increases' category includes all colonizing species. We excluded species that (i) were introduced by man; (ii) bred accidentally; (iii) bred rarely and in few pairs because the region is at the periphery of their normal range of distribution; and (iv) the cuckoo, *Cuculus canorus*, because it has special life-history adaptations to being a brood parasite. We used two sources, the *Breeding bird atlas of the Czech Republic* (Stastny *et al.* 1987) and the three volumes of *Fauna CSSR* (Hudec & Cerny 1972, 1977; Hudec 1983), to designate trend categories. The distinctions among groups were necessarily subjective because quantitative information on the trends was known for only a handful of species. Both sources use published literature to qualitatively estimate trends since the mid to late 1800s. Evidence generally fell into at least one of four categories: (i) a comparison of species range maps between early atlases (from the late 1800s and early 1900s) and more recent atlases; (ii) a comparison between current and past occurrence patterns at specific sites; (iii) a temporal comparison of numbers of individuals or breeding pairs

within regions or districts of the Czech Republic; and (iv) qualitative descriptions of species abundance (e.g. a species that was described as 'common throughout the Czech Republic' at the turn of the century and 'rare' in more recent times would be designated as 'rapidly declining'). If a species was described as showing no trend by both sources it was designated stable, if it was described as either declining or increasing we used quantitative criteria where available to place them into 'rapidly' or 'moderately' categories. Where there were no quantitative data we used the qualitative descriptions (e.g. 'have declined to near extinction', 'were once common but are now rarely found') to designate categories. Of course, any species that have gone extinct in or colonized the Czech Republic in the past 100 years are categorized as 'rapidly decreasing' and 'rapidly increasing', respectively. Thus, although it is likely that there has been some misclassification between adjacent groups (e.g. we may have classified some species as stable that should have been slightly declining or slightly increasing), it is unlikely that there has been misclassification among non-adjacent groups (e.g. it is unlikely that a rapidly declining species has been classified as stable). No information on the trends was available for 10 species and these species were excluded from further analyses.

Preliminary analyses indicated that body size, fecundity and longevity were strongly correlated. We have combined the variables with principal component analysis into a single index (PRIN1), which we interpret as measuring a species position along a life-history gradient, with small, high fecundity and short-lived species (r-species) at one end and large, low fecundity, long-lived species (K-species) at the other. We emphasize that r-K labels simply define a species position along a gradient of body size, fecundity and longevity and do not imply an endorsement of the r-K life-history strategies theory. The eigenvalue of the first component explained 70% of the standardized variance and the loadings on the first eigenvector were 0.86, -0.79 and 0.86 for log body mass, log fecundity and log longevity, respectively. The loadings are relatively large and approximately equal for the three life-history variables, so this first component (PRIN1) provides a good synthesis of the life-history traits and was used to measure a species' position along a life-history gradient.

We first tested to see if stability was randomly distributed among families and orders. To do this we categorized each species as stable (unity) or increasing or decreasing (zero). We then randomly shuffled the unities and zeros and calculated the proportion of stable species in each family or order. This was repeated 1000 times. We could then compare the observed and expected (under the null hypothesis of random distribution of stability) 'proportion stable' frequency distributions using a χ^2 -test.

We then related life-history strategies, as summarized by PRIN1, to population trends in two stages. In the first analysis each species is treated as an independent ecological unit and we use ANOVA to compare PRIN1 across the five trend categories. In the second analysis we used the independent contrasts method (Harvey & Pagel 1991; Oakes 1992) to control for phylogenetic relatedness because species are not truly independent ecological units, causing the true degrees of freedom to be less than the calculated degrees of freedom. Note, however, that the independent variable, in this case, is a categorical variable (i.e. population trend category) and thus, we use the 'sister-taxa' comparisons method and compare only pairs of closely related species that differ in population-trend category (Harvey & Pagel 1991; Bennett & Owens 2002). This approach

tends to have low power because (i) only select pairwise comparisons can be used, therefore sample sizes are small (i.e. n species can only provide, at most, $n/2$ contrasts) (Ackerly 2000; Larsen & Barrett 2000); and (ii) it ignores variation in population trends that occur at higher phylogenetic levels, such as families within orders or orders within class, because we only compare closely related species. Bennett & Owens (1997, 2002) have made a powerful case that much of the variation in many life-history traits and conservation status occurs at the family level or higher. It is possible, and even likely, that the same is true of population trends but higher level variation is ignored when one only compares closely related species. For example, the large, long-lived, low fecundity species from the orders Anseriformes (ducks and geese) and Galliformes (grouse and pheasants) show only two stable trends while eight out of the 17 species have seen extreme declines or increases over the past century. The two possible pairwise comparisons show no obvious correlation between PRIN1 and trend but these two orders show much more variable trends than orders made up of small, high fecundity, short-lived species (e.g. Passeriformes). We have used randomization techniques to test the hypothesis that population trends are random with respect to phylogeny.

3. RESULTS AND DISCUSSION

The long-term population trends were determined for 185 species belonging to 43 families and 14 orders. Out of this total, 31 (17%) species were classified as showing large declines, 31 (17%) as showing moderate declines, 76 (41%) as stable, 28 (15%) as showing moderate increases and 19 (10%) as showing large increases. Although more species showed large declines than large increases, the difference was not significant (binomial test: $p = 0.12$). The declining and increasing species were present in most families. Out of the 23 families containing more than one species, declining species were present in 19 (83%) families, stable species in 18 (78%) families and increasing species in 15 (65%) families.

At the family level we found little evidence that the frequency distribution of 'stable' species was non-random ($\chi^2 = 3.12$, d.f. = 3, $p = 0.37$). The χ^2 -test categories were 0–0.099, 0.1–0.499, 0.5–0.899 and 0.9–1.0 to ensure that each category had at least five counts. The categories are somewhat arbitrary but all possible ways of categorizing so that there were at least five counts in each category led to the same qualitative conclusion, that is, acceptance of the null hypothesis. However, order-level χ^2 -analysis suggested that stability may not be randomly distributed ($\chi^2 = 3.59$, d.f. = 1, $p = 0.06$). The χ^2 -test categories were 0–0.299, and 0.3–1.0 to try and ensure that each category had at least five counts (it was impossible to combine categories so that each category had five counts, so one category has four).

The orders Strigiformes and Passeriformes had more stable species than would be expected by chance whereas Charadriiformes and Falconiformes had fewer, although only the results for the order Passeriformes remained significantly different once we had corrected for multiple comparisons. In fact, 50 out of 75 passerine species had stable trends over the last 100 years while none of the 1000 randomizations has as many as 50 stable trends among passerine species.

Figure 1. (a) Mean ($\pm$ s.e.) values of PRIN1 for population-trend categories. PRIN1 combines body size, fecundity and longevity into a single value (31). Species with large PRIN1 have large body size, low fecundity and long lifespan, whereas species with small PRIN1 have the opposite life-history traits. Values shown are sample sizes. (b) Mean ($\pm$ s.e.) differences in PRIN1 of closely related species from different population-trend categories. PRIN1 difference equals trend category minus stable category. Values shown are sample sizes (number of species pairs). Stable comparison serves as a baseline.

Using an approach that treats each species as an independent ecological unit we found significant differences among mean PRIN1 values for different trend categories (ANOVA_{4,180}; $F = 6.88$; $p < 0.0001$). PRIN1 was high for species showing large declines and large increases, intermediate for moderately declining and increasing species, and low for stable species (figure 1a). A post-hoc Bonferroni pairwise comparisons test shows that the means for 'large decline' and 'large increase' species were significantly different from the mean for 'stable'. This means species that have seen large declines or increases tend to be large, have low fecundity and a long lifespan, whereas species that have shown a stable population size are small, have high fecundity and a short lifespan.

Despite the low power of the independent contrasts method, pairwise comparisons among trend categories

using closely related species found a significant difference in PRIN1 values between stable and rapidly increasing species ($t = 2.06$, $n = 13$, $p = 0.032$). Other comparisons were non-significant but in the expected direction (figure 1b). Thus, even when we control for phylogeny, K-species exhibit more variable population dynamics than r-species at the regional scale.

Our results confirm that bird declines and extinctions are correlated with body size, fecundity and longevity but, moreover, at the regional scale, K-species population trends are much more variable than r-species trends. Theoretical (Pianka 1970; Sæther *et al.* 2002), simulation (Chiba 1998) and empirical evidence (Saether *et al.* 2002) suggests species that are small and have high fecundity and mortality will have higher population variability than large, long-lived, low fecundity species and therefore, all other things being equal, be at greater risk of extinction. However, we found that r-species show much less population variation than K-species at the regional scale. That is, the life-history attributes that are presumed to confer stability and resistance to extinction at the local scale lead to large population fluctuations and, presumably, greater extinction risk at the regional scale.

One of the rarely discussed paradoxes in life-history extinction research is that life-history traits such as large body size, low fecundity, long lifespan and population variability are both positively correlated with population decline or extinction, but are generally considered to be negatively correlated with each other (Fagan *et al.* 2001). One explanation for this paradox may be that at local scales highly variable populations (generally, small, fecund, short-lived species) are more extinction prone, simply due to demographic and environmental stochasticity, but that this tendency to extinction does not hold at regional scales. Both demographic and environmental stochasticity and deterministic factors contribute to population extinctions (Lande 1998), but the relative importance of stochastic versus deterministic factors may vary across scales. In fact, species with high population variability may have evolved life-history traits such as high fecundity, good dispersal ability and small body size in response to natural environmental instability and be less vulnerable to anthropogenic stresses like habitat fragmentation that are occurring at regional scales.

Tilman *et al.* (1994) have recently suggested that in areas of high habitat fragmentation, the best competitors will be most extinction prone if there is a trade-off between competitive ability and dispersal ability. Theory suggests that K-species face increased competitive pressure and therefore have increased competitive ability (Smith 1980), and there has been some empirical support for this assertion (Connell 1983). It has also been shown that species with high intrinsic growth rates and large population fluctuations will have greater selection pressure for dispersal ability (Safriel & Ritte 1983; Olivieri *et al.* 1995), so there is evidence to support this putative trade-off. Further, there is evidence that environmental variability exerts strong selection pressures in favour of dispersal ability (McPeck & Holt 1992). It seems reasonable to infer from the trade-off between good competitive ability and good dispersal ability and the selection pressure in favour of dispersal ability in variable environments, that man-induced fragmentation will have a larger negative

impact on K-species than r-species. A logical consequence of Tilman's theory, that strong competitors are more likely to go regionally extinct in fragmented habitats, is that large-scale competitive release will follow extinction events and, in fact, Nee *et al.* (1997) make this explicit. K-species, as a result of their superior competitive ability, will be best able to exploit this competitive release. Thus, in fragmented habitats, K-species are more likely to go extinct or decline because of their low-dispersal ability, and to colonize or increase due to their superior competitive ability.

There are other potential explanations for this pattern. It may be that the modifications to the landscape have created large tracts of uninhabitable areas for some K-species and large tracts of improved habitat for other K-species, while having little impact on the habitat suitability for r-species. If this were true, however, one would expect the preferred habitat of declining species to be different from increasing species, but we find that for species showing both large increases and large decreases the most common preferred habitat is wetlands (13 out of 31 and 13 out of 19 species, respectively). This suggests that declining species are being replaced in wetlands by species undergoing competitive release.

Mechanisms aside, the evidence that life-history correlates of population variability change with scale has important conservation implications. It is well understood that local population variability is positively correlated with the probability of stochastic extirpations, and thus it is often assumed that populations showing large local population variability or species that have the life-history characteristics that we associate with large local population variability are most at risk of extinction. Our results suggest that the relationships among life-history characteristics, population variability and extinction risk are, almost certainly, scale-dependent, and that at large scales, life-history characteristics that contribute to local population variability confer regional stability.

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