

The relationship between population means and variances in reproductive success: implications of life history and ecology

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ABSTRACT

Within populations, individuals vary in breeding performance even under identical environmental conditions. Here, we present a model of logistic improvement in reproductive success (proportion of fledglings raised per egg laid) with environmental quality for breeders with different capacities. The mean reproductive success in our model denotes environmental quality for breeding. Our model establishes a space of potential combinations of means and variances in reproductive success. In this space, positive, negative or absent trends are possible. The literature and our own long-term studies show that life-history strategies may markedly affect the sign and shape of the relationship between mean and variance in reproductive success. Populations of long-lived birds rarely achieve a high mean reproductive success, and associations between the mean and variance of breeding success in different years tend to be positive. Conversely, populations of short-lived birds present negative mean–variance relationships with high mean reproductive success and variance in good environmental conditions approaching zero. Other factors, such as resource distribution and mating system, may also affect the variance in reproductive success and mean–variance trends. Plotting means and variances in reproductive success for different years or populations may indicate important aspects of the life history and ecology of organisms.

Keywords: life history, long-term studies, mean reproductive success, parental quality, variance in reproductive success.

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INTRODUCTION

Substantial annual variation in breeding success has been reported in most populations studied (Clutton-Brock, 1988; Newton, 1989). Annual variation in average reproductive success in populations under long-term study arises from variability in environmental factors such as food supply, predation, disease, climate or human disturbance (Newton, 1998), but also from quantitative changes among years in the mean parental quality of individuals in the population due to such factors as breeding experience (Saether, 1990). However, there is also considerable variability among pairs of breeders in reproductive success even under identical environmental conditions, which may be expressed as variance associated with the average breeding output (e.g. mean proportion of fledglings raised per egg laid). This variability arises from differences in the quality of territories occupied by individuals or in the reproductive performance of different pairs or individuals due to age, experience, mating system, body condition or genetic variation (Clutton-Brock, 1988; Newton, 1989; Kendall and Fox, 2002).

Differences in the mean and variance of reproductive success also exist among populations of the same species, probably related to different environmental restrictions on reproduction (e.g. Sanz, 1995). But population mean values of breeding success may also indicate the possible range of reproductive performance in different species. In particular, differences in the life-history strategies of species (Roff, 2002) may be an important factor determining variability in average fecundity. A restraint strategy with respect to reproductive effort in long-lived species may constrain reproductive performance (Drent and Daan, 1980; Curio, 1983; Moreno, 1998). In these cases, the range of mean values of reproductive success may be truncated well below a maximum of 1. Truncation implies substantial individual variation in breeding success even under the best environmental conditions, while no truncation would mean convergence in performance with decreasing variance. The level of truncation in reproductive success may be explored either with data from long-term studies of a single population or from studies covering several populations of the same species under different environmental conditions. Thus, positive mean–variance associations could denote reproductive restraint, while negative associations and convergence at zero variance would represent a high reproductive investment strategy.

Most published long-term population studies have presented mean annual breeding performances. Unfortunately, despite the relevance of data for variance in success, only a few of these studies have shown variability in annual reproductive success. Genotype fitness based on reproductive success is better measured by the mean reproductive output minus some function of its variance (Gillespie, 1977; Lacey *et al.*, 1983). Effective population size has become an important topic in conservation biology, since it indicates the sensitivity of a population to random genetic drift (Wright, 1938). A high variance in lifetime reproductive success lowers effective size, thus decreasing genetic variability and increasing the risk of local extinction (Hill, 1972; Nunney, 1996). Thus, for theoretical and applied reasons, it is important to know which factors could modulate variation in fecundity around the average among individuals of the same population. Among these factors, contagious environmental factors like predation (Oro *et al.*, 1999) or parasitism (Brown and Brown, 1986) may determine the rate of total breeding failure, which, in turn, may lead to increased variances. Also, the despotic social structuring of populations (Fretwell, 1972; Ens *et al.*, 1995) or age-dependent breeding performance (Saether, 1990) may be a source of increased variance.

Here, we present a model of logistic improvement of individual reproductive success with environmental quality. Henceforth, reproductive success or performance will be measured as the proportion of fledglings per number of eggs laid. We assume that, for a constant environmental quality, there is variation among breeders in expected reproductive performance, and we examine the implications of this assumption for the mean–variance relationship in long-term studies of reproductive performance. We will not consider demographic stochasticity due to random effects that are unaffected by differences in individual parental quality. We also examine if life history affects the shape of the relationship between mean and variance in breeding success in different years. Although the model can be applied to any sexually reproducing organism, we use the avian literature and our long-term field studies on different bird species to test the validity of the model. Finally, we discuss the use of these functions for synthetically portraying the implications of life history and ecology for fecundity and conservation prospects.

A MODEL FOR INDIVIDUAL IMPROVEMENT FUNCTIONS IN RELATION TO ENVIRONMENTAL QUALITY IN A POPULATION

We envisage breeding performance of each female, or pair, of a population varying continuously in relation to environmental quality. We will hereafter refer to pairs even in cases when females reproduce without significant male help. Our initial premise is that there is variation among breeders in expected breeding performance even under the same environmental conditions. Here, we only consider variation due to parental quality and not that due to random events (demographic stochasticity) that are independent of parental quality. Some apparently stochastic events are in fact related to parental performance (i.e. nest-site selection may affect apparently random predation events) and are thus included in the model. When conditions are extremely poor, reproductive success is zero for all categories of pairs of the population. The reproductive success of a pair, measured as the proportion of fledglings per egg laid, increases sigmoidally with improved conditions until it reaches an asymptote, the maximum reproductive potential, above which increased success is not possible (Fig. 1). Sigmoidal functions reflect the fact that improvements occur faster under normal environmental conditions, but slower when breeders experience very poor or very good environmental conditions.

In general, if x is environmental quality for breeding and y is reproductive performance (hereafter improvement function) of a female, family or pair, y will improve in a sigmoidal fashion with x :

$$y(x) = A \left(1 - \frac{2}{e^{Bx} + e^{-Bx}} \right) = A [1 - \cosh^{-1}(Bx)] \quad (1)$$

where A is the asymptote for y (i.e. maximum reproductive potential of the pair) and B represents the rate at which y improves with x (the faster the improvement, the higher B), which depends on parental quality or parental experience. The improvement function, y , may increase at different rates for pairs of different quality towards different asymptotes (Fig. 1a) or towards a common asymptote (Fig. 1b). Random events would induce decrements in performance independent of parental quality. Thus, these functions would represent maximum reproductive performance as they do not include completely random events. In the most general situation, families breeding in a population differ in both the A

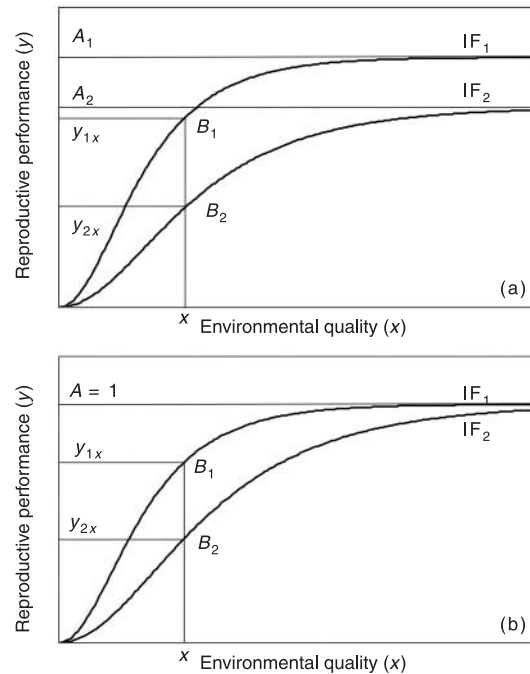


Fig. 1. (a) The improvement functions (IF) of reproductive success (y) with environmental quality (x) when females/pairs with high parental quality (B_1) and low parental quality (B_2) have different rates of improvement (B_1 and B_2) and different maximum reproductive potentials (A_1 and A_2). (b) The improvement functions (IF) when individuals/pairs differ with respect to improvement rates (B_1 and B_2), but all have a common maximum reproductive potential (A), attainable under the best conditions for breeding.

and B parameters (Fig. 1a). Even in the best environmental conditions, the differences in performance between the best and the poorest breeders would be maintained. There would be parallel improvement functions for different categories of breeders, with no convergence possible. There should be a range of variation in B , from a maximum of B_1 to a minimum of B_2 ($B_2 \leq B \leq B_1$), and in A , from a maximum of A_1 to a minimum of A_2 ($A_2 \leq A \leq A_1$). In practice, it is not rare that some pairs in the population attain maximum values of reproductive success. Therefore, it will not be a reduction of the generality of the model if we include the maximum value $A_1 = 1$.

We consider a population with 100 pairs of breeders and, consequently, with 100 different improvement functions. To explore the relationship of both population mean and variance in improvement functions with environmental quality, we assume normal distributions in both the A and B parameters of the population. One hundred data points were generated randomly to fit different prearranged means and standard deviations for each parameter. Success was expressed as a proportion of successfully raised offspring. Then, the normal distribution of the A parameter was readjusted and all generated data higher than a maximum of 1 were set to 1. Mean, μ , and variance, σ^2 , of the reproductive performance of the population for each value of environmental quality x can be obtained as a mean and variance for these 100 simulated improvement functions (Fig. 2a):

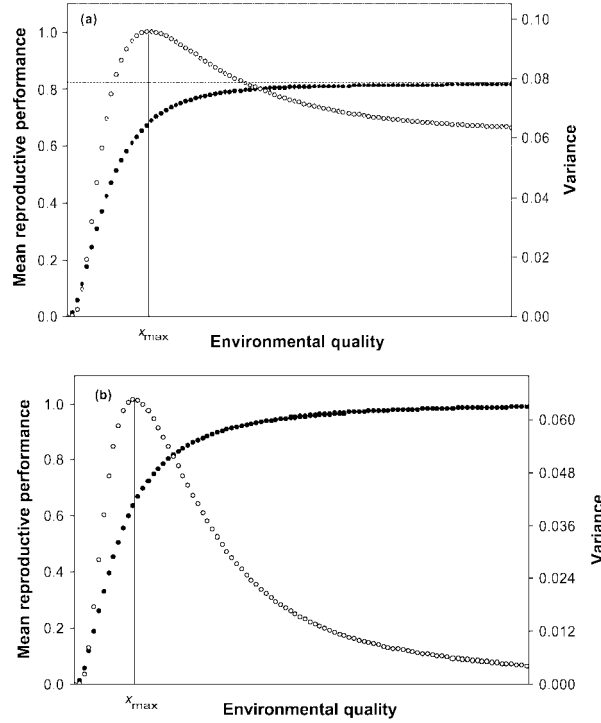


Fig. 2. (a) The mean and variance of reproductive success (expressed as proportions) as a function of environmental quality x for the case depicted in Fig. 1a. Data points (means = solid dots; variances = open dots) are based on simulations obtained for distributions of the A and B parameters (see equations in text) with $\mu_A = 0.82$, $\sigma_A = 0.24$ and $\mu_B = 1$, $\sigma_B = 0.24$. Data for B are in environmental quality units. Below the threshold x_{max} , variance increases with x , while it decreases above this threshold to a level above zero. The mean approaches asymptotically the difference between the maximum and minimum reproductive performances in the population. In the example presented, mean success approaches 0.82 while variance is maximal when mean success is 0.68. (b) The same functions but for the case represented in Fig. 1b. Data points are based on simulations obtained for a distribution of B with $\mu_B = 1$, $\sigma_B = 0.48$. A is 1 for all individuals. The mean now approaches the common asymptote while the standard deviation reaches zero under the best conditions for breeding. In the example presented, the variance in reproductive success reaches its maximum when the mean is 0.63.

$$\mu(x) = \frac{1}{100} \sum_{i=1}^{100} y_i(x) \quad (2)$$

$$\sigma^2(x) = \frac{1}{100} \sum_{i=1}^{100} [y_i(x) - \mu(x)]^2 \quad (3)$$

The maximum variance can be obtained by differentiating (3) with respect to x :

$$\frac{\partial \sigma^2}{\partial x} = 0 = \frac{1}{100} \sum_{i=1}^{100} y_i^2(x) - \mu^2(x) \quad (4)$$

The environmental quality value $x_{\max}$ (Fig. 2) that satisfies (4) is obtained as:

$$\sum_{i=1}^{100} (y_i(x_{\max}) - \mu(x_{\max})) \frac{\partial y_i}{\partial x} = 0 \quad (5)$$

The environmental threshold above which variance decreases (Fig. 2a) is well below the point at which the maximum reproductive potential of pairs is attained. For some distributions of A and B values, variance is far above zero for environmental qualities at which the maximum reproductive potential is attained (Fig. 2a).

What is the relationship between means and variances in reproductive success for different combinations of A and B values? The relationship between predicted mean and variance in reproductive success can be obtained by comparing (2) and (3) for the same x values (Fig. 3a). In all cases, variance increases with the mean up to a point and then declines, but the shape of the mean–variance relationship is dependent on the simulated distribution in

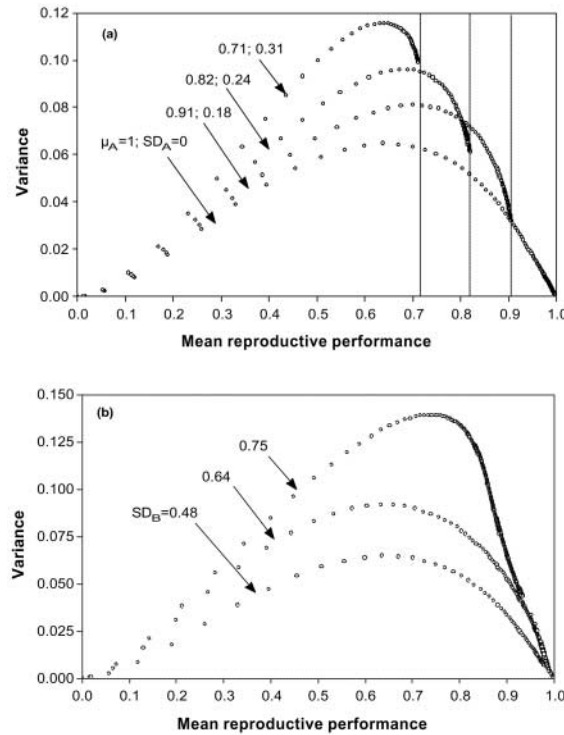


Fig. 3. (a) The association between the variance and the mean in reproductive success for the case depicted in Fig. 1a. The curves depicted are based on simulations obtained for a distribution of B with $\mu_B = 1$ and $\sigma_B = 0.46$ and the mean and standard deviation (SD) of distributions of A (expressed as proportions) indicated on the curves. Functions are truncated at or below 1 depending on the A distribution. (b) The same association for the case presented in Fig. 1b. The curves depicted are based on simulations with no variance around a mean value of 1 for A and a distribution of B with $\mu_B = 1$ and the variances presented on the curves.

the A and B parameters (Fig. 3a). There is a mathematical inevitability in this association, which means that as you approach the extreme values in mean performance, variance tends to zero. Simple mathematical reasoning leads to the conclusion that variance as a function of the mean is constrained between a maximum following a parabolic function that is independent of clutch size:

$$\sigma_{\max}^2 = \mu(1 - \mu) \quad (6)$$

and a minimum that can be written as n parabolic functions (n = clutch size):

$$\sigma_{\min}^2 = \left(\mu - \frac{i-1}{n} \right) \left(\frac{i}{n} - \mu \right) \quad \text{where } \frac{i-1}{n} \leq \mu \leq \frac{i}{n} \quad (7)$$

where $i = 1, 2, \dots, n$.

There is an upper limit of possible values in mean reproductive success at the mean of the simulated distribution of A values (see cases in Fig. 3a). The higher the standard deviation in the A and B parameters, the higher the variance in reproductive success of the simulated population.

An alternative would be when all families have the same maximum reproductive potential (Fig. 1b). In this case, variance would decline with improving conditions for breeding, as even poorly performing pairs could gradually approach the performance of good breeders in optimal environmental conditions. The improvement functions of good and poor breeders would converge in optimal conditions (hereafter convergence means the confluence of improvement functions at a common asymptote of 1). In this case, there is variation in the B parameter, but no variation in the A parameter (i.e. $A = 1$; see Fig. 1b). In this case, the population may attain its maximum reproductive potential under very good environmental conditions, when the mean approaches 1 and variance approaches zero (Fig. 2b). There is a near parabolic fit between the predicted mean (2) and variance (3) functions (Fig. 3b). The range of variation of mean reproductive success does not depend on the B parameter.

The main difference between the cases with or without convergence at maximum success and zero variance is that, in the case of non-convergence, the mean–variance function will be truncated somewhere below a mean value of 1 (Fig. 3a). No truncation is expected in the case with convergence of improvement functions (Fig. 3b). In cases of truncation below 1, the asymptote in performance is not attained in the best observable conditions. When truncation occurs near a success of 0.5, the improvement functions would still be diverging under the best conditions recorded (Fig. 1a) and only positive mean–variance relationships can be expected (Fig. 3a).

METHODS

Observational data

We have, over a number of years, obtained data on mean and variance in annual fledging success in populations of four species with contrasting phylogenies and life histories, the European storm petrel (*Hydrobates pelagicus*), the blue tit (*Parus caeruleus*), the pied flycatcher (*Ficedula hypoleuca*) and the spotless starling (*Sturnus unicolor*). It is important to

mention that of these species, only blue tits depend on exclusive territories for obtaining their food, so differences in improvement functions in the other species should be directly related to individual parental quality itself. Breeding success has been measured as the proportion of laid eggs that fledge.

The storm petrel study was carried out at Benidorm Island (38°30'N, 0°08'E), Mediterranean coast of Spain, from 1993 to 2001. The study area consisted of two high-density colonies inside caves (Mínguez, 1994, 1997), where petrels nest under boulders and in crevices. Fledging success was measured each year in the context of other studies and then with a variable number of breeding pairs. Every year, marked nests were checked at least weekly, from the onset (i.e. middle April) to the end (middle August) of the breeding season. We considered chicks to have fledged if they were at least 35 days old when last observed, as older chicks become highly mobile within crevices and are difficult to find.

The pied flycatcher (population 1) and blue tit studies were conducted between 1991 and 2001 (no flycatcher data for 1996) in a deciduous forest of Pyrenean oak *Quercus pyrenaica*, 1200 m above sea level in the vicinity of La Granja, Segovia province, central Spain (40°54'N, 4°01'W) (Sanz and Moreno, 2000). Another population (population 2) was studied at a pine *Pinus sylvestris* forest at 1900–2000 m elevation, a marginal habitat for pied flycatchers. In this area, the average temperature in May reaches barely 6°C, and it can snow in June. The contrasting breeding biology of these two populations, which are only a few kilometres apart, has been described elsewhere (Sanz, 1995).

The spotless starling study was conducted between 1996 and 2001 in a nest-box colony near Collado Villalba, central Spain (Moreno *et al.*, 1999; Veiga *et al.*, 2002). When incubation was about to end, we inspected the nest boxes daily until all chicks had hatched. Thereafter, we made two to four additional inspections until nestlings were 16 days old. During the last visit, we ringed and measured all nestlings, and those alive at that age were assumed to have fledged. Both first and second clutches were included as independent data points.

Literature review

While improvement functions and reproductive potentials are difficult to measure in the field, albeit not impossible, means and variances in annual reproductive output are routinely obtained in long-term population studies. However, a review of the literature reveals a striking fact: very rarely is any measure of yearly variance in reproductive success published, while many studies present the average values (e.g. studies reported in Clutton-Brock, 1988; Newton, 1989). Only studies including 5 or more years have been considered to derive correlations, restricting the sample even more. We found only data for two species of albatross *Diomedea melanophris* and *D. chrysostoma* (Prince *et al.*, 1994), one species of guillemot *Uria aalge* (Wanless and Harris, 1988) and the kittiwake *Rissa tridactyla* (Murphy *et al.*, 1991). The data for *D. chrysostoma* for the season 1984–85 (Prince *et al.*, 1994) were not considered in the analysis because there must be an error in either the mean and/or variance, as they do not correspond to the expected mathematically canalized association for single-egg layers. The information on non-seabirds is restricted to data on the Florida scrub jay *Aphelocoma coerulescens*, a cooperatively breeding species. The numeric values were obtained from Figure 20.5 of Fitzpatrick and Woolfenden (1988).

Statistical analyses

As a rough measure of the sign of the association (positive, negative or no association at all) between mean and variance in reproductive success, we used the sign and value of the slope of linear regressions, although tendencies should not be linear according to the mathematical model. Data for species with single-egg clutches were fitted to canalized mean–variance relationships. The slight dispersion of some data points around the fitted parabolic function are due to the lack of precision in the data presented in Table 5 of Prince *et al.* (1994). Curvilinear associations for species with multiple-egg clutches were fitted to quadratic polynomial functions. For the scrub jay and the kittiwake, number of chicks fledged was presented instead of proportional success data. Therefore, we have not been able to obtain annual means and variances at a comparable scale as in the other studies. We have presented the mean–variance relationships for these species assuming no significant among-year variation in clutch size. For the pied flycatcher, separate analyses for the two populations were performed.

RESULTS

The data discussed here represent realized reproductive success, which includes the effects of demographic stochasticity and not only the variation considered in our model. We assume that the effects of demographic stochasticity are less important than individual variation in expected performance.

Observational data

In the European storm petrel, there is no significant correlation between the annual means and variances in breeding success (Table 1, Fig. 4). As storm petrels only lay one egg, there is a strict parabolic association between means and variances. A truncation near 0.7 (Table 1) is suggested in this relatively long-lived bird. This means that even in the best conditions, about 30% of breeding pairs do not raise any young.

In the short-lived pied flycatcher, the annual means and variances in breeding were negatively correlated in the two populations studied (Table 1, Fig. 4). In the best years, breeding success approaches 1 and variance is very close to zero. However, an interesting difference between the two populations was identified: pied flycatchers living in the extreme environment (Sanz, 1995) (population 2) experience lower reproductive success and higher variance when conditions deteriorate. Therefore, although the correlations are similar, the slope of the mean–variance association is less negative in population 2 than in population 1 (Table 1). For pied flycatchers, convergence is a real possibility. In the spotless starling, there is no significant association between means and variances (Table 1, Fig. 4). Truncation appears close to 0.7. This means that, in this species of intermediate longevity, convergence is not even approached in the best years.

Literature review

In seabirds, the two forms of association between means and variances can be observed (Table 1). For albatrosses and the kittiwake, there were clear positive associations between mean and variance in reproductive success (Table 1, Fig. 4). Given the mean clutch sizes for

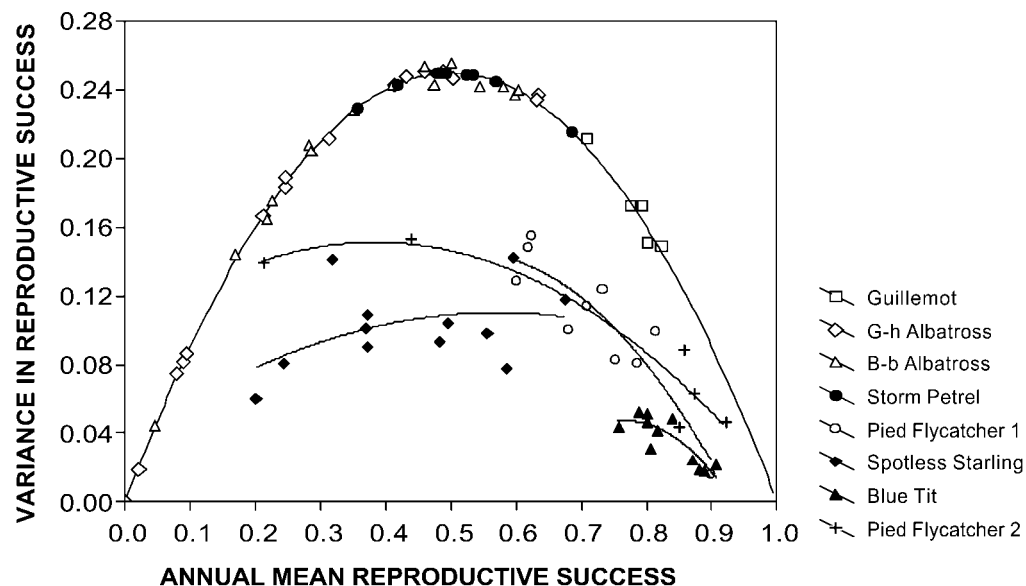
Table 1. Evidence for the relationship between annual breeding success and its variance in several species of birds

Species	Years of study	Correlation means–variances			Range in mean success	Source
		<i>B</i>	<i>R</i>	<i>P</i>		
<i>Diomedea melanophris</i>	17	0.40	0.92	<0.001	0.00–0.64	Prince <i>et al.</i> (1994)
<i>Diomedea chrysostoma</i>	16	0.29	0.88	<0.001	0.05–0.60	Prince <i>et al.</i> (1994)
<i>Hydrobates pelagicus</i>	9	–0.04	–0.34	0.38	0.36–0.68	This study
<i>Uria aalge</i>	5	–0.57	–0.97	<0.003	0.71–0.82	Wanless and Harris (1988)
<i>Ficedula hypoleuca</i> 1	10	–0.37	–0.89	<0.001	0.60–0.82	This study
<i>Ficedula hypoleuca</i> 2	6	–0.14	–0.89	0.017	0.21–0.92	This study
<i>Sturnus unicolor</i>	6 ^b	0.06	0.39	0.21	0.20–0.67	This study
<i>Parus caeruleus</i>	11	–0.23	–0.82	<0.003	0.76–0.91	This study
<i>Rissa tridactyla</i> ^a	11		0.64	0.034	0.00–0.61	Murphy <i>et al.</i> (1991)
<i>Aphelocoma coerulescens</i> ^a	12		–0.66	0.018	0.30–0.90	Fitzpatrick and Woolfenden (1988)

Note: Two different populations (1 and 2) of *Ficedula hypoleuca*, living in different environmental conditions, are included. Values of *B* (slope), *R* (correlation) and *P* refer to linear regressions.

^a Breeding success = no. of fledged chicks per pair.

^b Second clutches included each year.

**Fig. 4.** Associations between annual means and variances in breeding success (proportion of eggs that fledge) for different bird species.

kittiwakes in Murphy *et al.* (1991), we can estimate that mean reproductive success varies between 0 and 0.61. The same is true for albatrosses, which indicates that even under the best environmental conditions, nearly 40% of the pairs fail to produce young. The same

cannot be deduced for kittiwakes given that they are multiple-egg layers. This suggests for these three species a truncation in mean values close to 0.6. In guillemots *Uria aalge*, the association is negative and adjusted to the canalized function for species laying single-egg clutches (Table 1, Fig. 4). Mean performance is well above 0.5 of the maximum, with a suggested truncation close to 0.8. This means that close to 20% of pairs fail to raise young under the best environmental conditions. However, this conclusion should be treated with caution given the few years included in the study compared with the longevity of this species. In summary, in all seabird populations analysed, there was no indication of convergence.

For scrub jays, there is a strong negative correlation between annual means and variances for reproductive success (Table 1; Fitzpatrick and Woolfenden, 1988). The slight variances observed in the best years suggest convergence in improvement functions between different categories of breeders (Fig. 2a). Based on an average clutch size of 3.2 (Fitzpatrick and Woolfenden, 1988), we estimate a range in mean values of 0.3–0.9. This suggests that this cooperatively breeding species approaches convergence.

DISCUSSION

The proposed model is based on differences in the reproductive behaviour of different breeders in populations. It does not explicitly consider the effects of purely random events. However, our conclusions are general if one assumes that the effects of this stochasticity have less of an impact on the observed variation in realized reproductive success than the impact due to individual variation in parental quality. In addition, the variation due to demographic stochasticity is not heritable and so cannot play a role in life-history evolution.

Two scenarios were simulated. The first scenario represents the most general case, where improvement functions of different categories of breeders may differ in both the shape with which reproductive success increases with improved environmental conditions and in their maximum reproductive potential (Fig. 1a). Pairs of breeders that experience a slower increase in reproductive success with environmental conditions will be those with lower maximum reproductive potential. In these populations, there would be a constraint on reproductive potential operating through a fraction of poor breeders. This would be expressed as a truncation of mean values of reproductive success at some level below 1. The second and more particular case represents populations with a common observable reproductive potential but different improvement functions with respect to shape. This means that nearly all breeders may attain maximum reproductive performance in the best years. Thus, variance would approach zero and mean success approach 1 in very good conditions for breeding. Frequently met environmental conditions would favour the expression of maximum reproductive potential even for poor breeders. The relationship between means and variances in reproductive performance among years is a consequence of the two scenarios described above. According to the first scenario, means will be truncated at intermediate values. Therefore, there will be a positive or non-significant mean–variance relationship. In contrast, in the convergence scenario, truncation at high mean values will determine a negative mean–variance relationship.

The theory of life-history evolution is based on a trade-off between survival and reproduction (Stearns, 1992). This implies a gradient in the amount of resources devoted to present reproduction, based on the environmentally determined survival probabilities. At one extreme of this gradient are long-lived species which devote most resources to

self-maintenance, with the other extreme being represented by short-lived species which invest heavily in each reproductive attempt. We thus expect the conservative extreme of the life-history gradient to be associated with the scenario of low truncations and positive or non-significant mean–variance associations, while the short-lived extreme would be prevalent in the scenario with convergence and negative mean–variance associations.

The first extreme implies a conservative breeding strategy, constraining breeding success of some breeders in the population below the maximum potential to maximize survival probabilities (Saether *et al.*, 1993). In long-lived species, there is selection for delayed breeding and potential for improvement in performance with age and/or experience (Curio, 1983; Saether, 1990; Moreno, 1998). The positive associations in albatrosses *Diomedea* spp. and kittiwakes *Rissa tridactyla* suggest divergence in improvement functions well below the threshold at which the best performers can attain their maximum reproductive potential. The low truncation level and positive trend observed is in accordance with the model when applied to long-lived prudent reproducers (0.97 annual survival for albatrosses, 0.93 for kittiwakes; Weimerskirch, 1992; Hatch *et al.*, 1993). Storm petrels are shifted to the right compared with albatrosses, as expected from their smaller size and shorter lives (0.9 annual survival; Saether, 1989). Guillemots are shifted even more to the right, in accordance with their lower survival rates (0.87; Saether, 1989); their higher reproductive performance may not be due to life-history trade-offs. Seabirds exhibit a conservative strategy with respect to reproductive effort (Saether *et al.*, 1993; Mauck and Grubb, 1995; Erikstad *et al.*, 1998), so we would predict positive associations for many species.

In short-lived species, there is no strong selection for restraint in reproductive effort and no great scope for age effects on performance (Curio, 1983). Passerines show two different patterns. Pied flycatchers and blue tits approach convergence and show the expected negative association between means and variances as corresponds to their body size and life span. Annual survival rates are 30–48% for blue tits (Saether, 1989) and 45–52% for pied flycatchers (Sanz, 2001). Starlings show a totally different pattern, with truncation at lower mean values and no correlation between means and variances. This suggests that spotless starlings experience marked differences in performance among pairs within years, probably related to age or experience effects. A relatively long life span would be expected for this little studied species. However, its close relative, the European starling *Sturnus vulgaris*, exhibits a low annual survival rate (0.47; Saether, 1989). Scrub jays also show a negative mean–variance association and possible convergence.

Within these extremes determined by life history, ecological conditions may also affect the shape of the mean–variance function. In marginal habitats for breeding, variance may increase and means will be shifted towards lower levels. This increase in variance may be linked to an increased risk of total failure. Comparing habitats with different conditions for breeding, we expect the mean–variance function to be moved towards higher variance and lower mean values. That is the case with the two populations of pied flycatchers compared in our study. Pied flycatchers living near their altitudinal limit experience limiting conditions more frequently than those living in milder habitats and, accordingly, show a less negative slope in the mean–variance relationship.

The social breeding system may also impinge on variances and mean values and affect the shape of the improvement function. Thus, despotic resource distributions among breeding pairs/individuals may increase variances in the reproductive success of the population when compared to more equitable distributions (Fretwell and Lucas, 1970; Fretwell, 1972; Sutherland and Parker, 1985; Pulliam and Danielson, 1991). While not necessarily affecting

mean values, despotic/pre-emptive systems may be expected to show higher mean–variance functions. Cooperative breeding may also decrease variance in reproductive success, although the evidence for this effect is equivocal (Reed and Walters, 1996). Colonial breeding may protect against predation through cooperative nest defence, thus reducing the incidence of total failure and thereby reducing variance in breeding success (Andersson and Wiklund, 1978; Wittenberger and Hunt, 1985). The dilution effect of dense nest aggregation may also lower variance (Wittenberger and Hunt, 1985). This may also be a consequence of creche formation in certain species (Davis, 1982; Evans, 1984).

High variances even under the best conditions may imply low effective genetic population sizes, with important consequences for management and conservation (Nunney, 1996). On the other hand, Kendall and Fox (2002) have demonstrated that variation among individuals in the expected life-history parameters (e.g. survival or fecundity) will reduce the expected extinction risk of populations with respect to that predicted by stochastic demographic models that assume identical expected fates of all individuals. In any case, a survey of mean–variance associations derived from long-term studies may effectively depict the potential for serious conservation problems based on low effective population sizes.

This preliminary review of a few case studies highlights the importance of presenting the variance in annual reproductive success derived from long-term studies. The sign of the association between annual means and variances in long-term population studies may reveal the implications of habitat quality or life-history variation for the attainment of convergence in reproductive performance and for individual variation in reproductive potentials. The variance observed under the best conditions for breeding may reveal if convergence between different categories of breeders is at all possible. A continuum from positive functions (prudent reproduction) to negative ones (reckless reproduction) can be envisaged. The form of the mean–variance function thus summarizes in a simple way a whole set of life-history, behavioural and environmental variables. Therefore, authors should start to present the variances obtained in the calculations of annual average breeding success. Variances are as important as average values for estimating how the performance of different individuals changes with environmental quality.

ACKNOWLEDGEMENTS

Elena Arriero, Juan A. Fargallo and Santiago Merino helped in Valsain with the flycatchers and blue tits, and Belén Belliure helped in Benidorm Island with storm petrels. J.M., J.J.S. and J.P.V. have been supported throughout the years by projects PB91-0084, PB94-0070-C02-01, PB97-1233-C02-01 and BOS2001-0587 from the Spanish Ministry of Science and Technology. While writing this paper, V.P. was supported by a postdoctoral grant from the Spanish Ministry of Education and Science. Some of the records for storm petrels were obtained from the data set of the Environmental Monitoring Service of Benidorm Island (Life-Generalitat Valenciana) by E.M.

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