

Lifetime reproductive success in seabirds: interindividual differences and implications for conservation*

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SUMMARY: Seabirds share certain life history traits, most species being relatively longlived and reproducing at a low rate. Long-term population studies of seabirds have revealed that lifetime reproductive success differs widely among individuals, and that only a minor fraction of the population contributes importantly to future generations. These individuals have traditionally been termed of high “parental quality”. Quality is often defined tautologically as breeding success. Determinants of parental quality, and ways to measure it *a priori* without relying on breeding success, remain a challenge in seabird ecology. Parental health state and immunocompetence have been shown to be associated with breeding date, egg size, chick growth rate and breeding success in several field studies and may allow the identification of good breeders. Identifying the “high quality” fraction in a population may be worthwhile in order to better guarantee the productivity of declining populations.

Key words: conservation, health, immunocompetence, life histories, lifetime reproductive success, parental quality, seabirds.

RESUMEN: ÉXITO REPRODUCTOR A LO LARGO DE LA VIDA EN LAS AVES MARINAS: DIFERENCIAS ENTRE INDIVIDUOS E IMPLICACIONES PARA LA CONSERVACIÓN. – Las aves marinas comparten ciertas características en sus estrategias vitales, siendo la mayoría de las especies de vida larga y reproduciéndose a una baja tasa. Los estudios poblacionales a largo plazo en aves marinas han revelado que el éxito reproductor a lo largo de la vida difiere grandemente entre individuos, y que solo una pequeña fracción de la población contribuye de forma importante a las generaciones futuras. Estos individuos han sido tradicionalmente denominados como de alta “calidad parental”. No obstante, la calidad es a menudo definida tautológicamente como éxito reproductor. Los determinantes de la calidad parental, y las formas de medirlo *a priori*, sin recurrir al éxito reproductor, continúan siendo un desafío para la ecología de las aves marinas. El estado de salud parental y la inmunocompetencia han resultado estar asociadas a la fecha de reproducción, tamaño del huevo, tasa de crecimiento y éxito reproductor en varios estudios de campo y podrían permitir la identificación de los buenos reproductores. Identificar la fracción de “alta calidad” en una población pudiera ser útil para garantizar mejor la productividad de poblaciones en declive.

Palabras clave: aves marinas, calidad parental, conservación, estrategias vitales, inmunocompetencia, salud.

INTRODUCTION

The widespread idea that most breeding individuals in natural populations contribute to succeeding generations has been shattered in the last decades by

a series of long-term studies, many of them on birds. Newton (1995) summarised the information resulting from these studies as follows: (1) a large proportion of young that are raised to independence die before they can breed; (2) not all the individuals which survive to attempt breeding subsequently produce offspring and (3) successful individuals vary

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TABLE 1. – Proportion of any one generation of fledglings that breed, and proportions of breeders that raise some young throughout their lifetime and produce half the young in the next generation.

	Proportion fledglings that breed	Proportion breeders raising some young	Proportion breeders raising half next generation
Blue tit <i>Parus caeruleus</i>	0.14	0.93	0.21
Kingfisher <i>Alcedo atthis</i>	0.19	0.95	0.32
Meadow pipit <i>Anthus pratensis</i>	0.28	0.79	0.25
Sparrowhawk <i>Accipiter nisus</i>	0.28	0.81	0.18
Ural owl <i>Strix uralensis</i>	0.28	0.96	0.21
Osprey <i>Pandion haliaetus</i>	0.29	0.83	0.21
Barnacle goose <i>Branta leucopsis</i>	0.58	0.59	0.16

Based on studies reported in Newton (1989).

greatly in productivity. It is this latter point which is worth emphasising, as the variation revealed in these studies is really striking (Table 1). We are not as much concerned with the proportions of fledged or independent young that actually breed successfully, as with the proportions of individuals breeding at least once (i.e. individuals which we can find breeding in a population in a certain season). Actually, in 7 bird studies dealing with species ranging from the blue tit (*Parus caeruleus*) to the barnacle goose (*Branta leucopsis*), between 16 and 32% of breeders produced half the next generation (Table 1).

If we consider only seabirds and separate by sex, one third of breeders do not raise any young (Table 2). Also, two thirds or more of raised young do not become new breeders; hence most parents raising young never pass on their genes to future generations. In the kittiwake, although most breeders raise some young during their lifetime, only 41% of male and 50% of female breeders succeed in passing on their genes to the next generation. This is a very conservative estimate as most of these birds actually raise very few offspring. As an example, a third of the males and a fifth of the females that manage to raise some young during their lifetime in the short-

tailed shearwater (*Puffinus tenuirostris*) raise only one chick. In this latter study, half of the chicks are produced by 15% of the adults.

FACTORS EXPLAINING LIFETIME REPRODUCTIVE SUCCESS (LRS)

Seabirds are mostly long-lived, prudent reproducers, and long-term population studies have revealed that a large part of the variance in LRS is actually due to breeding lifespan (Table 3). This effect is most striking for species with a higher number of breeding years (compare the short-tailed shearwater with the red-billed gull *Larus novaehollandiae*). The long-lived individuals are in most cases the ones contributing most to the future gene-pool. This suggests a strong selection for viability in seabird populations. This effect may consist of two main components: (1) more breeding seasons implying more chances to raise young; and (2) the association between breeding success and breeding experience in most seabirds studied. This effect of breeding experience or age is very general (Moreno, 1998) and suggests that the last years of reproduc-

TABLE 2. – Proportion of fledged young that breed and proportions of breeders that raise some young and some recruits throughout their lifetime in several seabird species.

		Prop. fledged young that breed	Prop. breeders that raise young	Prop. breeders recruits
Little blue penguin <i>Eudyptula minor</i>	Males	0.35	0.57	0.20
	Females	0.28	0.64	0.18
Short-tailed shearwater <i>Puffinus tenuirostris</i>	Males	0.73	0.28	
	Females	0.69	0.31	
Red-billed gull <i>Larus novaehollandiae</i>	Males	0.22	0.64	0.17
	Females	0.18	0.61	0.24
Kittiwake <i>Rissa tridactyla</i>	Males	0.34	0.95	0.41
	Females	0.42	0.96	0.50

Based on studies by Dann and Cullen (1990), Wooller *et al.* (1988), Mills (1989) and Coulson (1988a).

TABLE 3. – Effects of breeding lifespan on lifetime reproductive success (r^2 from regression analyses) and breeding lifespan in years for several seabird species.

		Effect of breeding lifespan (r^2) on LRS	Breeding lifespan (years)
Fulmar	Males	61	21
<i>Fulmarus glacialis</i>	Females	54	21
Short-tailed shearwater		98	28
<i>Puffinus tenuirostris</i>			
Little blue penguin	Males	74	12
<i>Eudyptula minor</i>	Females	81	15
Kittiwake	Males	83	20
<i>Rissa tridactyla</i>	Females	80	20
Red-billed gull	Males	31	7
<i>Larus novaehollandiae</i>	Females	29	9

From studies by Ollason and Dunnet (1988), Wooller *et al.* (1989), Dann and Cullen (1990), Coulson (1988a) and Mills (1989).

TABLE 4. – Percentage of variability explained by life-history traits other than longevity in several seabird species.

	Trait	% of variability in LRS
Fulmar	Fecundity	12
<i>Fulmarus glacialis</i>	Offspring survival	48
Kittiwake	Fecundity	7
<i>Rissa tridactyla</i>	Offspring survival	4
Red-billed gull	Mean lifetime laying date	Females 32
<i>Larus novaehollandiae</i>		Males 15

From studies by Ollason and Dunnett (1988), Coulson (1988a) and Mills (1989).

tion in long-lived seabirds may be crucial for LRS. However, the linearity suggested in the associations found (Coulson, 1988a; Dann and Cullen, 1990) indicates that the effect of experience/age is not as important as one might think based on the seabird literature.

A considerable part of the variation in LRS is due to factors unrelated to longevity. These may be breeding frequency, egg size, breeding date or mate retention (Table 4). There is also a high consistency in fitness-related breeding parameters between years expressed as repeatability (Table 5). However, one should beware of repeatabilities obtained for a few years, as age effects may explain part of this consistency (Catry, 1999). Consistency in breeding performance has been interpreted as being due to differences between breeders in a highly elusive property called “parental quality”. Parental quality is a widely used term in the seabird literature and usually refers to consistent differences in some aspect of breeding success (e.g. Nisbet *et al.*, 1998; Wendeln

and Becker, 1999). There is a striking circularity in this description, as reproductive success is used to define parental quality, which is then used to explain differences in the same variable used in the definition. As such, parental quality is non-explanatory and just a catchword used to hide our ignorance of what is really happening. In some studies, parental quality is simply the variation in breeding performance which cannot be explained by other measured variables (Coulson and Porter, 1985; Saether *et al.*, 1997).

To avoid tautologous arguments it is necessary to define parental quality in terms of something different from reproductive success. One way is the same as has been proposed by philosophers of biology to avoid the tautology in the definition of natural selection as “the survival of the fittest”. Using an approach similar to Brandon (1990), we could define parental quality of an individual breeder as “the propensity to obtain a high reproductive success in a certain environment”. Lightning may kill a high-quality parent before the end of reproduction, but that individual would still have a high propensity to breed successfully. Once the philosophical side is solved, we confront the operational problem: is there any way to establish this propensity independently of actual breeding success? I think this is a crucial problem in seabird ecology for two reasons: (1) in basic science, it is necessary to determine what traits underlie parental quality to understand how variation in these presumably strongly selected traits is maintained (the alternative of no variation is unrealistic because we know that there is a great

TABLE 5. – Individual consistency in measures related to reproductive success expressed as repeatability (r) or percentage of variation explained by individuals.

	Trait	Consistency
Chinstrap penguin	Hatching date	$r = 0.89$
<i>Pygoscelis antarctica</i>		
Fulmar	Laying date	33 % variation
<i>Fulmarus glacialis</i>	explained	
Common murre	Laying date	$r = 0.20$
<i>Uria aalge</i>		
Arctic skua	Laying date	$r = 0.45$
<i>Stercorarius parasiticus</i>	Clutch volume	$r = 0.73$
	Chick growth	$r = 0.26$
Kittiwake	Breeding success	23% variation
<i>Rissa tridactyla</i>		

From studies by Moreno *et al.* (1998), Hatch (1990), Sydeman and Eddy (1995), Phillips and Furness (1998) and Thomas and Coulson (1988).

TABLE 6. – Correlation coefficients for associations of longevity with traits related to breeding performance in several seabird species.

	Sex	Trait	Correlation
Fulmar <i>Fulmarus glacialis</i>	Males	Fledging success	0.22 ($p < 0.05$)
	Females	Fledging success	0.26 ($p < 0.05$)
Kittiwake <i>Rissa tridactyla</i>		Chicks fledged	positive assoc.
Red-billed gull <i>Larus novaehollandiae</i>	Females	First laying date	-0.36 ($p < 0.01$)

From studies by Ollason and Dunnett (1988), Coulson (1988a) and Mills (1989).

deal of variation); and (2) in applied science, this understanding may help to identify the fraction of the population which will succeed in producing young, making it possible to either protect it or destroy it (culling).

A related question is whether individuals with a high viability (i.e. those with a propensity to attain a long life), can also be detected, and whether they are those with a high parental quality (Table 6). In some studies, reproductive rate and survival rate are significantly correlated (Table 6), which indicates that good parents are the long-lived individuals contributing to future generations, although more data are needed to strengthen this conclusion. However, this finding should not be interpreted as an absence of reproductive costs, as some seabird ecologists have stated (e.g. Coulson, 1988b). To detect life-history trade-offs one has to compare individuals with the same level of resources, i.e. one has to randomise reproductive effort levels among individuals (Stearns, 1992; Roff, 1992).

HOW CAN PARENTAL QUALITY BE MEASURED?

This positive correlation between fecundity and survival leads to our next question. In what crucial resources do the poor reproducers/survivors differ from the good ones? Seabirds offer the advantage that they do not inhabit territories, so resources must come from some other source than territoriality. The last question is related to the search for an operational measure of parental quality. We are looking for the basis of the propensity to survive and reproduce in a certain environment. This sounds like searching for the substrate of adaptedness or fitness, something which is not recommended by philosophers of biology like Brandon (1990). However, we are not dealing here with philosophical issues, but with operational ones. We need a rough approximation to adaptedness here and now, which may help

us to detect the good performers. If we have only resources to protect certain individuals in a population from destruction or impairment of reproduction, these are the only ones worth fighting for, as the rest are to a certain degree 'living dead' for evolution.

There are several variables which could give a hint about immediate reproductive prospects (Table 7). Condition measured non-destructively as mass in relation to structural size is probably less directly related to quality as it fluctuates too much in the short term. Fat or protein reserves may offer another operational measure of quality but require careful standardisation with respect to breeding stage, as reserve storage and utilisation may depend on the demands imposed by different breeding stages (Moreno, 1989). Fluctuating asymmetry of bilateral traits (Møller, 1999) also has its problems of inter-

TABLE 7. – Potential nondestructive measures of phenotypic quality which can be used to predict the reproductive performance of individuals a priori.

- Condition as mass in relation to structural size: is problematic as it fluctuates too much in the short term
- Fat or protein reserves: may offer another operational measure of quality but require careful standardisation with respect to breeding stage, as reserve storage and utilisation may depend on the demands imposed by different breeding stages
- Fluctuating asymmetry: related to developmental instability; contentious for interindividual comparisons, difficult to measure correctly
- Ptilochronology: related to conditions during moult, indirect association with conditions while breeding
- Locomotory capacity: could indicate something about the propensity to evade predators or forage efficiently, but is difficult to measure in the field in a standardised way
- Health state: healthy individuals have apparently the necessary resources to defend themselves against ubiquitous pathogens, can be derived from haematological measures
- Immunocompetence: is the substrate of health state; good health may be due to a high immunocompetence or to lack of pathogens

pretation. Locomotory capacity could indicate something about the propensity to evade predators or forage efficiently, but is difficult to measure in the field in a standardised way.

One promising avenue of research in the search for the basis of quality is general health state. Healthy individuals apparently have the necessary resources to defend themselves against ubiquitous pathogens. Finally we have immunocompetence, which is the substrate of health state. Good health may be due to a high immunocompetence or to lack of pathogens. Only the first association represents the propensity to survive, the other is just the consequence of external variation. Of course, all measures requiring the destruction of the study animals are completely unsuitable for our purposes. Is there any evidence linking some of these traits to actual reproductive success or survival probability? I have tried a first step in this direction through two recent studies on penguins. In the first performed on the chinstrap penguin on Deception Island, Antarctica, we were able to measure some variables related to health state and cell-mediated immunity in early and late breeders with a two-week difference in breeding date (Moreno *et al.*, 1998). We used leukocyte counts in blood smears and the PHA response test to that end. We measured these variables at hatching of the chicks. We found that early breeders had symptoms of a better health than late breeders as evidenced by lower numbers of lymphocytes and heterophils and higher levels of T-cell-mediated immunocompetence. Breeding date has important implications for reproductive success in this population (Viñuela *et al.*, 1996). Thus immunocompetence may assist us in identifying early and therefore successful breeders in this population. In Magellanic penguins breeding on the Atlantic coast of Patagonia, we measured hematological variables related to prior infection at hatching of their chicks (Moreno *et al.*, 2002). We found that females with leukocytosis laid smaller eggs, raised chicks with slow growth and failed in raising young to a higher degree than females with better health indicators. These studies pinpoint the importance of health and immunocompetence as indicators of parental quality in seabirds, but they are only a first step.

The detected variation in immunocompetence in wild populations may indicate either that this trait has a low heritability or that its genetic architecture is too complex to allow erosion of existant variation through selection (Merilä and Sheldon, 1999). The study of the genetic and environmental components

TABLE 8. – Percentage of variation explained by nest of origin (genetic component) and statistical significance of its effect on cell-mediated immunity in cross-fostering studies of different bird species.

Species	Percentage of variation explained	Significance
American kestrel <i>Falco sparverius</i>	12%	p<0.05
Great tit <i>Parus major</i>	15%	p<0.001
Pied flycatcher <i>Ficedula hypoleuca</i>	9.7%	NS
Swallow <i>Hirundo rustica</i>	20.1%	p<0.01

From studies by Tella *et al.* (2000), Brinkhof *et al.* (1999), Soler *et al.* (2003) and Saino *et al.* (1997).

of immunocompetence is still in its infancy although studies on a few non-seabird species suggest that the heritable component measured in cross-fostering studies is small but significant (Table 8).

A typical flawed argument expressed by some seabird ecologists when confronted with the need to monitor health state or immunocompetence is that it is only food availability that determines reproductive success, with parasites and pathogens looking from the sidelines. This argument confuses the environmental factor affecting reproductive success or mortality with the actual physiological mechanism determining proximately death or reproductive failure. It is not food scarcity which directly kills the animals or leads them to abandon their young but the increasing foraging costs interacting with condition and health state. When food gets scarce, some individuals survive or manage to breed and others do not. What determines the difference between these two categories of individuals? Here lies the crux of the matter because food is scarce for all.

IMPLICATIONS FOR CONSERVATION

There is a further added need to monitor immunocompetence in seabird populations. Global change in pollutant levels, radiation incidence and climate may already be affecting the immunocompetence of seabirds (Sagerup *et al.*, 2000), as they are doing for the more publicised marine mammals. Before confronting a sudden breakdown in immunocompetence of endangered seabirds, we should try to get baseline levels on populations little affected by human-induced changes yet. Sudden mass mor-

talities in the future may be associated with changes in immune defenses if we know what to expect. As a general point, the neglect until present of the immune system in ecological and conservation studies (Sheldon and Verhulst, 1996) should be replaced by a fuller consideration of its importance for life histories and population dynamics.

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