

S02-1 Prediction of individual reproductive success in short-tailed shearwaters, *Puffinus tenuirostris*

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Abstract Previous studies of the short-tailed shearwater, *Puffinus tenuirostris*, have identified assortative mating based on age from first breeding as a strong predictor of reproductive success. The physical traits of a large number of breeding pairs were measured on Great Dog Island, Tasmania, and their breeding success recorded. Modest sexual dimorphism was found, primarily in bill depth. Significant correlations between pair members were recorded in bill depth and tarsus length. In addition, those females having a lower absolute deviation from the mean in bill depth had a significantly greater likelihood of producing an egg, as did those males that had a higher absolute deviation from the mean in head length. Female body condition indices at hatching and at laying were also predictors of breeding success.

Key words Assortative mating, Breeding success, Morphometrics, Condition index, Natural selection, Darwinian fitness

1 Introduction

Short-tailed shearwaters *Puffinus tenuirostris* are medium-sized (500 g), burrow-nesting procellariiform seabirds which breed in southeastern Australia, mainly on islands around Tasmania. They are transequatorial migrants that return to colonies in late September and lay in late November. The single young leaves late April (Warham, 1990, 1996).

A small colony of 100–200 shearwaters on Fisher Island in Bass Strait has been studied annually since 1947. All individuals have been identified reliably since 1950 and their mates and reproductive performance recorded each year. Of the birds that have completed their life histories, 8% have produced over 50% of the birds that have returned to Fisher to breed (Wooller et al., 1988). Thus, a core of very successful breeders produces the majority of the subsequent generation.

Breeding age (measured from the year of first breeding) has a substantial effect on reproductive success (Bradley et al., 1995, 2000; Wooller et al., 1990). Bradley et al. (2000) found curvilinear relationships with age in the proportion of breeders attending the colony and, given the existence of an egg, the probability of producing a fledgling. In both cases, success increases with breeding age to an optimum, after which success declines as the birds grow old. However, the probability of an attending bird being associated with an egg continues to increase through life.

The number of years spent breeding with a particular mate is also a highly significant predictor of breeding success (Bradley et al., 1990; Wooller et al., 1990; Wooller and Bradley, 1995). Given age dependent effects, it is logical to

find evidence of assortative mating in breeding age. Bradley et al. (1995) used a random model of re-pairing birds (birds requiring a mate because of mate death, divorce or recruitment) to show that older birds had a greater probability of pairing with older birds than chance alone could predict.

The Fisher Island study has required minimal interference to breeding adults. Consequently, although they were handled to establish identity and burrow occupancy, they have never been weighed or measured. Although the Fisher data provide very high power in measuring variation in lifetime reproductive success, or in testing for age or historical effects, they do not, to date, provide information on physical predictors of success. Hence, since 1991, a second site on neighboring and much larger Great Dog Island, 5 km south of Fisher, has been used as a monitoring and experimental site to add to the information from Fisher and to provide some replication of our findings. In 1991, an extensive program was initiated on Great Dog to measure and weigh breeding birds at various stages of reproduction. Over a single season, this study provided an opportunity to use large sample sizes to search for evidence of physical predictors of breeding success.

Successful breeding is a joint and interactive process between two individuals (Black, 1995). Individual and joint measures can be used to predict breeding success on the basis that the pairings represent random subsets, at least from the aspect of physical variables. If, however, there is a degree of assortative mating associated with physical parameters, or the behavior of one individual through the breeding process affects the weight or body condition of the other, then there is the opportunity for a pair member to

influence, directly or indirectly, the physical attributes of the mate.

2 Breeding success and physical measures

Physical measures fall into two categories which behave in different ways. First, skeletal or body shape variables (e.g., tarsus length, wing length) have, in general, high heritabilities (e.g., Gustaffson, 1986) and are highly repeatable in adults. Where these variables provide a prediction of breeding success, which is itself a component of Darwinian fitness, they flag the action of natural selection and may change or stabilize gene frequencies at the polygenic loci modifying these traits (Gustaffson, 1986; Kruuk et al., 2001; Gibbs and Grant, 1987). The second category includes measurements of mass and condition indices. These variables have lower repeatabilities, and evidence from other procellariiform studies (e.g., Weimerskirch and Lys, 2000) indicate that they change in value systematically through the breeding process.

Differences in the mean values of skeletal variables between successful and unsuccessful birds indicate at least the possibility of directional selection. Heritable changes in beak shape and other morphological traits have been demonstrated in one of Darwin's finches (*Geospiza fortis*) in drought and heavy rainfall years (Gibbs and Grant, 1987). This example reinforces the point that selective change need not be constant from year to year. However, a more common situation, according to quantitative genetics theory (Robertson, 1955; Stearns, 1992; Falconer and MacKay, 1996), is that of stabilizing selection where individuals close to the mean are fitter than those at one or other of the extremes of the distribution of the trait. In this situation the convergence of the mean and optimum fitness is the outcome of past selection, and the mean tracks the optimum. Under this model, we would expect successful birds, on average, to exhibit a lower absolute deviation from the mean than unsuccessful birds. For example, in Bewick's swans (*Gygis columbianus bewickii*), large males tend to have the highest reproductive success (Rees et al., 1995), whereas medium-sized males have the highest success in whooper swans (*C. cygnus*) and mute swans (*C. olor*). A third form of natural selection, disruptive selection, acts in the opposite way to stabilizing selection. In this case, fitness should be lowest close to the mean; and thus, under this model, successful birds will exhibit a higher absolute deviation from the mean than unsuccessful birds.

3 Correlations in physical measurements between pair members

Skeletal traits are generally invariant and highly repeatable. If they have the potential to be indicators of reproductive success because, for example, they affect the individual's foraging efficiency, then we might expect them to be good indicators to a potential mate also. For example,

size in the pinyon jay (*Gymnorhinus cyanocephalus*) is a predictor of reproductive success, and is also a demonstrable factor in mate choice (Marzluff et al., 1995). The behavior of assortative correlations between trait values in pair members will depend upon which selection model applies to the skeletal traits.

Under stabilizing selection, individuals close to the mean should select each other, and more extreme individuals will be left with each other by default. However, this would not show up as a correlation in raw values since, presumably, an individual with an extreme low value would be just as likely to mate with an individual with an extreme high value. Under these circumstances, however, absolute deviations from the mean would be positively correlated. If the measure in question were subject to disruptive selection, the reverse would apply. Mates with extreme values would be preferred. In terms of correlation this would be indistinguishable from stabilizing selection. Under directional selection, if a trend was sufficiently long term, we would expect assortative mating to evolve on the raw value of the measure. However, as Merilä et al. (2001) point out, long term directional selection on heritable traits need not produce the expected shift in the trait mean.

4 Methods

In the 1991–1992 breeding season, 1 750 burrows on Great Dog Island were checked 1–3 times per week for their contents. Occupant adults were weighed, measured and banded; eggs were weighed and measured. The adult pre-laying mass was taken before the birds departed on the pre-laying exodus, from 15 October to 3 November. The adult laying mass was taken upon return from exodus, from 21 November to 4 December. Because of the extreme synchrony of laying in this species, all females at this point were still on the first incubation shift and had not fed. The adult hatching mass was taken from 16–30 January. Final checks to ascertain fledging of the chicks took place from 6–11 April.

The measurements taken of adults were: head length, bill length, bill depth, tarsus length and wing length. Condition indices were calculated for each bird at each weighing by transforming each morphological measurement into standard deviations from the mean (zscores), summing the zscores across variables and dividing the mass by this result. Joint or mid-parent values for each pair were calculated by averaging male and female measurements. Absolute deviations from the mean were also calculated for each variable by subtracting the mean of the appropriate sex and taking the absolute (unsigned) value of this difference.

Six binary indices of breeding success were used: from pair down a burrow to production of an egg (pair to egg); from pair down a burrow to hatching (pair to hatching); from pair down a burrow to fledging (pair to fledging); from egg to hatching; from egg to fledging; and from hatching to fledging. Some categories included others (e.g., pair to hatching includes egg to hatching), and therefore these

Table 1 Sexual dimorphism in breeding short-tailed shearwaters

Variable	Gender		Difference	F-test		
	Female	Male		df	F	P
Head length (mm)	80.83±0.09	82.75±0.08	2.34%	1 104	245.92	0.000
Bill length (mm)	31.84±0.06	32.72±0.04	2.71%	1 104	150.21	0.000
Bill depth (mm)	8.15±0.02	8.85±0.02	8.22%	1 104	872.05	0.000
Tarsus length (mm)	58.22±0.09	58.97±0.07	1.28%	1 104	44.50	0.000
Wing length (mm)	270.90±0.29	273.13±0.24	0.82%	1 104	34.58	0.000
Pre-laying mass (g)	533.80±2.74	555.83±2.75	4.04%	469	30.73	0.000
Laying mass (g)	617.63±4.37	630.87±2.74	2.12%	760	7.09	0.000
Hatching mass (g)	639.18±8.52	660.83±7.26	3.33%	119	3.79	0.054

Mean ± standard error is given. The column "Difference" gives the female mean subtracted from the male mean expressed as a percentage of the average of the two means.

variables were not independent of each other. However, because all members of each pair were not included at each weighing, sample sizes, and hence the power of each test, will differ within each of these measures.

Using the SPSS statistical package, unequal sample size *t*-tests were performed for each of the body measurements, masses, condition indices and absolute deviation variables, using the success indices as categorical variables. Because of the substantial repeat testing involved for each breeding success variable, nominal significance levels were set at one in 100 rather than one in twenty (Bonferroni correction).

5 Results and discussion

The measurements of breeders within pairs demonstrate that detectable but small sexual dimorphism exists in this species (Table 1). The most marked difference occurs in bill depth, where the difference between the sexes is 8%. Bill length and head length are approximately 2% different, and tarsus and wing length 1%. Mass measurements vary between 2% and 4% depending on the stage of the breeding cycle. The male is the bigger bird for all variables.

No linear (i.e., untransformed) skeletal variables are

significantly different between successful and unsuccessful birds for any of the measures of reproductive success (Table 2). The only linear (as opposed to absolute deviation) variables for which $P < 0.01$ are female condition index variables. There are two absolute deviation variables which are significant at this level: male head length and female bill depth. This would indicate that skeletal variables are not subject to detectable fluctuating or directional selection. However, female bill depth appears to be subject to stabilizing selection where the production of the egg is concerned. The effect is stronger, with a deviation 20% greater on average, in unsuccessful females than in successful ones. Also, male head length appears to be subject to disruptive selection because males successful in egg production have a deviation from the mean which is 25% greater than in unsuccessful ones.

It is obvious that male head length is unlikely to be a direct determinant of the ability of the female to lay an egg, and it is difficult to envisage how disruptive selection will act on this trait unless an assortative mating effect is involved. Male head length deviation also approaches significance for the pair-to-hatching reproductive success measure, but since this includes the pair-to-egg measure,

Table 2 Proportionate differences between individuals showing reproductive success or failure

	Pair to egg	Pair to hatching	Pair to fledging	Egg to fledging	Hatching to fledging
Female hatching index	0.176	0.145	0.401	0.392	0.377
<i>P</i>			0.002	0.003	0.014
Female laying index	-0.071	-0.072	0.008	0.039	0.136
<i>P</i>					0.010
Male head length deviation	0.253	0.297	0.273	0.178	0.013
<i>P</i>	0.006	0.020			
Female bill depth deviation	-0.205	-0.136	-0.210	-0.074	-0.157
<i>P</i>	0.01				

Difference of success-failure is standardized by dividing by the average. Only variables with a significant difference have been included. *P* = probability value.

and the magnitude is only slightly larger (30%), this is probably measuring the effect of egg production alone.

The strongest effects on fledgling production are produced by the female hatching condition index (Table 2). The reproductive success measures of pair to fledging and egg to fledging are all significant at $P < 0.01$; and hatching to fledging approaches this ($P = 0.014$). The magnitude of the effect is large in that the successful females have a condition index which is approximately 40% greater than the unsuccessful ones in each case. The fact that pair to egg, pair to hatching, and egg to hatching measures are not significant suggests that the effect is restricted to the fledgling from hatching stage. In addition, since both birds feed the chick, the question remains why the difference occurs in the condition index for the female and not for the male.

The female laying condition index has a significant effect (14%) on hatchling to fledgling production. One possible mechanism explaining this effect is that female condition is correlated with egg quality and that the effect is transmitted through the egg. On the hand, Nager et al. (1999) point out that egg production has a major effect on female condition in the lesser black-backed gull (*Larus fuscus*). In the shearwater, it is possible that females are more prone to desert than males because of poor condition during chick feeding, brought on by egg production, so threatening their future reproduction.

Some evidence exists of assortative mating in linear variables (Table 3). There are modest correlations between tarsus lengths and bill depths among pairs. Male head length also correlates with female bill depth, as does male summed zscore. Male prelaying mass and prelaying condition index correlate negatively with female bill length. Male laying condition index negatively correlates with female bill depth, and vice versa. While we might expect the strongest correlations between sexes to exist between like variables, this need not be the case. Forero et al. (2001) have demonstrated the occurrence of assortative mating from bill depth and body mass in magellanic penguins (*Spheniscus magellanicus*).

Adult prelaying mass is substantially correlated across the sexes (Table 3). This may be evidence that pair members feed together before laying, or, at least, share common experiences. Alternatively, such a correlation could be generated by assortative mating for foraging skills. There is evidence of a modest degree of assortative mating for breeding age in this species (Bradley et al., 1995). It is possible that increasing the age of breeding tends to generate heavier prelaying birds because they are more efficient foragers. In addition, there is a strong correlation between the male prelaying condition index and female laying condition index. This suggests that good male condition early in the reproductive period is linked to good female condition later. A possible explanation for this effect is that prelaying males in better condition are replaced later in the first incubation shift, allowing females to build up better condition.

6 Conclusion

We have found evidence in the short-tailed shearwater that individual quality, which is a constant attribute from year to year, is related to, and indicated by, specific physical traits, notably condition and bill depth. Such traits are predictors of reproductive success and, since studies of other avian species (e.g. Gustaffson, 1986; Gibbs and Grant, 1987) indicate that they have substantial heritability, the evidence suggests the operation of some form of natural selection.

Previous studies of this species have established assortative mating based on age from first breeding, which is itself a strong predictor of reproductive success (Bradley et al., 1995). Thus, it is likely that mate selection involves cues that give some indication of an individual's reproductive abilities. In this study, bill depth, which shows strong sexual dimorphism, also exhibits correlation between pair members, and, in the female, predicts reproductive success. It is possible that a mixture of significant sexual and stabilizing selection acts upon this trait, and that its strong dimorphism is the outcome of the balance between these effects.

Table 3 Correlations between physical traits of pair members

Female variables	Male variables					
	Head length	Bill depth	Tarsus length	Prelaying mass	Summed zscores	Prelaying condition index
Bill depth	0.164	0.135	0.056	-0.009	0.151	-0.118
<i>P</i>	0.003				0.007	
Tarsus length	0.062	0.053	0.163	-0.045	0.065	0.001
<i>P</i>			0.004			
Prelaying mass	-0.048	0.027	0.019	0.277	0.032	0.095
<i>P</i>				0.000		
Laying condition index	-0.103	-0.253	-0.200	-0.016	-0.194	0.378
<i>P</i>		0.002				0.007

The top figure is the Pearson correlation coefficient. Only variables with a significant correlation between pair members have been included. *P* = probability value.

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