How slow breeding can be selected in seabirds: testing Lack's hypothesis

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The historical debate of the 1960s between group and individual selection hinged on how the slow breeding of seabirds could be explained. While this debate was settled by the ascendance of individual selection, championed by David Lack, explanations for slow breeding in seabirds remain to be tested. We examined the slowest breeding of these birds, the albatrosses and petrels (order Procellariiformes), using analyses that statistically controlled for variations in body size and phylogeny. Incubation and fledging periods appeared strongly correlated, but this turned out to be largely explained by phylogeny. Nonetheless, developmental and reproductive rates were associated with the distance to the foraging range, as predicted under the hypothesis of ecological constraints on breeding pairs, and these results were independent of body size and phylogeny. Slower breeding in these seabirds appeared associated with the rigors of farther pelagic feeding, as Lack originally hypothesized.

Keywords: albatrosses; David Lack; slow breeding; individual selection; petrels

1. INTRODUCTION

An epiphany occurred in evolutionary biology during the 1960s, produced by a disagreement between two ornithologists. This well-known argument was between the concept of group selection or 'the good of the species' (articulated by the ornithologist Wynne-Edwards in 1962) and Darwin's (1859) concept of individual selection (championed by Williams (1966) and Lack (1968), the latter an ornithologist). Central to this debate was the extremely slow reproductive rate of seabirds, especially in procellariiform (petrel and albatross) species. Slow breeding appeared to be difficult to explain in terms of individuals maximizing the numbers of their offspring. Petrels and albatrosses are indeed the largest group of birds with extremely slow reproductive rates, some species laying a single egg every two years and rearing one chick about every four years (Ricklefs 1990; Jouventin *et al.* 1999; Tickell 2000). At the same time, sexual maturity is delayed up to 12 years, annual survival is as high as 96%, and lifespan extends up to 60 years (Jouventin & Mougin 1981; Jouventin & Weimerskirch 1988). While the debate over group versus individual selection was resolved in favour of the latter, tests have not been made of Lack's (1968) explanation of these slow reproductive rates as reflecting the difficulties of feeding in pelagic environments that are considerable distances from breeding colonies.

Lack's (1968) explanation of slow breeding in seabirds was limited by a dearth of natural history information, because only a few demographic field studies of pelagic birds had been conducted. Therefore, he was forced to compare species with extremely different lifestyles. For example, his argument that pelagic ecology could explain

limited reproduction in seabirds rested on a comparison of a near-shore feeding penguin and a relatively far-pelagic shearwater. These species differ not only in the ability to fly but also in body size. Nonetheless, he made several predictions about how characteristics of life history should vary with the distance the seabird species must travel to forage. Primary among these was that farther-foraging pelagic species should show strongly curtailed reproductive rates, but he also predicted the dependence of care and growth of young on the distance to feeding areas. Lack (1968) not only had to work with limited field data, but also did not have the statistical tools available for incorporating possible confounding influences, such as body size (and phylogeny, see §2) into his analyses.

The purpose of our study was to test Lack's (1968) predictions, derived from his Darwinian view of seabird populations, with extensive information on pelagic bird demography and ecology at sea. We chose to examine only species in the order Procellariiformes, because they are a large group of closely related species that share a basic lifestyle of foraging over the ocean by flight, rather than comparing extremely different groups of seabird species that exhibit highly divergent lifestyles. All the 125 extant procellariiform species exhibit slow reproduction (Brooke 2004), laying only one egg every year or every other year, but also exhibit the most extensive variation in body size of any avian order (Warham 1990). Body size is an important life-history trait that must be taken into account in any interspecific study (Roff 1992; Stearns 1992). With data on petrels and albatrosses, we examined body size, reproductive rate and developmental periods of young. Several species of pelagic seabirds have been studied through numerous and detailed observations in breeding colonies on land and with satellite transmission of locations of foraging range at sea (well known for large

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seabirds, Jouventin & Weimerskirch 1990; Catard & Weimerskirch 1999). Although they remain to be accurately documented for all seabird species, foraging ranges can be generalized. Thus, it was possible to examine how rates of reproduction and subsequent development of young vary with general estimates of the distance that parents have to travel to forage.

A further problem in studying reproductive and ecological patterns among species is the extent to which history has resulted in groups of species that share traits owing to common ancestry (Dobson 1985; Felsenstein 1985). Non-independence of related species can cause sampling problems that bias estimates of significance of statistical tests (Harvey & Pagel 1991). Lack (1968) partly accounted for historical relationships among species by comparing both within groups of seabirds like the Procellariiformes, and among species from different groups of birds that were of similar body size. He considered his predictions to be mostly independent of body size and phylogeny, but he had no statistical tools for evaluating their influence. Thus, in our analyses, we considered both the influences of body size and phylogeny as possible confounding factors, and we analysed seabird breeding with and without statistical adjustment for these variables (after Price 1997).

2. MATERIAL AND METHODS

We used a long-term dataset on 43 species of petrels and albatrosses that was derived from literature sources and particularly from studies conducted by the French Polar Institute in the French Southern and Antarctic Territories. These data had been collected for up to 40 years, though this varied among species (Jouventin & Mougin 1981; Warham 1990; Tickell 2000; electronic supplementary material, appendix A). Banded birds were monitored on marked nests for several years (usually more than 10 years) for reproductive success. Species' foraging ranges were estimated first using visual observations of foraging individuals (from islands and from ships), and more recently by satellite tracking of breeding individuals in the southern oceans of the world (Jouventin & Weimerskirch 1990). Species were classified into three categories: near-shore feeders (foraging range less than 200 km offshore); mid-distance feeders (foraging range between 200 and 1000 km offshore); and far-pelagic feeders (foraging range more than 1000 km offshore).

We examined associations of traits that were explicitly mentioned by Lack (1968). These were average body mass of adults, egg mass, length of the incubation and fledging periods, mean duration of incubation shifts (mates take turns incubating, so the length of a 'sit'), average number of feeds delivered per day to the chick, average number of chicks produced per year, number of eggs produced per year and probability of fledging success given production of an egg. Egg mass was estimated from egg length and width (from Brooke 2004) using Hoyt's (1979) formula. Variables were log-transformed (adult body mass, egg mass, incubation shift, feeding frequency, incubation period, fledging period, growth period, chicks per year and feeding zone) or square-root arcsine transformed (eggs produced per year) where necessary to conform to normality. The direction of relationships was specified hence, we used unilateral significance of correlation coefficients (SAS statistical software, SAS Institute Inc.

Table 1. Maximum and minimum characteristics of body mass, developmental periods, parental attendance and reproduction of procellariiform species. (The growth period is the summed incubation and fledging periods, and chicks per year is the product of reproductive frequency (egg production per year per mated pair) and fledging success (the probability that an egg results in a fledged chick)).

trait	minimum	maximum	N
adult body mass	28 g	9600 g	43
egg mass	7 g	476 g	42
incubation period	40 days	79 days	42
fledging period	46 days	278 days	42
growth period	92 days	357 days	42
incubation shift	1.3 days	20.2 days	37
feeding frequency	0.26 feeds per day	1 feed per day	28
chicks per year	0.20 chick	0.88 chick	25
reproductive frequency	0.51 eggs per year	0.90 eggs per year	26
fledging success	0.11 per egg	0.80 per egg	30

1990). Statistical adjustments for body size were made by extracting residuals from linear regressions of variables on log-transformed body mass. Since predictions were made *a priori*, tests were independently conducted, though most associations were so strong that adjustment for bilateral testing and multiple testing would make little or no difference to conclusions.

The consensus phylogeny for petrels and albatrosses that was produced by Kennedy & Page (2002) was used in two ways. First, we examined the relationship of body mass of adult females to phylogenetic structure with application of network autocorrelation (after Cheverud *et al.* 1985; Dunham & Miles 1992). This analysis was a preliminary test of whether body size and phylogeny co-varied. For phylogeny-free comparisons, we removed the influence of the phylogenetic tree on pairs of traits using the software PDAP (Garland *et al.* 1999; Garland & Ives 2000). Pearson's correlation coefficients are produced by this software hence, to facilitate comparisons, we used these coefficients throughout. Rank correlations (Spearman's and Kendall's- τ) produced similar coefficients and the same conclusions. A change in correlation coefficient between data that were and that were not adjusted for the phylogeny indicated phylogenetic influence and associations that were historical, and thus could reflect either historical organism–environment co-occurrence or constraints on character change (Dobson 1985).

3. RESULTS

In our sample of procellariiform species, body mass varied by over two orders of magnitude (table 1). This unique group of birds includes large albatrosses and small storm petrels, the former weighing more than 300 times the latter. Developmental traits, such as incubation and fledging times, varied by only two- to fivefold. Two ecological traits, shifts by partners during incubation and feeding frequencies of chicks, varied by 15 and 4 times, respectively. Even though all of the species lay only one egg at a time, the rate of chick production per year varied fourfold. This was due to eightfold variation in fledging success and twofold variation in the successful annual production of an egg by a mated pair (annual or biennial egg production; Jouventin & Dobson 2002).

Figure 1. Association between incubation and fledging periods for 43 species of Procellariiformes (albatrosses and petrels). Incubation and fledging periods were log-transformed. Ordinary least squares regression line is given.

Egg mass relative to adult body mass was virtually uncorrelated with length of the incubation period ($r = -0.029$, $N = 42$, $p = 0.86$) and incubation period relative to the length of the fledging period ($r = 0.033$, $N = 42$, $p = 0.84$). The incubation and fledging periods were strongly associated (figure 1), and this association was only partly due to body size (table 2; reduction in the correlation coefficient, when the influence of body mass was statistically controlled, was significant, $\Delta r = 0.295$, $N = 42$, $p < 0.02$). This strong association disappeared completely when the influence of phylogeny was removed. Adult size was closely associated with many of the characteristics of the species, including incubation period ($r = 0.895$, $N = 42$, $p < 0.0001$), fledging period ($r = 0.811$, $N = 42$, $p < 0.0001$), duration of incubation shift ($r = 0.570$, $N = 37$, $p < 0.001$), feeding frequency ($r = -0.478$, $N = 28$, $p < 0.01$) and their feeding zone ($r = 0.376$, $N = 39$, $p < 0.01$).

Body size and phylogeny strongly co-varied (network autocorrelation $\rho = 0.780$, $N = 43$, $p < 0.0001$). Since these characteristics appear statistically confounded, removing the phylogenetic influence would also result in a reduction in variation due to body mass. Thus, we examined three types of analyses: (i) correlations of transformed data that reflect actual traits and conditions in the field, (ii) correlations of data adjusted for body mass by regression, to evaluate possible influences of size (though these could also be due to history) and (iii) correlations adjusted for body mass and phylogeny using PDAP, to reveal variation unexplained by either a life-history axis of body size or historical patterns of species relationships.

Both incubation period and fledging period were significantly associated with the feeding zone, as was the developmental or growth period for young (combined incubation and fledging periods). Adjustment to remove the influence of body size did not greatly alter these relationships, but removal of phylogenetic influence resulted in the loss of an association of incubation period and feeding zone. Parents take turns incubating eggs, and the time between turns (*viz.* the incubation shift) was significantly associated with the feeding zone, regardless of body size and phylogeny. However, feeding frequency of the chick was only weakly associated with the feeding zone.

The average number of chicks produced in a year was not significantly associated with the feeding zone (table 2). Surprisingly, this association was stronger when the influence of phylogeny was statistically controlled, suggesting partial masking of the pattern by historical relationships among species. This association appeared to be most strongly influenced by the average number of eggs that a pair can produce per year (*viz.* reproductive frequency), rather than by fledging success. In particular, the relationship between reproductive frequency and the feeding zone was not strongly influenced by body size, and the phylogenetic pattern appeared to mask the strength of this association.

4. DISCUSSION

David Lack (1968) predicted a positive correlation between the incubation and chick-rearing periods, suggesting that the association should be only partly explained by body size. It should take larger birds longer to both incubate an egg and rear a chick, because the fledging size of the chick will also be large (usually heavier than the parents). In accordance with this prediction, we found a positive and significant correlation between the duration of incubation and that of chick-rearing (the fledging period), even after controlling for body mass (table 2). However, surprisingly, this pattern was completely accounted for by the influence of phylogeny. Thus, the variation in this association lies deep within the history of the clade. Within the ecological time frame of the present, we might expect that the incubation period is less labile to environmental conditions, probably due to physiological constraint. In addition, incubating an egg is energetically much less expensive than raising a chick to fledging, and the latter might undergo stronger ongoing selection by feeding conditions. During incubation, parents have to forage only for themselves. During chick-rearing, parents forage for chick and for themselves, and chicks can fledge at greater weights than their parents (Warham 1990). Associations with incubation period were not influenced by variation among species in the relative size of their eggs. As Lack (1968) predicted, relative egg size was not associated with incubation period, whether adjusted for the length of the fledging period or not.

A series of predictions about developmental periods and the general distance to foraging ranges were generally upheld. The incubation and fledging periods were significantly associated with the zone within which species feed, with the farthest foragers having the slowest developmental times (table 2). An exception was the lack of significance of distance to the foraging range on the incubation period when adjustment was made for body size and phylogeny. Our above argument might explain this pattern: incubation periods should be less likely to be constrained by the distance to the feeding zone. However, the length of time that each parent spent incubating before being relieved by the mate was influenced by the feeding zone, an ecological pattern that was largely independent of body size and phylogeny. This was not same for the feeding frequency of chicks and the feeding zone. This pattern was not strong, and it appeared to at least partly reflect the body size of the species, with little additional variation explained by the phylogeny. However, a possible

Table 2. Correlations between characteristics of development and reproduction of procellariiform species and the zone in which they commonly feed (near-shore, mid-distance and far-pelagic). (* $p \leq 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$.)

correlated traits	prediction	unadjusted correlation	body mass adjusted	body mass & phylogeny adjusted
incubation period and fledging period	+	0.878 (42)****	0.583 (42)****	0.076 (41)
incubation period and feeding zone	+	0.521 (38)***	0.420 (38)**	0.264 (37)
fledging period and feeding zone	+	0.576 (38)****	0.532 (38)***	0.455 (37)**
growth period and feeding zone	+	0.578 (38)****	0.552 (38)***	0.510 (37)***
incubation shift and feeding zone	+	0.596 (35)****	0.449 (35)**	0.380 (34)*
feeding frequency and feeding zone	—	−0.377 (27)*	−0.213 (27)	−0.254 (26)
chicks per year and feeding zone	—	−0.305 (25)	−0.239 (25)	−0.331 (24)*
reproductive frequency and feeding zone	—	−0.407 (26)*	−0.347 (26)*	−0.591 (25)***
fledging success and feeding zone	—	−0.046 (30)	−0.098 (30)	−0.107 (29)

bias is that neither volume nor quality of food for the chick was recorded.

Lack (1968) knew that all Procellariiformes lay only one egg; therefore, he proposed that coastal-feeding petrels would have abnormally short developmental time, rather than more eggs. This was generally borne out, with developmental period of fledging shorter for near-shore feeders (table 2). We also used the length of the summed incubation and fledging periods as an indicator of the rate of development of the young, and got the same result. As predicted by Lack, the further a species has to go to forage, the slower the growth of the chick is, even when influences of body mass and phylogeny were statistically removed. While Lack expected that the critical variable would actually be the rate at which chicks were fed, we found weak support at best for this prediction, especially after adjustment for body mass and phylogeny. It appears that Lack's predictions about developmental rate generally hold, though details remain to be elucidated. Nonetheless, we found that incubation and fledging periods should be examined separately, and they may well be influenced by different patterns of historical and ecological factors.

Reproduction in Procellariiformes is perhaps more variable than Lack (1968) anticipated, because in some species pairs only produce an egg every two years, while in others an egg is produced in most years (Jouventin & Dobson 2002). In addition, annual egg production and fledging rates vary greatly among the species (table 1). We found that the rate of chick production per year was significantly associated with the range during foraging (table 2); but this appeared to be due to the frequency at which pairs produce eggs, rather than success at fledging. This observation was somewhat surprising, because fledging success varies more broadly than reproductive frequency. Nonetheless, the lack of phylogenetic influence on reproductive rate suggests that variations in breeding may be due to ecological constraints that result from difficulties in foraging for these pelagic birds, as Lack predicted.

In conclusion, Lack (1968) was correct in most of his inferences, at least those concerning the dependence of developmental and reproductive rates on ecological factors like the distance to the feeding range. Our analyses differ in detail, some surprising, such as the decoupling of the association of incubation and fledging periods when

phylogeny is taken into account. With a group of species with remarkably unimodal reproductive abilities, laying only one egg at a time, we also documented that considerable variation in reproductive rate was associated with distance to the feeding range, as Lack predicted for seabirds in general. Even when Lack (1968) doubted that the Procellariiformes might follow his predicted pattern due to their production of a single egg, they in fact followed his expectation. Thus, our results supported Lack's explanation of extremely slow breeding patterns, from within the clade of Procellariiformes. In turn, our results provide support for Lack's (1968) view of slow breeding in birds being favoured by individual Darwinian selection under the harsh limitation of pelagic feeding.

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