



# Do marine birds use environmental cues to optimize egg production? An experimental test based on relaying propensity

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According to the environmental cues hypothesis, female birds use information available to them in the early-season environment to fine-tune egg production annually. However, support for the hypothesis derives largely from correlational studies. In each year from 2002 to 2006, which spanned a period of extreme variation in environmental conditions, we removed eggs from early-laying rhinoceros auklets *Cerorhinca monocerata*, burrow-nesting seabirds that lay a single-egg clutch. We then measured their relaying rates, relaying intervals, and breeding success. We also monitored the timing and success of breeding in control pairs, and control chick diets. If the experimental females base their relaying decision on early-season cues, then we predict that few will relay in years in which early-laying control birds breed unsuccessfully, and in which a preferred prey species, Pacific sand lance *Ammodytes hexapterus*, is in short supply in nestling diets. Results matched neither prediction. In each year, almost all (88–90%) of the experimental females relaid, despite that the control pairs' breeding success (32–87% fledged chicks), and their chicks' diets (twofold variation in proportion of sand lance), varied markedly. We conclude that female rhinoceros auklets did not modify their relaying decision in response to variation in environmental conditions, although relaying intervals and their own breeding success (0–78%) covaried negatively. Our results may have important implications related to using seabirds as monitors of the marine environment.

Female birds are widely held to fine-tune egg production, including laying propensity, the timing of laying, number and size of eggs, and allocation of resources within the clutch, using early-season environmental cues that predict what feeding conditions will be like weeks to months later, when they are raising chicks (van Noordwijk et al. 1995, Forbes and Mock 1996, Rutstein et al. 2005). Appropriate external cues could include ambient temperature (Meijer et al. 1999), or chemical (Bourgault et al. 2006) or visual (Perfito et al. 2004) indicators. That fine-tuning could be especially important to fitness in seasonal environments, where deteriorating feeding conditions often drive seasonal declines in breeding success (Perrins 1970). However, with notable exceptions (e.g., Wingfield et al. 2003), support for the “environmental cues” hypothesis derives largely from correlational studies, which potentially fail to distinguish between internal, physiological constraints operating during egg production (Stevenson and Bryant 2001) and the strategic use of external, environmental cues.

Theory suggests that marine birds should be flexible in their reproductive investment, due to the extreme variability of their breeding environments (Erikstad et al. 1998). Previous studies have shown that many seabird species exhibit flexibility in the rate at which they provision offspring, which they vary in response to feeding conditions, chick demands, and their own self-maintenance needs

(Lorentsen et al. 1999, Weimerskirch et al. 2001). However, because most research has focused on post-hatching investment in seabirds, we know little about how flexible the investment in eggs might be across a range of environmental conditions.

We tested predictions of the environmental cues hypothesis in the rhinoceros auklet *Cerorhinca monocerata*, during a five-year period of extreme and well-described variation in the marine environment of the northeast Pacific (Sydeman et al. 2006, Mackas et al. 2007). We focused on an important facet of egg production, and one that is easily manipulated: the probability that a female relays following egg loss. In each year, we removed first eggs from early-laying females, then measured egg size and the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable isotopic signatures in yolks, the latter to assess interannual variation in foraging ecology during egg production. We then measured the proportion of experimental females that relaid, as well as the length of time taken to relay, and their success with the replacement egg. We simultaneously monitored the breeding success of control pairs, as well as the size and species composition of food loads delivered to nestlings.

If females modify their relaying decision in response to early-season cues that forecast feeding conditions later in the breeding episode, then we predict that: (1) more experimental females will relay in years in which their peers

early-laying control pairs – breed more successfully, and (2) more experimental females will relay in years in which Pacific sandlance *Ammodytes hexapterus*, a putatively preferred prey species at our study site (Hedd et al. 2006), figures more prominently in chick diets. Two assumptions are inherent in our approach. First, that the control pairs' breeding parameters respond to environmental variation, an assumption strongly supported by empirical evidence at our study site (Bertram et al. 2001, Gjerdrum et al. 2003) and at others within the California Current system (Ainley and Boekelheide 1990, Sydeman et al. 2001). And second, that the environmental factors that affect breeding success encompass the cues that females would use to decide whether or not to relay. A more direct, but less holistic approach would be to compare relaying rates directly to environmental predictor variables, alone or in combination. However, in reality we do not know what specific cue(s) the birds might use, so that negative statistical results from those analyses could not be considered definitive evidence against the hypothesis.

As experimental subjects, we used females that laid early in the season. In other species of Alcidae, early-laying females tend to be older, more experienced, and more successful birds (de Forest and Gaston 1996, Pyle et al. 2001), those in better body condition and with greater capacity to invest in their offspring (Gaston and Hipfner 2006). In this way, we are removing internal physiological constraints on relaying propensity as a factor as best we can, enabling us to conduct stronger tests of the hypothesized role of external factors (i.e., environmental cues).

## Methods

We conducted our study at Triangle Island, British Columbia, Canada (50° 52'N, 129° 05'W) from late April (prior to the start of laying) to late August (by which time all but a few chicks had fledged) of 2002–2006. On a control plot, we inspected all breeding burrows at 5 d intervals to determine laying dates. When an egg was found, the burrow was then left undisturbed for 40 d, based on a 45 d incubation period (Gaston and Deschene 1996). Burrows were then checked at 5 d intervals until a hatchling was found. When first found, we measured hatchling wing length (to within 1 mm) and mass (to within 1 g), and estimated hatching date (age 0) using a calibration of wing length against age for known-aged chicks at Triangle Island. We weighed and measured nestlings at ages 5, 10, 40 and 45 d, and then every other day until they disappeared (nestling periods average 54 d; Gaston and Deschene 1996).

We sampled control pairs' nestling diets by intercepting ca. 10 adult birds returning to the colony to feed their chicks, in areas away from monitoring plots, at 7–10 d intervals throughout the chick period. Rhinoceros auklets, which provision nocturnally with one to many fish or large invertebrates, were caught on the ground with fishing nets before they could scramble into burrows. Food loads were placed in whirlpak bags. We weighed complete food loads to within 0.1 g using an electronic balance, and also the masses of all individual prey items within all loads. Items were identified to the lowest possible taxonomic level, usually species.

Experiments were conducted on a neighbouring plot, on which we inspected burrows at 2 d intervals from the start of the season. When an egg was found, we collected it, measured its length and breadth (to within 0.1 mm) and mass (to within 1 g), then preserved it (n = 31 eggs in 2002 in a pilot project, see Hipfner et al. 2004), and n = 10 eggs in 2003–2006). Eggs were collected prior to the median laying date on the control plot (Fig. 1). As a measure of egg size, we used an index of volume (length × breadth<sup>2</sup>), that has a strong linear relationship with fresh egg mass (Hipfner et al. 2004).

In 2003–2006, we rechecked experimental burrows every 5 d beginning 10 d after eggs were removed. Methods were slightly different in 2002 (Hipfner et al. 2004), which precludes use of 2002 data in the comparisons of relaying intervals. When a second egg was found in a burrow, we measured its length and breadth, then put it back in place. Based on studies on alcids in which eggs laid by the same female can be indentified by their background colour and markings, individual females lay first and replacement eggs of consistent shape (length:breadth ratio) at the same site (Hipfner et al. 2003). In addition, other alcids tend to use the same burrow from year to year (Pyle et al. 2001). As a result, the shape of first and second eggs found in the same burrows can be used to test whether they were laid by the same bird.

Based on these protocols, we defined burrow occupancy as the proportion of all burrows on the control plot in which eggs were laid, hatching success as the proportion of eggs laid that hatched, and fledging success as the proportion of chicks that survived at least 45 d before disappearing. Breeding success and fledging mass are the proportion of eggs laid that produced chicks that fledged, and the last mass recorded prior to the chick's departure, respectively. Finally, the annual representation of Pacific sandlance in diets is a single value calculated as the total mass of sandlance collected across all sampling sessions within the year divided by the total mass of all fish collected in that year. Note that individual food loads tend to include either exclusively sandlance, or to be entirely devoid of sandlance.

In the laboratory, we extracted ca. 1 ml samples of yolk and placed them in eppendorff tubes. Lipid-free prepared samples were sent to the stable isotope facilities at University of Saskatchewan (2002 yolks) or University of California, Davis (2003–2006 yolks) for analysis of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  signatures. Nitrogen stable isotope ratios can be used to assess the trophic level at which a consumer has fed, because  $^{15}\text{N}$  becomes systematically enriched at successive trophic levels (Peterson and Fry 1987). Carbon stable isotope ratios can be used to infer the type of marine habitat in which a consumer has fed, because  $^{13}\text{C}$  is enriched in benthic and inshore environments relative to pelagic and offshore environments (De Niro and Epstein 1978). While  $^{13}\text{C}$  also tends to exhibit trophic enrichment, that effect is much less marked than the  $^{15}\text{N}$  enrichment.

## Statistical analyses

To test the two predictions of the environmental cues hypothesis, we regressed the annual proportion of experimental females that relaid against the annual breeding

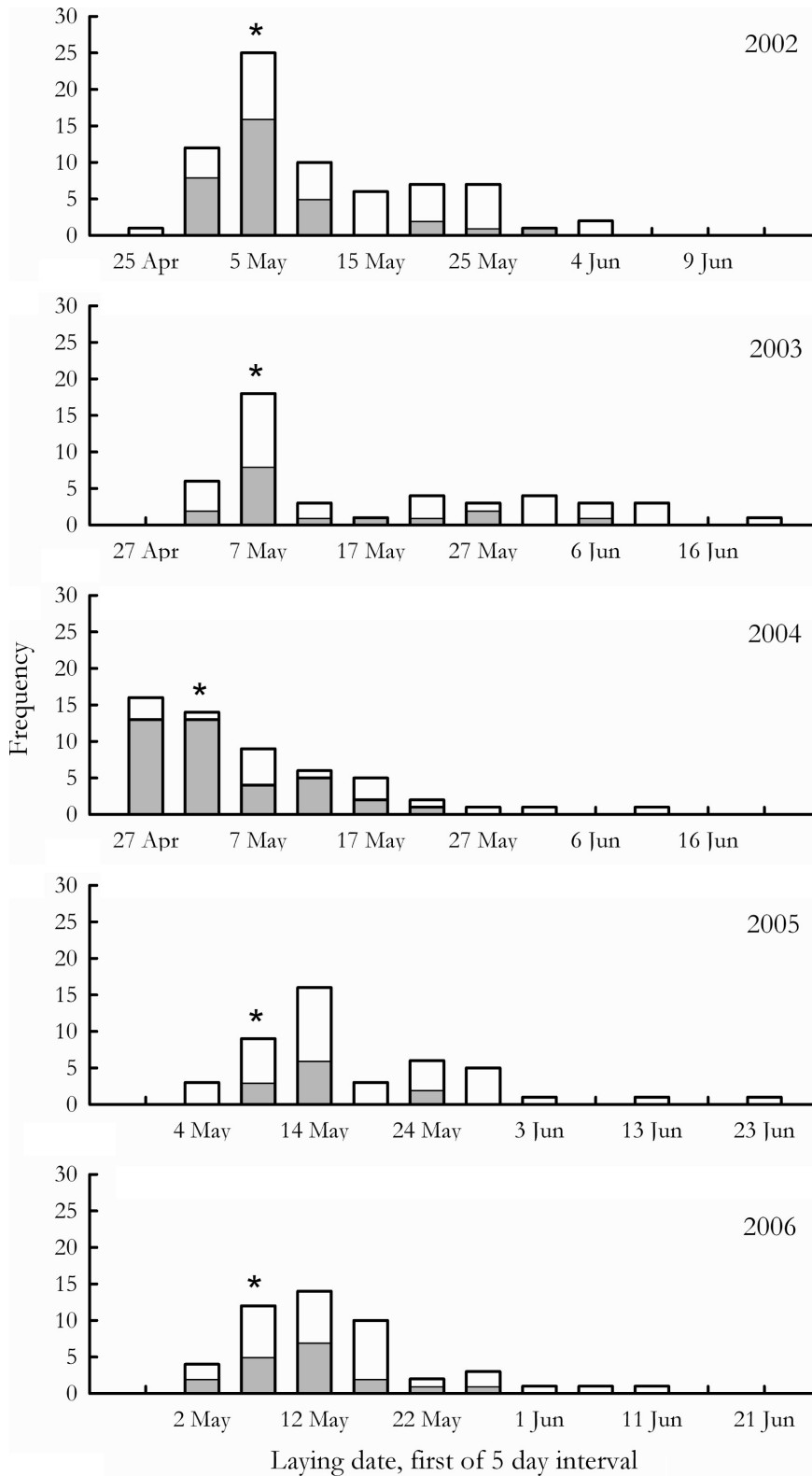


Figure 1. Distribution of control rhinoceros auklet laying dates in 2002–2006. Eggs that resulted in fledged chicks are in grey, unsuccessful eggs are in white. Dates of final egg removals in each year are indicated by asterisks.

success and fledging masses of early-laying control pairs, and against the annual proportion of sandlance in control chicks' diets. Otherwise, we used discriminant analysis to test whether combined  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  signatures in yolks

varied among years, which would provide evidence that variation in early-season environmental conditions affected feeding conditions. In these analyses, Wilks' lambda tests for the equality of the centroids in bivariate plots. We also

used logistic regression and analysis of covariance (ANCOVA) to explore the effects of year (as grouping variable) and date (as covariate) on breeding success and fledging masses of control pairs. In follow-up analyses to assess whether annual and seasonal factors had similar effects on control and experimental pairs, we included the treatment term (i.e., control or experimental pair) and all possible interaction terms. Non-significant ( $P > 0.1$ ) interaction terms were sequentially dropped from the models (three-way interaction term first, then two-way terms, starting with the two-way term with the higher P-value).

## Results

### Observations on control pairs

Burrow occupancy rates on the control plot were similar in the four years for which we had data (Table 1). For all control pairs, median laying dates varied by about two weeks, based on midpoints of the 5 d check intervals (Table 1, Fig. 1). Similarly, median hatching dates estimated from hatchling wing lengths varied by 17 d (Table 2).

Hatching success, fledging success and breeding success of early-laying control pairs varied markedly among years (Table 1). Breeding success was lower in years in which the median laying date was later ( $r^2 = 0.81$ ,  $P < 0.05$ ). Success also declined within seasons: based on logistic regression ( $-2\log\text{Likelihood} \geq 22.07$ ,  $df = 4$ , all  $P < 0.001$ ), and after controlling for year, all three measures of success declined with laying or hatching date as appropriate (all Wald  $\chi^2 \geq 19.66$ , all  $P < 0.001$ ; see Fig. 1).

In contrast to breeding success, fledging masses of chicks of early-laying controls varied little among years (Table 1). Fledging mass also was little affected by hatching date within years: after controlling for year in an analysis of covariance (for the whole model,  $F_{4,97} = 2.32$ ,  $P < 0.05$ ), fledging mass declined only weakly with later hatching ( $P = 0.1$ ).

Diet sampling spanned most of the chick period in each of the five years (Table 2). As a proportion of total annual biomass, the representation of Pacific sandlance in nestling diets varied more than two-fold across the five years (Table 2). As expected (Hedd et al. 2006), fledging masses were higher in years in which parents delivered more sandlance to their nestlings ( $r^2 = 0.92$ ,  $P < 0.01$ ).

### Observations on experimental pairs

The shape indices of the first and second eggs found in the same burrows were strongly correlated ( $r^2 = 0.67$ ; Fig. 2). By comparison, randomization tests ( $n = 100$ ) produced  $r^2$ -values of 0.001 to 0.06, with relationships equally likely to be positive or negative. Moreover, the strength of the correlation is very similar to that relating an older ( $\geq 8$  years old) female murre's *Uria* spp. egg mass in one year to her egg mass in the following year ( $r^2 = 0.62$ ; M. Hipfner unpubl. data). These observations suggest that the second eggs were in fact replacements laid by the same females. Egg size varied little among years, but first eggs ( $145.9 \text{ cm}^3 \pm 8.72 \text{ SD}$ ) tended to be larger than replacements ( $143.0 \text{ cm}^3 \pm 8.28 \text{ SD}$ ; two-factor ANOVA: for year,  $F_1 = 0.41$ ,  $P = 0.5$ ; for egg number  $F_1 = 3.88$ ,  $P = 0.05$ ; Fig. 2).

Combined  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable isotopic signatures in yolks indicated that foraging ecology during egg production varied among years (Discriminant analysis: Wilks' lambda = 0.30,  $F_{2,42} = 8.61$ ,  $P < 0.001$ ). Examination of bivariate plots suggests that females fed at higher trophic levels and in more inshore or benthic environments in 2003 (a close match to a Pacific sandlance diet), but at lower trophic level and in more offshore or pelagic environments in 2006. Other years were intermediate (Fig. 3).

Contrary to predictions of the environmental cues hypothesis, relaying rates were consistently very high: 88–90% across five years (Table 3). Thus, in our regression analyses, there was essentially no variation in the response variable (relaying rate), despite dramatic variation in the predictor variables (especially breeding success, but also proportion of sandlance in diets). Despite the constancy in relaying rates, however, relaying intervals varied significantly among the five years (Kruskall-Wallis test statistic = 14.40,  $P < 0.01$ ), with medians being especially long in 2005 and to less extent in 2003 (Fig. 4). The annual breeding success of the 90% of experimental females that did relay also was extremely variable (0–78%; Table 3).

We reran the logistic regression for breeding success, this time including the treatment term (control or experimental pairs), and including the treatment  $\times$  year  $\times$  date, treatment  $\times$  laying date, and treatment  $\times$  year terms. None of the interaction terms were significant in any run of these models in which they were included (all  $P > 0.4$ ). In the final model ( $-2\log\text{Likelihood} \geq 31.54$ ,  $df = 6$ ,  $P < 0.001$ ), which included only the three main effects, the year and date effects were significant but the treatment effect was not

Table 1. Median laying dates and burrow occupancy rate for the entire population, and breeding success for control females that laid on or prior to the median laying date in each year from 2002–2006. The P-values are results of interannual comparisons based on logistic regressions (for hatching, fledging and breeding success) or ANCOVAs (for fledging mass).

Year	Population		Early layers				
	Median lay period	Percent burrow occupancy (n)	No. eggs	No. hatch (%)	No. fledge (%)	No. success (%)	Fledging mass, g (mean $\pm$ SD)
2002	5–9 May	67 (76)	38	24 (63)	23 (96)	23 (61)	312 $\pm$ 26
2003	7–11 May	72 (76)	24	11 (46)	10 (91)	10 (42)	294 $\pm$ 34
2004	2–6 May	64 (72)	30	28 (93)	26 (93)	26 (87)	298 $\pm$ 40
2005	14–18 May	65 (79)	28	16 (57)	9 (56)	9 (32)	258 $\pm$ 14
2006	10–14 May		30	21 (70)	14 (67)	14 (47)	271 $\pm$ 32
		$P = 0.78$		$P = 0.001$	$P = 0.003$	$P < 0.001$	$P = 0.08$

Table 2. Median hatching dates, sampling periods for rhinoceros auklet nestling diets, and representation of Pacific sandlance in diets.

Year	Median hatching date	Sampling period (d relative to median hatch)	No. loads (no. complete)	Percentage biomass sandlance, all loads
2002	15 June	0–63	124 (100)	43.1
2003	18 June	2–59	97 (90)	31.6
2004	10 June	10–60	71 (45)	38.5
2005	27 June	4–55	63 (47)	20.5
2006	21 June	5–65	53 (35)	20.0

(for year: Wald  $\chi^2 = 18.30$ ,  $df = 4$ ,  $P = 0.001$ ; for laying date: Wald  $\chi^2 = 24.06$ ,  $df = 1$ ,  $P < 0.001$ ; for treatment, Wald  $\chi^2 = 0.01$ ,  $df = 1$ ,  $P > 0.9$ ). Thus, both year and laying date within the year had similar effects on the breeding success of control and experimental pairs.

## Discussion

Ambient conditions in the marine environment, including sea-surface temperature (a warming trend through the five-year period), the timing and intensity of upwelling, the strength of primary production, and the timing of the peak in zooplankton biomass in surface waters (an advance over the five years, associated with the warming trend)-all varied

dramatically across the northeast Pacific during our study (Sydeman et al. 2006, Mackas et al. 2007). Of note, our five-year study included an El Niño year (2003), often associated with reduced seabird breeding success (Schreiber and Schreiber 1984, Ainley et al. 1990), and also the very extreme 2005 season, in which spring upwelling virtually failed across the California Current system. That caused widespread seabird breeding failure and elevated adult mortality rates (Sydeman et al. 2006).

Not surprisingly, effects of the environmental variability were evident on key rhinoceros auklet breeding parameters: early-season foraging ecology (interannual variation in yolk  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable isotopic values suggested that feeding conditions varied while females formed eggs), timing of laying (median dates varied by 2 weeks), hatching, fledging and breeding success (32–87% of early pairs fledged chicks, with success being lower in years of later laying) and chick diets (including two-fold variation in the amount of Pacific sandlance delivered, with more sandlance being linked to higher mean fledging masses). Despite this, there was no variation in the relaying rates of the experimental females (88–90%). Thus, we conclude that the high-quality females used in our experiments did not modify their relaying decision in response to early-season environmental cues. We might also have predicted that the success of females that did relay would be consistently high from year to year (having read the cues available to them, only those females likely to succeed should have relaid). That prediction also was contradicted by our results.

Nonetheless, environmental effects were evident on the experimental birds while they formed their replacement eggs: relaying intervals were especially long in the very late and very unsuccessful 2005 season, and to less extent in the 2003 El Niño year. That is consistent with a role for

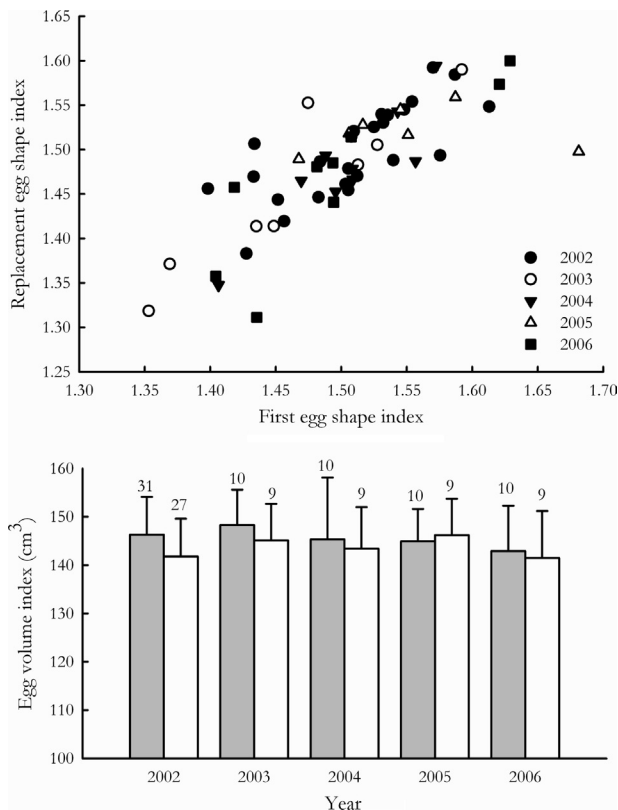


Figure 2. Bivariate plot of egg shape index (length/breadth) for first and second eggs found in the same experimental rhinoceros auklet burrows. With all eggs included  $r^2 = 0.67$ , but excluding the one clear outlier (likely a result of measurement error, since the shape index of the first egg is well outside the range for all other eggs),  $r^2 = 0.74$  (top panel). Volume indices (length  $\times$  breadth<sup>2</sup>) for all first (in grey) and replacement (in white) eggs (bottom panel).

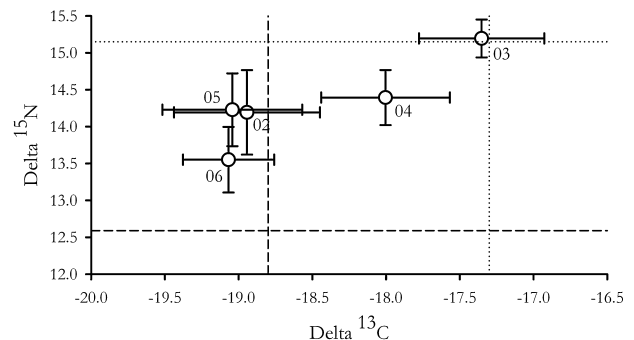


Figure 3. Bivariate plot of  $\delta^{15}\text{N}$  vs  $\delta^{13}\text{C}$  in rhinoceros auklet egg yolks in each year from 2002–2006. Dashed lines indicate  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values predicted in yolk for a bird feeding on a 100% euphausiid diet; dotted lines indicate  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values predicted in yolk for a bird feeding on a 100% Pacific sandlance diet.

Table 3. Breeding success of experimental female rhinoceros auklets that relaid. The P-values are results of interannual comparisons based on logistic regressions (for hatching, fledging and breeding success) or ANOVAs (for fledging masses).

Year	No. eggs (% relaying)	No. hatch (%)	No. fledge (%)	No. success (%)	Fledging mass, g (mean $\pm$ SD)
2002	27 (88%)	11 (41)	8 (73)	8 (30)	290 $\pm$ 25
2003	9 (90%)	2 (22)	2 (100)	2 (22)	244 $\pm$ 20
2004	9 (90%)	7 (78)	7 (100)	7 (78)	275 $\pm$ 20
2005	9 (90%)	0 (0)	–	0 (0)	–
2006	9 (90%)	8 (89)	6 (75)	6 (67)	295 $\pm$ 23
		P < 0.001	P = 0.22	P < 0.001	P = 0.07

physiological constraint related to unfavourable feeding conditions. Moreover, environmental conditions associated with both the year and the laying/hatching date within the year tended to have similar effects on the breeding success of experimental pairs as on the control pairs.

In a previous study on Brünnich's guillemots *Uria lomvia*, the date of egg removal also had no effect on the relaying rates of early females (Hipfner et al. 1999). In that study, however, breeding success was unaffected, unlike in the current study. How then do we account for the fact that nearly all of the experimental rhinoceros auklets relaid? On the proximate level, we suggest that those females capable of laying earliest and breeding most successfully (by way of comparison with the control pairs) also were in adequate physiological condition to produce replacement eggs in all years, although the amount of time they took varied. However, there is no obvious ultimate explanation for the

lack of regulation of reproductive effort beyond that, in response to environmental cues, given that in several years few or even none of the offspring from replacement eggs fledged. Regulation of effort during the chick-rearing period, in response to environmental conditions, is a characteristic strategy of many marine birds (Weimerskirch et al. 2001). We suggest four possibilities, which are not mutually exclusive, and that could in fact be interrelated.

First, rhinoceros auklets might simply lack the neural and physiological mechanisms to recognize and adapt to environmental cues available to them while they form eggs. This seems unlikely, given that interannual variation in the timing of breeding within seabird populations tends to be marked (Gjerdrum et al. 2003, Durant et al. 2004). However, Frederiksen et al. (2004) noted that variation in timing could be a product of physiological constraints imposed on individuals by feeding conditions, as well as by their strategic use of environmental cues. Second, because seabirds tend to have long incubation periods (Lack 1968), conditions during egg formation might not strongly predict conditions during chick rearing (unlike in short-breeding passerines; Both and Visser 2001). In our study, the lack of any systematic relationship between foraging ecology during egg production and subsequent breeding success is consistent with this idea. Third, their single eggs might be relatively inexpensive to produce, although they are large; 30% larger than predicted for body mass (Hipfner et al. 2004). Under these conditions, natural selection could favour a fixed investment in egg production. We note that both the size (this study) and the yolk androgen concentrations (Addison et al. 2008) of the same eggs varied little among years. Instead, adjustments to environmental conditions could be made later in the breeding attempt, either by abandoning eggs or chicks in extreme cases, or by modifying feeding rates to chicks in more moderate cases.

And fourth, the indirect fitness benefits of relaying might outweigh the direct fitness costs. In particular, relaying might be a sexually-selected trait whereby females display their high quality so as to retain mates for the future (Ainley and Boekelheide 1990). In other alcids, behavioural deficiencies often cause individuals to become victims of divorce (Moody et al. 2005), and increased mate fidelity is linked to higher lifetime reproductive success (Pyle et al. 2001). The fact that almost all females relaid even in moderately (2003) and extremely (2005) unsuccessful seasons, and then only after extended periods spent producing their second eggs, is consistent with the idea that rhinoceros auklets have a very strong drive to relay that is not simply related to the potential for fledging offspring in the current year.

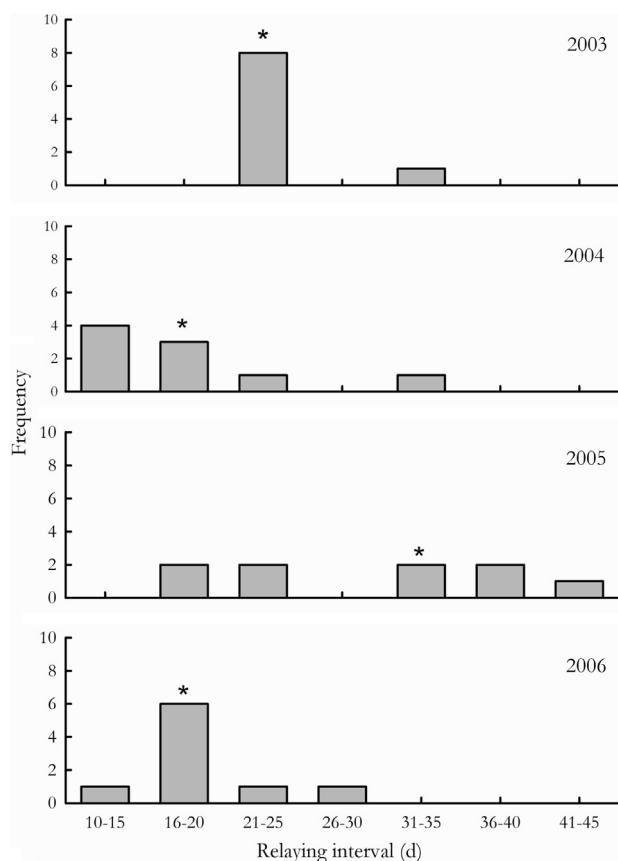


Figure 4. Time elapsing between egg removal and the laying of a replacement egg in experimental rhinoceros auklet burrows in each year from 2003–2006. Asterisks indicate median relaying intervals.

Seabirds are effective and practical monitors of conditions in marine ecosystems, because their demographic and behavioural parameters respond strongly and predictably to environmental variation (Cairns 1987, Wanless et al. 2007). However, that was not the case in our study. We found that the relaying decisions made by the population's more capable rhinoceros auklets were made independently of variation in environmental conditions, even though annual and seasonal conditions affected the ultimate fate of the replacement eggs. We suggest that care needs to be taken in choosing seabird parameters for use as environmental indicators. More generally, we suggest that a more comprehensive understanding of the relationship between seabirds' life histories and the marine environment will require further studies that address questions integrating proximate mechanisms with ultimate causation (Pinaud and Weimerskirch 2002).

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