JOURNAL OF AVIAN BIOLOGY 35: 224–236, 2004

Rates and consequences of relaying in Cassin's auklets *Ptychoramphus aleuticus* and rhinoceros auklets *Cerorhinca monocerata* breeding in a seasonal environment

J. Mark Hipfner, Kristin Charleton and W. Eric Davies

Hipfner, J. M., Charleton, K. and Davies, W. E. 2004. Rates and consequences of relaying in Cassin's auklets *Ptychoramphus aleuticus* and rhinoceros auklets *Cerorhinca monocerata* breeding in a seasonal environment. – J. Avian Biol. 35: 224–236.

We removed first eggs from early-laying females to measure rates and consequences of relaying in Cassin's auklets *Ptychoramphus aleuticus* and rhinoceros auklets *Cerorhinca monocerata* at Triangle Island, British Columbia, Canada. Based on egg size and composition, the investment that Cassin's auklets made in first eggs was very close to that predicted from adult body mass, whereas rhinoceros auklets invested more. In both species, a high percentage of females relaid (90% of Cassin's and 87% of rhinoceros auklets). Breeding success declined weakly with later laying among control Cassin's auklet pairs, but pairs that we induced to relay bred more successfully than naturally late pairs, and similar to values predicted from laying dates of their first eggs. Their chicks also fledged heavier and younger than late control chicks, and similar to values in early control chicks, but followed the population-wide seasonal decline in wing length at fledging. Nestling diets were dominated by *Neocalanus* copepods until late in the season, a sign that feeding conditions remained favourable until late. In contrast, rhinoceros auklet pairs induced to relay followed the population-wide seasonal decline in breeding success, which was driven by a decline in hatching success. Pacific sandlance *Ammodytes hexapterus*, thought to be a preferred prey species, virtually disappeared from nestling diets in mid-to-late season, yet there was no seasonal decline in fledging mass. However, chicks from replacement eggs followed the declines among control chicks in both age and wing length at fledging. Despite the female having produced a replacement egg, and despite delayed breeding, there appeared to be little immediate consequence associated with relaying for Cassin's auklets, except for a tendency for their chicks to fledge with short wings. Consequences were more marked in rhinoceros auklets (greatly reduced hatching success, and having their chicks fledge with short wings), and this may have been due to the large investment made in eggs, and/or to delayed breeding. Results of this study show that attributes of Cassin's and rhinoceros auklets that lay at different times in the season can be important in driving seasonal declines in breeding performance, as found in studies on other Alcidae. They also show how decisions taken during the egg stage can have variable yet potentially important implications for fitness, even in relatively long-lived species that lay single-egg clutches.

J. M. Hipfner (correspondence), K. Charleton and W. E. Davies, Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada, and Canadian Wildlife Service, Pacific Wildlife Research Centre, RR#1 5421 Robertson Road, Delta, British Columbia, V4K 3N2, Canada. E-mail: mark.hipfner@ec.gc.ca

Lack (1947) argued that egg production was not a particularly demanding process for birds, at least compared to chick-rearing, a conclusion he reached based largely on the apparent ease with which many species replace lost eggs and clutches. That idea, combined with others related to avian egg production, was important to the development of life-history theory, in large part because it set the stage for future experimental studies

(Stearns 1992, Monaghan and Nager 1997). In fact, studies of the relaying ecology of birds continue to provide much insight into the evolution of life histories, perhaps because the topic neatly links ultimate factors such as potential costs of late breeding or risk of nest predation on individual fitness (e.g. Milonoff 1989, Arnold 1993), with proximate factors such as the immediate effects of an individual female's nutritional state on her capacity to provide parental care (e.g. Hegyi and Sasvári 1998, Wendeln et al. 2000). However, the view that has emerged from recent studies is that egg production can be demanding for birds, and certainly more demanding than Lack envisaged, with evidence accumulating of trade-offs for females between the production of extra eggs and their own immunocompetence (Oppliger et al. 1996), survival (Visser and Lessells 2001), future breeding propensity (Nager et al. 2001), provisioning capacity later that season (Heaney and Monaghan 1995, Monaghan et al. 1998), and the inherent quality of their individual offspring (Sorci et al. 1997, Nager et al. 2000).

The Alcidae is a family of marine birds that exhibits marked variation in certain aspects of their breeding ecology, variation that in some cases is unmatched within any other avian family (Gaston and Jones 1998). Relaying capacity is one life-history trait that appears to vary widely among species within the family, although that is largely speculative because so little information is available for most species. Experimental studies of relaying in murres *Uria* spp. have shown that early-laying females have a very high capacity to relay (Hatchwell 1991, Hipfner et al. 1999), and early females include the older and more experienced members of the population (Hipfner et al. 1997), individuals less likely to be phenotypically constrained (Hipfner et al. 2003). Given the supposed seasonality of the boreal and arctic marine environments in which they breed, it seems somewhat surprising that these studies also have consistently found that relaying females suffer no reduction in breeding success, despite having incurred the costs of producing a replacement egg and despite the consequent delay in their timing of breeding (Hatchwell 1991, De Forest and Gaston 1996, Hipfner 2001). Observational studies often have arrived at very different conclusions about rates and consequences of relaying in murres (e.g. Gaston and Nettleship 1981, Boekelheide et al. 1990), which points to the need to address phenotypic attributes of individual females as factors affecting not only their decision about whether or not to relay, but also the potential fitness consequences of that decision. Because most reports of rates and consequences of relaying in other alcid species have derived from observational studies of breeding biology (e.g. Ashcroft 1979, Piatt et al. 1990), they may provide relatively little insight about the adaptive significance of relaying within the species' life history (Hipfner et al. 2001).

We used experimental egg removals to study the ecology of relaying in Cassin's *Ptychoramphus aleuticus* and rhinoceros *Cerorhinca monocerata* auklets, members of the auklet (Aethiini) and puffin (Fraterculini) tribes, respectively, of the family Alcidae. Both are pelagic, nocturnal, burrow-nesting seabirds that lay a single-egg clutch. Previous studies have found Cassin's auklet to be a species with a protracted egg-laying period (Hatch and Hatch 1990) and a high capacity to relay (Manuwal 1979, Astheimer 1986). It is also the only alcid known to double brood, albeit only in the southern portion of its range (Ainley et al. 1990). In contrast, there is very little information on any aspect of egg production, including relaying, in rhinoceros auklets (Gaston and Dechesne 1996), although an analysis by Sealy (1975) indicated that they lay large eggs compared to their body mass. Where they breed in multi-species colonies, both Cassin's and rhinoceros auklets lay relatively early in the season compared to other species (Hatch and Hatch 1990). The specific goals of our study were to: (1) measure egg size and egg composition in both species, (2) measure relaying rates, and examine causes of variation in the size of replacement eggs, (3) measure breeding success of relaying pairs and compare it to natural, seasonal variation among control pairs, (4) measure fledging condition of offspring from replacement eggs and compare it to natural, seasonal variation among control offspring from first eggs, and (5) document background seasonal variation in nestling diets to examine whether seasonal trends in the availability of prey might have driven patterns detected in (3) and (4).

Biological production within the California Current system, in the southern and central portion of the breeding range of both study species, is highly seasonal and this can impart a strong seasonality to seabird breeding (Ainley and Boekelheide 1990). For example, long-term studies at the Farallon Islands, California, have shown that while Cassin's auklets frequently relay following egg loss, few offspring from replacement eggs normally survive to fledge in the face of strong, seasonal deteriorations in feeding conditions (Ainley et al. 1990). Likewise, research at our study site to the north has suggested that breeding by Cassin's auklets is normally timed to match annual peaks in the populations of planktonic prey (Vermeer 1981), but peaks occur too early in the season in some years, potentially creating a seasonal mismatch (Bertram et al. 2001). Mismatch years feature marked, seasonal changes in the diets fed to nestlings, low breeding success, and slow and declining chick growth rates (Hedd et al. 2002). Factors affecting food availability for larger seabirds in this marine zone, including rhinoceros auklets, are not well understood. However, breeding success, nestling growth rates, and nestling diet composition vary both within and among years, apparently in response to oceanographic factors that influence key prey species

(Vermeer and Westrheim 1984). Consequently, characteristics of the breeding environment provide a compelling backdrop against which to examine relaying ecology.

Methods

Study area

The study was conducted at Triangle Island, British Columbia, Canada (50°52′ N, 129°05′ W) during the 2002 breeding season. Triangle Island supports the world's largest colony of Cassin's auklets (500,000 breeding pairs), a population that recently appeared to be in decline (Bertram et al. 2000). It also supports a large and apparently stable population of rhinoceros auklets (40,000 breeding pairs).

Collection of eggs

We monitored breeding of 93 Cassin's auklet pairs and 103 rhinoceros auklet pairs. Observations began on 28 March (early in the laying period of Cassin's auklets, and prior to the start of laying in rhinoceros auklets), and continued until 28 August (by which time all Cassin's auklet chicks and all but a very few rhinoceros auklet chicks had fledged). Early in the laying period of each species, burrows were inspected at 2 day intervals and samples of eggs were collected at random when first found ($n = 30$ eggs for both species). Eggs were collected under permit from the Canadian Wildlife Service. We left in burrows similar numbers of early-laid eggs as the number collected, to facilitate comparison of success of experimental and early-laying control pairs. We measured the length and maximum breadth (to within 0.1 mm using dial calipers) and mass (to within 0.1 g on an electronic balance) of each collected egg. To examine egg composition, 21 Cassin's auklet eggs and 20 rhinoceros auklet eggs were boiled for 12 minutes, allowed to cool, reweighed, and then separated into shell + membranes, albumen, and yolk. Shell + membrane and yolk were weighed to within 0.1 g on an electronic balance, and albumen mass was taken to be the mass of the fresh, preboiled egg minus the mass of the shell + membranes and yolk. The remaining eggs were immediately frozen for use in a separate study of stable isotope ratios.

Relaying rates and replacement egg sizes

For both species, we first rechecked the burrows from which first eggs had been collected for second eggs 17 days after the last egg had been collected (no experimental burrow that did not contain an egg on that check later contained an egg). We adopted this approach to minimize disturbance to experimental pairs, hoping to reduce the risk that they would abandon their burrows. As a consequence, however, we did not directly determine relaying dates or relaying intervals (see below). When a second egg was first found in a burrow, we measured its length and maximum breadth, and put it back in place. Because auklets lay white, unmarked eggs, background colours and marking patterns cannot be used to ascertain whether the new egg was laid by the same female, as is commonly done with murres (e.g. Birkhead and Nettleship 1982). However, a relaying female's relative egg size and egg shape (ratio of length to breadth) are consistent (e.g. Astheimer 1986, Hipfner et al. 2003), so that the size and shape of the first egg will strongly predict that of the second egg in the same burrow if it was laid by the same female. Studies that involved banded females have shown that other species of Alcidae tend to relay at the same breeding site (JMH pers. obs.), and that Cassin's auklets tend to breed at the same site from year to year (Pyle et al. 2001).

Breeding success and condition of offspring at fledging

As noted, burrows were inspected at 2 day intervals prior to laying to obtain fresh eggs, and after the egg collections were completed, burrows were checked at 5 day intervals. Therefore, laying dates for all first eggs were known only to within 2–5 days. Because we did not know the laying dates of replacement eggs, we derived estimates by backdating from hatching dates of replacement eggs, estimated to within 1 day (see below), and assuming an incubation period of 38 days for Cassin's auklets (Astheimer 1991), and 45 days for rhinoceros auklets (Gaston and Dechesne 1996). Using this method, estimated relaying intervals averaged 15.2 days ± 2.7 SD for Cassin's auklets ($n = 17$), and 17.3 days ± 2.5 SD for rhinoceros auklets ($n = 11$), and these estimates seem reasonable (e.g. Astheimer 1986). Laying dates for all first and replacement eggs were grouped into six 5-day intervals for analysis, so small errors in estimating relaying dates should be of little consequence. In Cassin's auklets, these groups were: prior to 1 April (group 1), 1–4 April (2), 5–9 April (3), 10–14 April (4), 15–19 April (5), and after 19 April (6). All replacement eggs fell in groups 4, 5 and 6, so there were control and experimental pairs breeding at the same time. In rhinoceros auklets, the groups were: prior to 5 May (group 1), 5–9 May (2), 10–14 May (3), 15–19 May (4), 20–24 May (5), and after 24 May (6). All relaid eggs fell in groups 4, 5 and 6.

After an egg was found in a burrow, whether a control first egg or a putative replacement, the burrow was then left undisturbed for 30 days in Cassin's auklets and 40 days in rhinoceros auklets. At that time, burrows were again inspected at 5 day intervals until a hatchling was found. When first found, we measured hatchling wing length (to within 1 mm using calipers) and mass (to within 1 g using a 50 g Avinet spring scale). We derived estimates of hatching dates using a calibration of wing length against age for known-aged chicks using measurements made in previous years at Triangle Island (Hedd et al. 2002). Cassin's auklet chicks subsequently were measured and weighed at ages 5 days, 10 days, 25 days, 35 days, and then every two days until they disappeared, and rhinoceros auklet chicks were weighed at ages 5 days, 10 days, 40 days, 45 days, and then every two days until they disappeared.

Based on this protocol, for all control (first egg) and experimental (replacement egg) pairs, we defined *hatching success* as the proportion of eggs laid that hatched, *fledging success* as the proportion of chicks that survived at least 35 days (Cassin's auklet) or 45 days (rhinoceros auklet) before disappearing, and *reproductive success* as the proportion of eggs laid that produced chicks that fledged. For analyses of fledging condition, we defined *fledging mass* as the last mass recorded prior to departure of a successful chick, *fledging wing* as the last wing length recorded prior to departure of a successful chick, and *fledging age* as the age of the chick on the day between the next-to-last and last inspections (separated by 2 days) prior to its departure. (At one control rhinoceros auklet site, the egg hatched and the chick survived to 49 days of age but lost mass at a dramatic rate prior to disappearing. When last seen, the chick had a wing length of only 120 mm, 16 mm shorter than any other fledgling and 3.9 SD below the population mean fledging wing, so data for this pair were excluded from all analyses pertaining to breeding success and offspring fledging condition). We used measures at fledging, rather than measures of growth, because the offspring's condition when it leaves for an independent life at sea is probably what is most important, and because timing of nest departure in alcids has been a topic of considerable interest to evolutionary ecologists (e.g. Birkhead 1977, Ydenberg 1989).

Food loads delivered to nestlings

We sampled nestling diets by intercepting 5–15 adult birds returning to the colony at night to feed their chicks, on occasions spread through the chick period. Cassin's auklets, which carry zooplankton to their young in a sublingual pouch, were trapped in a large pheasant net set between two large poles, and induced to regurgitate through a funnel into a small, preweighed, screw-top plastic bottle, later filled with buffered formalin, by gently massaging the full pouch. Samples were categorized as full or partial, depending on whether the observer was confident of having obtained a complete food load. Sampling for Cassin's auklets was done on 18–19 May, 28 May, 7 June, 20–21 June, and 27 June. In the laboratory, samples were transferred to stacked sieves, and rinsed repeatedly with water to remove preservative. Individual items present in subsamples were identified to the lowest possible taxonomic level, enumerated, blotted dry, and weighed on an electronic balance.

Rhinoceros auklets, which carry one to many individual items per load (fish or large invertebrates), were trapped on the ground at night using long-handled nets before they were able to scramble into burrows to feed their chicks. Collected samples were placed in whirlpak bags, and categorized as whole or partial. Sampling was carried out on 15, 23, and 29 June; 6–7, 13, 18, and 28 July; and 3, 11, and 17 August. We determined load weights to within 0.1 g using an electronic balance, then each individual item within each load was identified to the lowest possible taxonomic level, and weighed on an electronic balance.

Statistical analyses

We analysed data pertaining to hatching, fledging and reproductive success using logistic regression. Based on previous work at Triangle Island and elsewhere, we expected success to decline with laying date, due either to seasonal environmental effects, or to late laying of less capable birds (e.g. inexperienced females). Therefore, we started with logistic regression models that included the constant, plus as continuous independent variable either laying date grouped by 5 day intervals (for hatching success and reproductive success), or hatching date estimated to within 1 day (for fledging success), treatment as the grouping variable (two levels: control first eggs and experimental replacement eggs), and the interaction between treatment and laying date. If the interaction term was non-significant ($P > 0.05$) in the first run, it was removed and the analysis re-run including only the constant, plus date and treatment terms.

Data on fledging mass, fledging wing length, and fledging age were analysed using analysis of covariance. As with measures of breeding success, we expected measures of fledging condition to decline with hatching date due to environmental effects, late laying of presumably less capable birds, or behavioural decisions taken by chicks based on the time in the season. Therefore, we used analyses similar to those used to analyse data on breeding success: we started with ANCOVA models that included the constant, plus date as continuous independent variable, treatment as grouping variable, and the date x treatment interaction. Non-significant ($P > 0.05$) interaction terms were removed and analyses re-run including only the constant, date and treatment.

Nestling diets were analysed by summing the masses of major prey taxa across all loads obtained on a single sampling session (Cassin's auklet), or on 2 consecutive sessions (rhinoceros auklet), and then calculating the percentage contribution by mass of each taxon.

Otherwise, we used single factor analyses (linear and logistic regressions, paired t-tests, ANOVA), visually examining residuals from linear analyses for normality and equality of variances. All data were analysed using SYSTAT v. 10.2 (SPSS Inc. 2002). Means are presented ±1 SD, and statistical significance was assumed at $P < 0.05$.

Results

Egg size and composition

Laying dates for 93 Cassin's auklet first eggs at Triangle Island in 2002 ranged from prior to 28 March (some eggs were present when burrows were first inspected) until 14 May. The median laying date fell on 31 March–1 April (Julian date 90–91). From among these eggs, 30 were collected between 28 March and 5 April. In addition, we collected one egg that was cracked while we inspected the burrow, and one that was found outside a burrow (the latter was used only in analysis of egg composition). Information on the size and composition of Cassin's auklet eggs is presented in Table 1. Eggs ranged from 23.2 g to 34.3 g in mass, with the mean (29.2 g) averaging 16.0% of the mean mass of 38 adult birds weighed during mid-incubation in 2002 (182.9±13.0). The mean egg mass also was 6.9% lower than predicted from mean adult mass, based on Rahn et al. (1975) equation for Charadriiform birds (egg mass $= 0.61 \times$ adult mass$^{0.73}$, $r^2 = 0.96$). The equation relating the fresh mass of Cassin's auklet eggs to volume index, which can be measured at any time prior to hatching, was:

$$\text{Fresh weight (g)} = 0.54 \text{ volume index (cm}^3) + 0.04 \ (r^2 = 0.95, n = 32).$$

By mass, the ratio of yolk to albumen in Cassin's auklet eggs averaged 0.57 (Table 1).

Laying dates for 103 rhinoceros auklet first eggs at Triangle Island in 2002 ranged from 22 April to 6 June, and the median fell on 4–5 May (Julian date 124–125). Thirty-one eggs were collected between 22 April and 6 May, and we also removed one other egg cracked during the burrow inspection, although it was damaged too badly to be used for analysis of size or composition. Information on egg size and composition is presented in Table 1. Egg mass ranged from 70.0 to 89.6 g, with the mean (79.2 g) averaging 14.6% of the mean mass of 15 adult birds weighed during mid-incubation (543.7 g± 37.5), or 31% heavier than predicted from adult mass (based on Rahn et al.'s equation). As with Cassin's auklets, the volume index of a rhinoceros auklet egg was a very strong predictor of its fresh mass:

$$\text{Fresh weight (g)} = 0.52 \text{ volume index (cm}^3) + 3.86 \ (r^2 = 0.94, n = 31).$$

Ratios of yolk to albumen in rhinoceros auklet eggs averaged 0.66 (Table 1).

Relaying rates and replacement egg sizes

In Cassin's auklets, comparisons of the volume and shape indices of the first egg with that of the egg later found and measured in the same burrow strongly suggest that most of these eggs, if not all, were replacements laid by the same females (for volume index, $r^2 = 0.50$, $F_{1,25} = 25.26$, $P < 0.001$; for shape index, $r^2 = 0.67$, $F_{1,25} = 49.88$, $P < 0.001$; Fig. 1). Assuming that they were all replacements, 90% of 30 Cassin's auklets relaid, but we were unable to determine with certainty whether a replacement might have been laid in one other burrow. The mass of the female's first egg was a marginally effective predictor of whether a female would relay (logistic regression, $\chi^2_1 = 3.50$, $P = 0.06$), because the two smallest eggs in the sample were produced by females that failed to relay after their eggs were collected. Replacement eggs averaged 2.5% smaller in volume index than first eggs laid by the same female (Table 1; range 16.3% smaller to 6.4% larger), a small but significant difference (paired-$t_{26} = 2.44$, $P = 0.02$). The percentage difference was not strongly related to the size of the first egg laid ($r^2 = 0.03$).

In rhinoceros auklets, comparisons of the volume and shape indices of first eggs with that of the egg later found

Table 1. Size and composition of eggs laid by Cassin's and rhinoceros auklets.

Egg number	Parameter	Cassin's auklet (n)	Rhinoceros auklet (n)
First	Volume index (cm^3)	53.9±4.6 (32)	146.3±7.8 (31)
	Mass (g)	29.2±2.6 (32)	79.2±4.2 (31)
	Percent shell	7.2±0.5 (21)	7.7±0.4 (20)
	Percent albumen	59.1±2.4 (21)	55.8±1.9 (20)
	Percent yolk	33.8±2.3 (21)	36.5±1.8 (20)
	Yolk:albumen	0.57±0.06 (21)	0.66±0.05 (20)
Replacement	Volume index (cm^3)	52.5±4.0 (27)	141.8±7.8 (26)

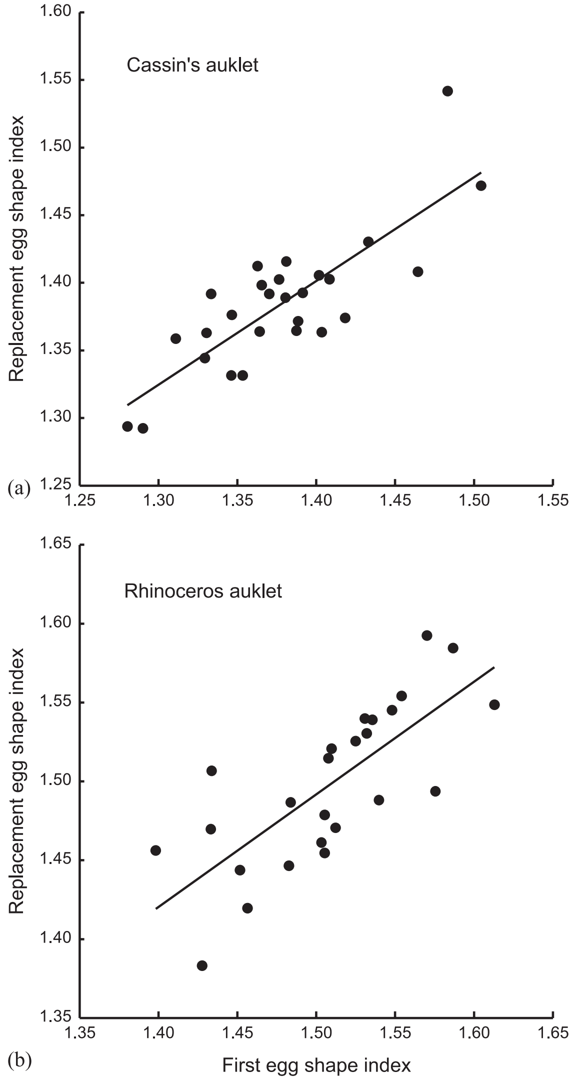


Fig. 1. The relationship between shape index (ratio of egg length to breadth) of first eggs and second eggs found in the same burrows in (a) Cassin's auklets ($r^2 = 0.67$), and (b) rhinoceros auklets ($r^2 = 0.56$). The strong relationships suggest that most, or perhaps all, of the second eggs were replacement eggs laid by the same females.

and measured in the same burrows suggest that most or all were replacements (for volume index, $r^2 = 0.31$, $F_{1,23} = 10.38$, $P = 0.004$, and for shape index, $r^2 = 0.56$, $F_{1,23} = 29.71$, $P < 0.001$; Fig. 1). We were unable to measure two putative replacements, and as mentioned could not accurately measure the one first egg damaged during the initial burrow inspection. Nonetheless, assuming that all eggs later found in the same burrows were replacements, 88% of 32 rhinoceros auklets relaid (the estimate excluding these three burrows is 86%). Probability of relaying was not predicted by first egg size (logistic regression, $P > 0.6$). Replacement eggs averaged 2.9% less in volume index than first eggs laid by the same female (paired-$t_{24} = 2.83$, $P = 0.009$; Table 1), and ranged from 10.4% smaller to 7.7% larger. There was some tendency for females that laid larger first eggs to show a greater percentage of reduction in the size of their replacement egg ($r^2 = 0.20$, $F_{1,23} = 5.61$, $P = 0.03$).

Breeding success

For Cassin's auklets, information on measures of breeding success for early- (groups 1 and 2), middle- (3 and 4), and late-laying control (5 and 6) pairs as well as experimental relayers is presented in Fig. 2. Among all 63 control pairs, 60% succeeded in producing fledglings from eggs. In none of the logistic regressions for hatching, fledging, or breeding success was the date × treatment interaction term statistically significant (all $P > 0.4$). This indicates that slopes relating success to date did not differ between pairs raising offspring from first and replacement eggs. Therefore, analyses were rerun including only the constant plus date and treatment terms. In these analyses, neither timing (laying date by 5 day intervals for hatching and reproductive success; hatching date to within 1 day for fledging success), nor treatment (control first egg or experimental replacement egg), had significant effects on any measure of success. Among control pairs, there was only a weak, non-significant tendency for breeding success to decline with later laying ($P = 0.1$).

For rhinoceros auklets, information on measures of breeding success for early- (groups 1 and 2), middle- (3 and 4) and late-laying (5 and 6) control pairs as well as experimental relayers is presented in Fig. 2 (one of the 28 experimental relaying pairs was removed from the analyses because we were unable to determine the fate of the egg with certainty). Among all 71 control pairs, 45% succeeded in raising fledglings from eggs. Three experimental chicks that remained when observations ceased were considered to have fledged because they were over 45 days of age. In none of the logistic regressions for hatching, fledging or reproductive success was the date × treatment interaction term significant (all $P > 0.3$). In analyses including only the constant plus date and treatment terms, later laying was associated with reduced hatching success ($t = 2.48$, $P = 0.01$), whereas fledging success was unaffected by hatching date ($P > 0.9$), after controlling for treatment effects. Due to the seasonal decline in hatching success, reproductive success also declined with later laying ($t = 2.87$, $P = 0.004$). Conversely, treatment had no significant effect on hatching success, fledging success, or reproductive success (all $P > 0.4$), after controlling for date effects.

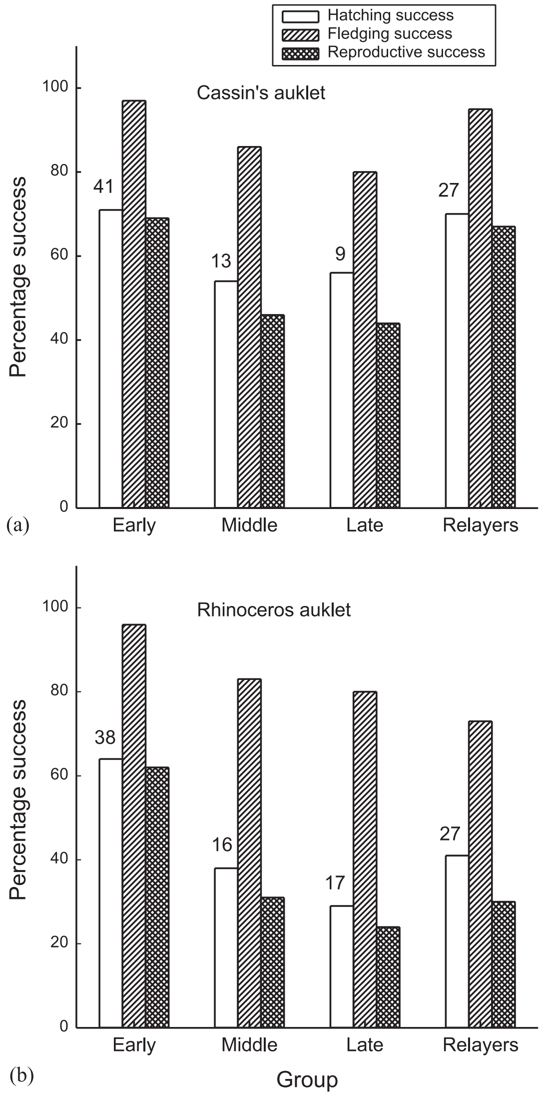


Fig. 2. Measures of breeding success for early (groups 1 and 2), middle (3 and 4), and late-laying (5 and 6) control pairs, compared to relaying pairs in (a) Cassin's auklets and (b) rhinoceros auklets. Initial sample sizes are shown above bars. In rhinoceros auklets, experimental relayers followed the population-wide seasonal declines in hatching and reproductive success, and there were no significant seasonal declines in measures of breeding success in Cassin's auklets.

Condition of offspring at fledging

Among control Cassin's auklets, the mean fledging mass was 159.8 g ± 19.3, mean fledging wing was 119.5 mm ± 4.6, and mean fledging age was 47.6 d ± 4.1 ($n = 38$). In none of the ANCOVA for fledging mass, wing length or age was the hatching date × treatment interaction term significant, although the interaction term for age was marginal ($P < 0.1$). This indicates that the slopes relating condition at fledging to hatching date did not differ strongly between chicks hatching from first and replacement eggs. With the interaction term excluded, both mass ($F_{1,53} = 9.82$, $P = 0.003$) and wing length ($F_{1,53} = 18.84$, $P < 0.001$) at fledging declined with hatching date, while fledging age increased with hatching date ($F_{1,53} = 10.32$, $P = 0.002$), after controlling for treatment effects (Fig. 3). After controlling for date, chicks from replacement eggs fledged heavier ($F_{1,53} = 4.93$, $P = 0.03$) and younger ($F_{1,53} = 8.81$, $P = 0.004$) than those from first eggs, while wing length at fledging differed little between groups ($P > 0.3$; Fig. 3).

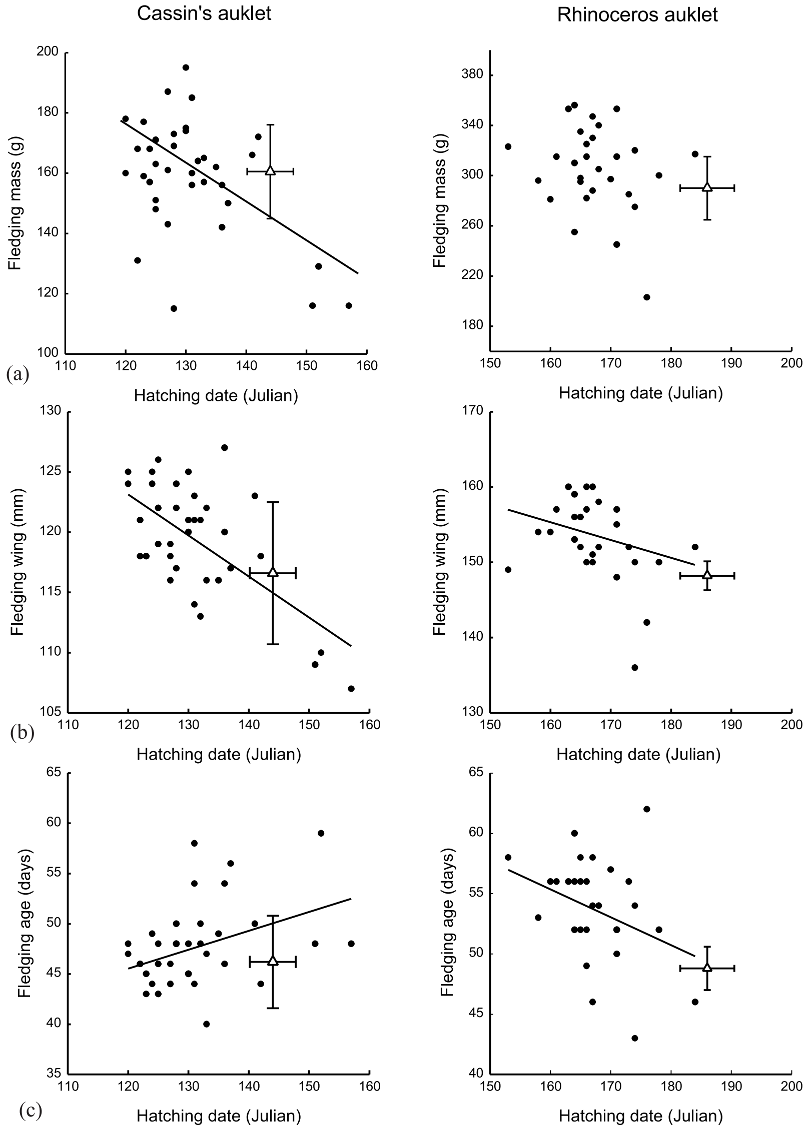
Among control rhinoceros auklets, mean fledging mass was 305.5 g ± 34.1, mean fledging wing was 153.1 mm ± 5.4, and mean fledging age was 53.8 d ± 4.2 ($n = 29$). The three experimental rhinoceros auklet chicks that remained when observations ceased were not included in the following analyses (their masses just prior to fledging were, however, similar to other experimentals at the same stage). In none of the ANCOVA for fledging mass, wing length, or age was the hatching date x treatment interaction significant (all $P > 0.8$). With the interaction term excluded, fledging mass was unrelated to hatching date ($P > 0.3$), whereas both fledging age ($F_{1,31} = 5.07$, $P = 0.03$) and fledging wing length ($F_{1,31} = 5.28$, $P = 0.03$) declined with later hatching, after controlling for treatment effects (Fig. 3). No measure of fledging condition differed between offspring from first and replacement eggs, after controlling for date (all $P > 0.7$; Fig. 3).

Food loads delivered to nestlings

The mass of complete food loads delivered to Cassin's auklet nestlings varied little among sampling sessions ($F_{4,20} = 0.26$, $P = 0.90$), although samples sizes were too small to provide meaningful tests (Table 2). Diets were dominated by invertebrates, especially copepods (almost entirely *Neocalanus cristatus* throughout the season) and euphausiids (especially *Thysanoessa spinifera*, and to a less extent *Euphausia pacifica*), on all but one sampling occasion when unidentified fish predominated (28 May). Other prey types, all forming very small proportions of nestling diets, included Hyperiids, Brachyurans, Molluscs, and Carideans.

Mean load masses delivered to rhinoceros auklet nestlings varied significantly across the five sampling groups ($F_{4,97} = 3.50$, $P = 0.01$), tending to increase to a peak in mid-season and then decrease (Table 3). Early in the season, diets were dominated by Pacific sandlance and salmon *Oncorhynchus* spp., with a small contribution from juvenile rockfish *Sebastes* spp. However, sandlance in particular virtually disappeared from nestling diets between late July and early August, being replaced by Pacific saury *Calolabis saila*. Late in the season squid *Gonatus* spp. also appeared in nestling diets.

Fig. 3. The relationship between hatching date and (a) fledging mass, (b) fledging wing length, and (c) fledging age in Cassin's auklets and rhinoceros auklets. The symbols represent mean ± SD values for chicks hatched from replacement eggs (n = 18 in Cassin's auklets, and 5 in rhinoceros auklets). Least squares regression lines are shown for significant relationships.



Discussion

Timing of breeding at Triangle Island in 2002 was similar to that recorded in recent years in both Cassin's and rhinoceros auklets (Bertram et al. 2001, Hedd et al. 2002). In addition, eggs were similar in size to those recorded previously (Morbey and Ydenberg 1997, Blight et al. 1999). Among control Cassin's auklets, breeding success in 2002 (60%) was in the upper end of the range recorded in previous years at Triangle Island (21–67% in the eight years in which observations spanned all or most of the breeding season), and the mean fledging mass (160 g) also was quite high (121–186 g in 11 years; cf. Vermeer 1981, 1987, Morbey and Ydenberg 1997, Triangle Island Research Station unpubl. data). Neither observation is surprising, because both mass and species composition of food loads delivered to nestlings were quite similar to those in previous successful years (Vermeer 1981, Bertram et al. 2001, Triangle Island Research Station unpubl. data). Bertram et al. (2001) showed that strongly seasonal, warm-water years are characterized by low overall prevalence of the copepod *Neocalanus cristatus* in nestling diets, with declines in its occurrence through the season. In 2002, this species remained important in nestling diets until late in the season. Taken together, these observations on control pairs suggest that feeding conditions were generally favourable for Cassin's auklets in 2002, a year in which

Table 2. Seasonal variation in composition (% wet mass) and mass of food loads brought to Cassin's auklet nestlings.

Prey species	Julian dates (n)				
	138, 139 (10)	148 (11)	158 (10)	171–172 (14)	178 (4)
Copepods	88.9	3.3	26.2	64.0	77.7
Euphasiids	5.7	21.0	70.0	27.9	21.9
Other invertebrates	3.1	3.3	< 0.1	< 0.1	0
Fish	0.4	66.9	1.0	1.6	0
Unidentified	1.9	5.6	2.7	6.4	0.4
Total	100	100	100	100	100
Mean load mass, g(n)	17.2±11.3 (2)	21.9±12.7 (6)	24.8±10.9 (7)	23.7±9.5 (8)	19.8±8.2 (2)

Table 3. Seasonal variation in compositon (% wet mass) and mass of food loads brought to rhinoceros auklet nestlings.

Prey species	Julian dates (n)				
	166, 174 (20)	180, 187–188 (26)	194, 199 (21)	209, 215 (24)	223, 229 (19)
Pacific sandlance	54.8	60.5	72.1	12.2	1.9
Salmon	33.1	39.5	4.2	14.9	14.5
Rockfish	12.1	0	7.7	9.9	1.1
Pacific saury	0	0	16.0	61.1	73.6
Squid	0	0	0	1.9	8.9
Total	100	100	100	100	100
Mean load mass, g(n)	19.0±8.6 (17)	29.5±11.1 (26)	29.9±12.2 (18)	26.6±10.1 (21)	23.3±9.8 (19)

sea-surface temperatures off the coast of British Columbia remained cooler than average throughout the summer (BC lighthouses database).

In contrast, both overall breeding success (46%) and mean fledging mass (306 g) of control rhinoceros auklet pairs were poor to average in 2002 compared to previous years at Triangle Island (21–67% success, and 220–361 g mean fledging masses; Vermeer and Cullen 1979, Triangle Island Research Station unpubl. data). Low breeding success was due more to events during the egg stage (50% hatching success) than during the chick stage (92% fledging success), and low hatching success is normal at Triangle Island (Triangle Island Research Station unpubl. data), although not at many other rhinoceros auklet colonies (e.g. Wilson and Manuwal 1986). In addition, masses of food loads delivered to nestlings in 2002 were quite low compared to previous years at Triangle Island and elsewhere (usually > 30 g; Vermeer and Westrheim 1984, Bertram et al. 1991), although species composition of diets was typical for Triangle (Vermeer and Cullen 1979, Triangle Island Research Station unpubl. data). The late-season switch from sandlance to sauries observed in 2002, and the concurrent diversification of nestling diets late in the season, are both common phenomena at Triangle, and likely reflect decreased availability of sandlance. However, the cause(s) is not known (Vermeer 1980). On the whole, these observations on control pairs suggest that feeding conditions in 2002 were less than favourable for rhinoceros auklets, unlike Cassin's auklets, and perhaps especially early in the season.

Investment in first and replacement eggs

The composition of eggs laid by Cassin's and rhinoceros auklets at Triangle Island was similar to that elsewhere (Kuroda 1963, Astheimer 1986), and was similar to that of eggs laid by other alcids that employ semi-precocial development (33–37% yolk by mass is typical; e.g. Birkhead and Nettleship 1984). There was, however, a striking difference between the two species in relative egg size. Whereas the mean mass of Cassin's auklet eggs closely matched that predicted from mean adult mass (within 7%), those laid by rhinoceros auklets were about 30% larger than predicted. This appears to be a general difference between auklets (Aethiini) and puffins (Fraterculini; as mentioned, rhinoceros auklet is placed in the puffin tribe). For example, least auklets *Aethia pusilla* laid eggs that averaged 2% heavier than predicted from adult mass at the Pribilof Islands, Alaska (data in Roby and Brink 1986), conversely, Atlantic puffins *Fratercula arctica* laid eggs 26% heavier than predicted at the Gannet Islands, Labrador (JMH unpubl. data), horned puffins *Fratercula corniculata* laid eggs 29% heavier at Talan Island, Russia (data in Piatt and Kitaysky 2002), and tufted puffins *Fratercula cirrhata* laid eggs 11% heavier at Triangle Island in 2002 (G. Blackburn unpubl. data). We can only speculate on the reasons for the difference between the two tribes. Kitaysky (1999) found that puffin chicks are much better adapted to short-term food shortages than are auklet chicks, and suggested that this reflected the inherent unpredictability of pelagic fish as compared to plankton as a food source. Perhaps the extra resources available in the puffins' relatively larger eggs act as a buffer against the possibility that feeding conditions will be inadequate soon after hatching.

Cassin's auklet is known to be a species with a high capacity to replace lost eggs (e.g. Astheimer 1986), so the 90% relaying rate recorded in this study is not surprising. A high relaying capacity also would be expected based on the species' extended laying period (Hatch and Hatch 1990), and the relatively small investment made in the first egg (Hipfner et al. 2001). Ainley et al. (1990) suggested that Cassin's auklets high relaying capacity might be a lingering life-history trait that reflects its strong evolutionary affinities to northern oceans, where the breeding season begins months later but appears to terminate at about the same time as it does further south. Alternatively, they suggested that it might have evolved as a means for females to display their high quality so as to retain mates and breeding sites. They based their arguments on, first, the apparent lack of direct fitness benefits associated with relaying (in their study, few pairs that lost eggs naturally and relaid produced fledglings), and second, the low relaying capacity of more northerly, and thus later-laying, members of the auklet tribe (species of the genus *Aethia*). However, early-laying Cassin's auklets that we induced to relay bred successfully, suggesting that under favourable conditions at least, relaying can confer considerable direct fitness benefits for pairs of high quality. This has been repeatedly found in studies of murres, wherein pairs that lose eggs and relay naturally do poorly, but early-laying pairs induced to relay fare well (Hatchwell 1991, Hipfner et al. 1999). Moreover, there is no experimental evidence to suggest that *Aethia* auklets have little capacity to relay, and very little information generally (Piatt et al. 1990). A thorough analysis of relaying ecology in the Aethiini will require more research.

It is difficult to put the high relaying rate observed in rhinoceros auklets (87%) into an evolutionary context because so little information is available for this and other puffin species (and we know of no experimental information). A high relaying capacity would be expected based on the species' relatively early laying (Hatch and Hatch 1990), but not expected based on its nesting habits and the large size of the first egg (Hipfner et al. 2001). However, unlike in Cassin's auklets, there was evidence of a possible trade-off for rhinoceros auklets between the investment made in the first and in the replacement egg, in that females that laid larger first eggs showed a greater percentage reduction in the size of their replacement. That is consistent with the large investment made in the first egg (large size, large yolk), and in rhinoceros auklets, unlike in Cassin's auklets, relaying females bred much less successfully than predicted based on their original laying date. Fitness trade-offs associated with producing additional eggs have now been documented in a variety of avian species (e.g. Heaney and Monaghan 1995, Oppliger et al. 1996), and alcids that lay large eggs appear to be suitable subjects for further study.

Breeding success

Overall, breeding success in 2002 was about normal for Triangle Island among control Cassin's auklet pairs, and there was only a weak tendency, not statistically significant, for success to decline among late-layers. In contrast, a strong seasonal decline in breeding success was reported previously at Triangle Island (Vermeer 1981), and occurs frequently at the Farallon Islands (Ainley et al. 1990). Given the lack of strong seasonality to breeding among control pairs in 2002, it is perhaps not surprising that neither production of the replacement egg, nor the delay in timing of breeding that resulted, had overt effects on the success of experimental pairs. As mentioned, sea-surface temperatures off the coast of British Columbia remained cool throughout the summer, and probably as a result, feeding conditions remained favourable until late in the season, as judged from the high prevalence and persistence of *Neocalanus* copepods in nestling diets (Vermeer 1981, Bertram et al. 2001). Success of offspring from replacement eggs could well be lower in years of less favourable feeding conditions (Manuwal 1979).

In contrast, breeding success was low overall and showed a strong decline with later laying in rhinoceros auklets. As in other alcids, a seasonal decline in success is probably normal for rhinoceros auklets (Wilson and Manuwal 1986). In our study, early-laying pairs that were experimentally induced to relay followed the population-wide decline in breeding success, which was driven mainly by a decline in hatching success. Given the strong concordance with naturally late pairs, the simplest explanation for the low success of experimental pairs is that it was somehow related directly to late laying, rather than being related to costs of producing the replacement egg. However, an alternative explanation would be that late-layers, and birds that produced an additional egg, were in some way in worse condition than early-layers incubating first eggs, which perhaps caused them to neglect their eggs in order to feed. Keen's mice *Peromyscus keeni* are effective predators on unattended seabird eggs at Triangle Island: Blight et al. (1999) estimated that up to 34% of rhinoceros auklet eggs could be lost to mice at this colony. Because the incubation period of late pairs would have overlapped with mid-to-late incubation and early chick-rearing of early pairs, and because chick-rearing appears to be more energetically demanding than incubation for rhinoceros auklets (Niizuma et al. 2002), it seems plausible that characteristics of relayers and naturally late-layers, rather than late laying *per se*, caused them to experience low hatching success.

Condition of offspring at fledging

In Cassin's auklets, both mass and wing length at fledging declined with later hatching, even though late-hatched control chicks remained longer in their burrows. A seasonal decline in growth rate and fledging mass is normal in Cassin's auklets (Vermeer 1981, Ainley et al. 1990, Morbey and Ydenberg 1997). However, pairs raising offspring from replacement eggs fledged chicks that were heavier than naturally late chicks, and similar to masses of early chicks. Experimental chicks also fledged younger than predicted from their hatching dates, but followed the population-wide seasonal decline in wing length at fledging. The tendency for their chicks to depart with short wings was the only clear signal we found of a potential fitness consequence associated with relaying for Cassin's auklets, compared to values expected based on first egg dates.

It has been suggested that seasonal declines in fledging mass represent strategic responses of alcid chicks to hatching late (Ydenberg et al. 1995). However, the observed differences in Cassin's auklets between experimental relayers (all of which initially laid early, therefore were probably high quality birds) and late controls suggest that the decline in fledging mass, and perhaps also the increase in fledging age, were more likely due to the low quality of late parents, rather than to their lateness (Morbey and Ydenberg 2000). Seasonal increases in fledging age are very rare in alcids (Ydenberg et al. 1995), and it is perhaps not just a coincidence that late control chicks tended to delay fledging in a year in which feeding conditions remained favourable until late (Morbey et al. 1999). We suggest that the naturally late chicks might have remained longer in order to complete further development, in an effort to improve their chances of successfully making the transition from life at the colony to an independent life at sea. Growth of wing feathers is one component of development widely thought to influence timing of nest departure in alcids (Birkhead 1977, Øyan and Anker-Nilssen 1996, Hipfner and Gaston 1999), yet the fact that experimental chicks tended to fledge young and with short wings suggests that even under favourable feeding conditions, it may be advantageous for faster-growing chicks to get to sea quickly late in the season (Ydenberg 1989). This tendency is also observed in thick-billed murres *Uria lomvia* (Hipfner 1997, 2001).

Consistent with that idea, we found that in the absence of a seasonal decline in fledging mass, all late rhinoceros auklet chicks, including those hatched from experimental replacement eggs, tended to fledge young and with short wings. The seasonal decline in fledging age is a common phenomenon in rhinoceros auklets, but a seasonal decline in fledging mass is also normal (Wilson and Manuwal 1986, Harfenist 1995, Ydenberg et al. 1995, Triangle Island Research Station unpubl. data). However, because few late-laying rhinoceros auklets produced fledglings in our study, neither experimentals nor controls, the lack of decline in fledging mass may reflect the fact that only very capable pairs managed to do so. We also note that Pacific sauries, the major prey species in nestling diets late in the season, are not notably lower than other prey in caloric content (Vermeer and Devito 1986). In our study, consequences of relaying for rhinoceros auklets, compared to expectations based on their original laying dates, were manifested clearly in greatly reduced hatching success, and also in the reduced quality of the few fledglings produced. However, as in Cassin's auklets, results of a study investigating the relative costs and benefits of relaying might vary with feeding conditions in a particular year.

Acknowledgements – We thank BriAnne Addison, Gwylim Blackburn, Stephen Hureau, Glen Keddie, Valerie Lebrecque, Andrea Lonon, Laura MacFarlane-Tranquilla, Brianna Newton and Natasha Schorb for help with fieldwork. In addition, we thank Moira Galbraith (Institute of Ocean Sciences, Sidney) for identifying prey species in Cassin's auklet food loads. This research was supported by a grant from the *Nestucca* Oil Spill Trust Fund to Douglas F. Bertram and Gary W. Kaiser. Other funding for the 2002 Triangle program came from the Centre for Wildlife Ecology (Simon Fraser University and the Canadian Wildlife Service, Pacific and Yukon Region), and by grants from World Wildlife Fund Canada (through the Endangered Species Recovery Fund), and the Science Horizons program of Environment Canada. As in previous years, we received invaluable ship and helicopter support from the Canadian Coast Guard. Thanks also to Judy Higham and Connie Smith for logistical support of our field camp from back home in Vancouver. The original manuscript was greatly improved by constructive reviews from BriAnne Addison, Scott Hatch, Ron Ydenberg and two anonymous reviewers.

References

Ainley, D. G. and Boekelheide, R. J. 1990. Seabirds of the Farallon Islands. – Stanford University Press, Stanford.

Ainley, D. G., Boekelheide, R. J., Morrell, S. H. and Strong., C. S. 1990. Cassin's auklet. – In: Ainley, D. G. and Boekelheide, R. J. (eds). Seabirds of the Farallon Islands. Stanford University Press, Stanford, pp. 306–338.

Arnold, T. W. 1993. Factors affecting renesting in American coots. – Condor 95: 273–281.

Ashcroft, R. E. 1979. Survival rates and breeding biology of puffins on Skomer Island, Wales. – Ornis Scand. 10: 100–110.

Astheimer, L. B. 1986. Egg formation in Cassin's auklet. – Auk 103: 682–693.

Astheimer, L. B. 1991. Embryo metabolism and egg neglect in Cassin's auklets. – Condor 93: 486–495.

Bertram, D. F., Jones, I. L., Cooch, E. G., Knechtel, H. A. and Cooke, F. 2000. Survival rates of Cassin's and rhinoceros auklets at Triangle Island, British Columbia. – Condor 102: 155–162.

Bertram, D. F., Kaiser, G. W. and Ydenberg, R. C. 1991. Patterns in the provisioning and growth of nestling rhinoceros auklets. – Auk 108: 842–852.

Bertram, D. F., Mackas, D. L. and McKinnell, S M. 2001. The seasonal cycle revisited: inter-annual variation and ecosystem consequences. – Progr. Oceanogr. 49: 283–307.

Birkhead, T. R. 1977. Adaptive significance of the nestling period of guillemots *Uria aalge*. – Ibis 199: 544–549.

Birkhead, T. R. and Nettleship, D. N. 1982. Adaptive significance of egg size and laying date in thick-billed murres *Uria lomvia*. – Ecology 63: 300–306.

Birkhead, T. R. and Nettleship, D. N. 1984. Egg size, composition, and offspring quality in some Alcidae (Aves: Charadriiformes). – J. Zool. Lond. 202: 177–194.

Blight, L. K., Ryder, J. L. and Bertram, D F. 1999. Predation on rhinoceros auklet eggs by a native population of *Peromyscus*. – Condor 101: 871–876.

Boekelheide, R. J., Ainley, D. G., Morrell, S. H., Huber, H. R. and Lewis, T. J. 1990. Common murre. – In: Ainley, D. G. and Boekelheide, R. J. (eds). Seabirds of the Farallon Islands. Stanford University Press, Stanford, pp. 245–275.

De Forest, L. N. and Gaston, A. J. 1996. The effect of age on timing of breeding and reproductive success in the thick-billed murre. – Ecology 77: 1501–1511.

Gaston, A. J. and Dechesne, S. B. C. 1996. Rhinoceros auklet (*Cerorhinca monocerata*). – In: Poole, A. and Gill, F (eds). The birds of North America. The Academy of Natural Sciences and the American Ornithologists Union, Philadelphia, number 212, pp. 1–23.

Gaston, A. J. and Jones, I. L. 1998. The Auks. – Oxford University Press, Oxford.

Gaston, A. J. and Nettleship, D. N. 1981. The thick-billed murres of Prince Leopold Island. – Can. Wildl. Serv. Monogr. Ser. No. 6.

Harfenist, A. 1995. Effects of growth rate variation on fledging of rhinoceros auklets (*Cerorhinca monocerata*). – Auk 112: 60–66.

Hatch, S. A. and Hatch, M. A. 1990. Breeding seasons of oceanic birds in a subarctic colony. – Can. J. Zool. 68: 1664–1679.

Hatchwell, B. J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of the common guillemot *Uria aalge*. – J. Anim. Ecol. 60: 721–736.

Heaney, N. and Monaghan, P. 1995. A within-clutch trade-off between egg production and rearing in birds. – Proc. R. Soc. Lond. B 261: 361–365.

Hedd, A., Ryder, J. L., Cowen, L. L. and Bertram, D. F. 2002. Inter-annual variation in the diet, provisioning and growth of Cassin's auklet at Triangle Island, British Columbia: responses to variation in ocean climate. – Mar. Ecol. Progr. Ser. 229: 221–232.

Hegyi, Z. and Sasvári, L. 1998. Parental condition and breeding effort in waders. – J. Anim. Ecol. 67: 41–53.

Hipfner, J. M. 1997. Effects of parental quality and timing of breeding on the growth of nestling thick-billed murres. – Condor 99: 353–360.

Hipfner, J. M. 2001. Fitness-related consequences of relaying in an arctic seabird: survival of offspring to recruitment age. – Auk 118: 1076–1080.

Hipfner, J. M. and Gaston, A. J. 1999. Timing of nest departure in the thick-billed murre and razorbill: tests of Ydenberg's model. – Ecology 80: 587–596.

Hipfner, J. M., Gaston, A. J. and de Forest, L. N. 1997. The role of female age in determining egg size and laying date of thick-billed murres. – J. Avian Biol. 28: 271–278.

Hipfner, J. M., Gaston, A. J., Martin, D. L. and Jones, I. 1999. Seasonal declines in replacement egg-layings in a long-lived, arctic seabird: costs of late breeding or variation in female quality? – J. Anim. Ecol. 68: 988–998.

Hipfner, J. M., Gaston, A. J. and Storey, A. E. 2001. Nest-site safety predicts the relative investment made in first and replacement eggs by two long-lived seabirds. – Oecologia 129: 234–242.

Hipfner, J. M., Gaston, A. J., Herzberg, G. R., Brosnan, J. T. and Storey, A. E. 2003. Egg composition in relation to female age and relaying: constraints on egg production in thick-billed murres. – Auk 120: 645–657.

Kitaysky, A. S. 1999. Metabolic and developmental responses of alcid chicks to experimental variation in food intake. – Phys. Biochem. Zool. 72: 462–473.

Kuroda, N. 1963. A comparative study on the chemical constitutions of some bird eggs and the adaptive significance. – Misc. Rep. Yamashina Inst. 3: 311–333.

Lack, D. 1947. The significance of clutch size. – Ibis 89: 302–352.

Manuwal, D. A. 1979. Reproductive commitment and success of Cassin's auklet. – Condor 81: 111–121.

Milonoff, M. 1989. Can nest predation limit clutch size in precocial birds? – Oikos 55: 424–427.

Monaghan, P. and Nager, R. G. 1997. Why don't birds lay more eggs? – Trends Ecol. Evol. 12: 270–274.

Monaghan, P., Nager, R. G. and Houston, D. C. 1998. The price of eggs: increased investment in egg production reduces the offspring-rearing capacity of parents. – Proc. R. Soc. Lond. B 265: 1731–1735.

Morbey, Y. and Ydenberg, R. C. 1997. Intraspecific variability in nestling growth and fledging behavior of Cassin's auklets at Triangle Island, British Columbia. – Condor 99: 361–371.

Morbey, Y. and Ydenberg., R. C. 2000. Seasonal decline in nestling growth: support for the parental quality hypothesis in Cassin's auklets. – Auk 117: 1065–1068.

Morbey, Y., Ydenberg, R. C., Knechtel, H. A. and Harfenist, A. 1999. Parental provisioning, nestling departure decisions and pre-fledging mass recession in Cassin's auklets. – Anim. Behav. 57: 873–881.

Nager, R. G., Monaghan, P. and Houston, D. C. 2000. Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. – Ecology 81: 1339–1350.

Nager, R. G., Monaghan, P. and Houston, D. C. 2001. The cost of egg production: increased egg production reduces future fitness in gulls. – J. Avian Biol. 32: 159–166.

Niizuma, Y., Araki, Y., Mori, H., Takahashi, A. and Watanuki, Y. 2002. Responses of body components to energetic demand throughout the breeding stages of rhinoceros auklets. – Can. J. Zool. 80: 1549–1555.

Oppliger, A., Christe, P. and Richner, H. 1996. Clutch size and malaria resistance. – Nature 381: 565.

Øyan, H. S. and Anker-Nilssen, T. 1996. Allocation of growth in food-stressed Atlantic puffin chicks. – Auk 113: 830–841.

Piatt, J. F. and Kitaysky, A. S. 2002. Horned puffin (*Fratercula corniculata*). – In: Poole, A. and Gill, F (eds). The birds of North America. The Academy of Natural Sciences and the American Ornithologists Union, Philadelphia, no. 603, pp. 1–28.

Piatt, J. F., Roberts, B. D., Lidster, W. W., Wells, W. W. and Hatch, S. A. 1990. Effects of human disturbance on breeding least and crested auklets at St. Lawrence Island, Alaska. – Auk 107: 342–350.

Pyle, P., Sydeman, W. J. and Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. – J. Anim. Ecol. 70: 1088–1097.

Rahn, H., Paganelli, C. V. and Ar, A. 1975. Relation of avian egg weight to body weight. – Auk 92: 750–765.

Roby, D. D. and Brink, K. L. 1986. Breeding biology of least auklets on the Pribilof Islands, Alaska. – Condor 88: 336–346.

Sealy, S. G. Egg size of murrelets. – Condor 77: 500–501.

Sorci, G., Soler, J. J. and Møller, A. P. 1997. Reduced immunocompetence of nestlings in replacement clutches of the European magpie. – Proc. R. Soc. Lond. B 264: 1593–1598.

Stearns, S. C. 1992. The evolution of life histories. – Oxford University Press, Oxford.

Vermeer, K. 1980. The importance of timing and type of prey to reproductive success of rhinoceros auklets *Cerorhinca monocerata*. – Ibis 122: 343–350.

Vermeer, K. 1981. The importance of plankton to Cassin's auklets during breeding. – J. Plankt. Res. 3: 315–328.

Vermeer, K. 1987. Growth and nestling periods of Cassin's auklets: adaptations of planktivorous auklets to breeding at northern latitudes. – Can. Tech. Rep. Hydr. Ocean Sci. 93.

Vermeer, K. and Cullen, L. 1979. Growth of rhinoceros auklets and tufted puffins, Triangle Island, British Columbia. – Ardea 67: 22–27.

Vermeer, K. and Devito, K. 1986. Size, caloric content, and association of prey fish in meals of nestling rhinoceros auklets. – Murrelet 67: 1–9.

Vermeer, K. and Westrheim, S. J. 1984. Fish changes in the diets of nestling rhinoceros auklets and their implications. – In: Nettleship, D. N., Sanger, G. A. and Springer, P. F. (eds). Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa, pp. 96–105.

Visser, M. E. and Lessells, C. M. 2001. The costs of egg production and incubation in great tits (*Parus major*). – Proc. R. Soc. Lond. B 268: 1271–1277.

Wendeln, H., Becker, P. H. and Gonzalez-Solis, J. 2000. Parental care of replacement clutches in common terns (*Sterna hirundo*). – Behav. Ecol. Sociobiol. 47: 382–392.

Wilson, U. W. and Manuwal, D. A. 1986. Breeding biology of the rhinoceros auklet in Washington. – Condor 88: 143–155.

Ydenberg., R. C. 1989. Growth-mortality trade-offs and the evolution of juvenile life histories in the Alcidae. – Ecology 70: 1494–1506.

Ydenberg, R. C., Clark, C. W. and Harfenist, A. 1995. Intraspecific fledging mass variation in the Alcidae, with special reference to the seasonal fledging mass decline. – Am. Nat. 145: 412–433.

(*Received 2 April 2003, revised 10 July 2003, accepted 18 July 2003.*)