

- THRALL, P. H., J. ANTONOVICS, AND W. G. WILSON. 1998. Allocation to sexual versus nonsexual disease transmission. *American Naturalist* 151:29–45.
- WHITTINGHAM, L. A., P. O. DUNN, AND R. D. MARGRATH. 1997. Relatedness, polyandry and extra-group paternity in the cooperatively breeding White-browed Scrubwren (*Sericornis frontalis*). *Behavioral Ecology and Sociobiology* 40:261–270.
- WRIGHT, J., AND I. CUTHILL. 1989. Manipulation of sex differences in parental care. *Behavioral Ecology and Sociobiology* 25:171–181.

Received 18 August 1999, accepted 28 April 2000.
Associate Editor: J. Ekman

The Auk 117(4):1065–1068, 2000

Seasonal Decline in Nestling Growth: Support for the Parental-Quality Hypothesis in Cassin's Auklets

YOLANDA E. MORBEY¹ AND RONALD C. YDENBERG

Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

Growth rates of nestlings often decline over the breeding season (e.g. Birkhead and Nettleship 1982, Gaston et al. 1983, Morbey and Ydenberg 1997, Lepage et al. 1999). Although several mechanistic hypotheses have the potential to explain this phenomenon (see Nilsson 1999), we investigated the two that are considered most often. Under the date hypothesis, nestling growth depends indirectly on current environmental conditions through direct effects on parental provisioning. A seasonal decline in nestling growth is expected if feeding conditions deteriorate over the season. Under the parental-quality hypothesis, young or inexperienced parents, or those with lower provisioning ability, initiate breeding later, leading to a seasonal decline in nestling growth. We determined which hypothesis could best explain the observed seasonal decline in nestling growth rates of Cassin's Auklets (*Ptychoramphus aleuticus*) by comparing growth of nestlings whose hatching dates were normal versus experimentally delayed.

Study area and methods.—Breeding phenology and nestling growth of Cassin's Auklets were monitored in 1994 on Triangle Island (50°52'N, 129°05'W; Morbey and Ydenberg 1997). Cassin's Auklets lay one egg and incubate it for approximately 38 days, with parents switching incubation duties approximately every 24 h (Astheimer 1991). Prior to egg laying, we excavated 82 burrows to create access holes and began daily monitoring. If twigs that we placed in burrow entrances were knocked down the following day, we inferred that the burrow had been visited the previous night. Active burrows were checked every third day for eggs. Upon discovery of a newly laid

egg, we alternately assigned the burrow to one of two experimental groups. In the delayed group ($n = 27$), the egg was replaced with a hard-boiled chicken egg for five days. In the interim, the auklet egg was left in a carton buried in the sand to keep it safe and cool. Enforcing egg neglect at the beginning of the incubation period was done to minimize any negative effects of interrupting embryonic growth. In the control group ($n = 25$), eggs were handled as in the delayed group but were not removed for more than a few seconds. Hatching dates of these experimental burrows were expected to span the natural range.

During the hatching period, we checked all burrows every three days and estimated hatchling ages using wing length (Morbey and Ydenberg 1997). Mass and wing length were measured at hatching, 5 days of age, 25 days of age, then every fifth day until chicks were fully feathered, and then every second day until chicks fledged (i.e. left their burrows). We measured nestling growth as the daily rate of mass increase during the linear growth phase, which occurs from 5 to 25 days of age (Vermeer 1981). We also measured nestling growth rates for an additional 70 chicks whose burrows were found after egg laying; these were considered controls for the experimental manipulation (low-disturbance group in Morbey and Ydenberg [1997]) and will be referred to as the natural group. These burrows likely represented the entire range of hatching dates (see Morbey and Ydenberg 1997: fig. 1).

We obtained growth rates for only 9 nestlings in the delayed group and 13 in the control group because of egg abandonment or predation (12 in the delayed group and 8 in the control group), nestling mortality (4 in the delayed group and 1 in the control group), extreme lateness (1 in the control group), and

¹ E-mail: ymorbey@sfu.ca

extreme low growth (2 in each group). Nestlings with extreme low growth (less than 3.25 g/day during linear phase) were excluded from analyses because their growth rates were lower than those observed in the natural group.

Under the date hypothesis, growth rates of delayed nestlings should match those of nestlings hatched on the same (actual) dates because growth is determined by current environmental conditions. Delayed nestlings should grow slower than nestlings hatched on the same intended dates (i.e. dates on which delayed eggs would have hatched in the absence of experimental delay). Under the parental-quality hypothesis, growth rates of delayed nestlings should match those of nestlings hatched on the same intended dates because growth rate and laying date are determined by parental quality. Delayed nestlings should grow faster than nestlings hatched on the same actual dates because the latter would have parents of lower quality.

We tested these predictions by comparing nestling growth in the delayed group with the natural seasonal pattern of growth, using either intended or actual hatching dates. Because of the small number of nestlings in the experiment, we did not use ANCOVA but instead tested if the residuals for the delayed group, in relation to the seasonal pattern for the natural group, were significantly different from zero using *t*-tests (one-tailed for directional predictions; two-tailed otherwise). The two hypotheses make different predictions about the same residuals. We also used the mean error (i.e. mean of the residuals) to determine which hypothesis was more consistent with the data (Power 1993). The parental-quality hypothesis is supported if the mean error for the delayed group members is lower when using their intended rather than their actual hatching dates, and the date hypothesis is supported if the mean error is lower when using their actual rather than their intended hatching dates.

Results.—The manipulation delayed hatching by 5.6 days (mean period between laying and hatching for delayed group = $44.3 \pm$ SD of 1.9 days, $n = 12$, hatching date unknown for three chicks; mean for control group = 38.6 ± 3.1 days, $n = 16$, hatching date unknown for one chick), so for delayed nestlings, the intended hatching date equaled the actual hatching date minus 5.6.

The experiment did not appear to have significant negative consequences on hatching and fledging success. Among all burrows, prolonging incubation did not significantly reduce hatching success in the delayed group (15 of 27, 56%) versus the control group (17 of 25, 68%; $\chi^2 = 0.85$, $df = 1$, $P = 0.36$). Hatching success was 79% in nonexperimental burrows (Morbey and Ydenberg 1997), but these burrows were found after egg laying and so are not comparable. Prolonging incubation did not significantly reduce fledging success in the delayed group (11 of 15, 73%)

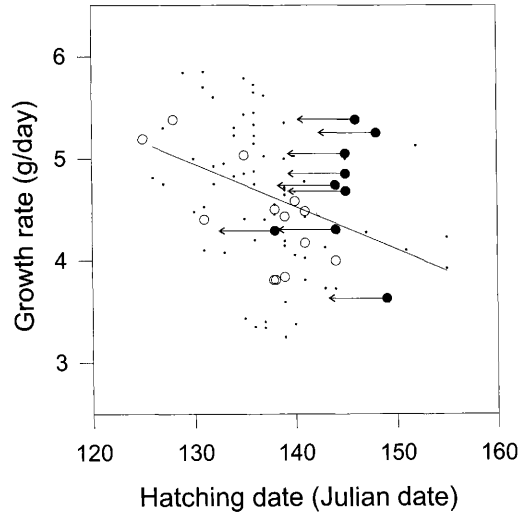


FIG. 1. Seasonal variation in nestling growth in natural (dots), control (open circles), and delayed (filled circles) groups of Cassin's Auklets. Filled circles denote actual hatching date, and arrow tips indicate intended hatching date. Overlapping data points are slightly offset to distinguish them. The best-fit line for the natural group is $y = 10.40 - 0.04x$, which corresponds to an expected decline of 0.23 g per day over 5.6 days under the date hypothesis.

compared with the control group (16 of 17, 94%; $\chi^2 = 2.61$, $df = 1$, $P = 0.11$), and fledging success in both experimental groups (84%) was similar to that of nonexperimental nestlings (88%; Morbey and Ydenberg 1997; $\chi^2 = 0.27$, $df = 1$, $P > 0.50$). Hatching success and fledging success for nonexperimental nestlings included the natural group and other nestlings that were measured more frequently.

Nestling growth rates declined significantly over the season in the natural group ($t = -3.13$, $df = 68$, $P = 0.003$; Fig. 1; see Morbey and Ydenberg 1997: fig. 4). Although this simple linear model had poor explanatory power ($R^2 = 0.13$) and appeared to overestimate nestling growth in mid-season, the addition of a quadratic or cubic term was not significant. As a consequence of the poor fit of this model, nestlings in the control group grew significantly slower than expected based on the seasonal pattern (mean error = -0.238 g/day; $t = -2.20$, $df = 12$, $P = 0.048$). If instead the control group is compared with the natural group modeled with a third-order polynomial, which does slightly better at describing the seasonal trend ($R^2 = 0.16$), nestling growth did not differ from expected (mean error = -0.095 g/day; $t = -0.91$, $df = 12$, $P = 0.38$).

Regardless of which model (linear or polynomial) is used to describe the natural seasonal pattern in

growth, the data for the delayed nestlings more strongly supported the parental-quality hypothesis. Using the linear model, growth rates of delayed nestlings more closely matched natural nestlings hatched at the same intended time (mean error = 0.124 g/day) rather than at the same actual time (mean error = 0.358 g/day; Fig. 1). As predicted under the parental-quality hypothesis, delayed nestlings grew faster than nestlings hatched at the same time (one-tailed $t = 1.88$, $df = 8$, $P = 0.049$) but at a similar rate to nestlings hatched 5.6 days earlier ($t = 0.65$, $df = 8$, $P > 0.50$). Counter to the date hypothesis, delayed nestlings did not grow slower than nestlings hatched at the same intended time (one-tailed $t = 0.65$, $df = 8$, $P > 0.50$), but in fact grew faster. However, in support of the date hypothesis, growth rates of delayed nestlings were statistically similar to those of nestlings hatched at the same time ($t = 1.88$, $df = 8$, $P = 0.098$).

Under the polynomial model, both predictions of the parental-quality hypothesis were supported: delayed nestlings grew faster than nestlings hatched at the same time (mean error = 0.617 g/day; one-tailed $t = 3.06$, $df = 8$, $P = 0.008$) and at similar rates to nestlings hatched at the same intended time (mean error = 0.305 g/day; $t = 1.50$, $df = 8$, $P = 0.17$). Both predictions of the date hypothesis were refuted: delayed nestlings did not grow slower than nestlings hatched at the same intended time (one-tailed $t = 1.50$, $df = 8$, $P > 0.50$), nor did they grow at similar rates to nestlings hatched at the same actual time ($t = 3.06$, $df = 12$, $P = 0.016$).

Discussion.—Our results are more consistent with the parental-quality hypothesis than with the date hypothesis. Regardless of the small sample size in our experiment, the small expected difference in growth rate under the date hypothesis (-0.23 g/day), and the poor description of the natural seasonal trend (low R^2 -values), the data indicate that delayed nestlings grew faster than nestlings with similar hatching dates. In fact, growth rates of delayed nestlings more closely matched those of nestlings hatched 5.6 days earlier, corresponding to the time they should have hatched. The simplest explanation for our results is that parents that breed early are of higher quality and better able to provision their nestlings than are parents that breed later.

Another hypothesis is that late-breeding parents reduce their provisioning effort because late nestlings are worth less than earlier nestlings owing to their lower contribution to parental reproductive success (Gaston 1985). Given our experimental design, this hypothesis cannot be distinguished from the date hypothesis because it predicts that delayed parents should reduce their effort, and nestling growth rates should match nestlings with similar hatching dates. For the reasons above, our results are more consistent with the parental-quality hypothesis than with the reduced-effort hypothesis because

delayed parents did not appear to reduce provisioning rates.

We can say little about feeding conditions, but the parental-quality hypothesis works if feeding conditions remain constant, or if they decline seasonally (Hipfner 1997). Perhaps high-quality parents are more efficient at finding and capturing prey than are poor-quality parents and thus can compensate for poor feeding conditions by increasing provisioning. High-quality parents also may be better at other parenting tasks, such as brooding. Parents brood their newly hatched nestling for up to six days to aid in thermoregulation (Manuwal 1974), and brooding could allow nestlings to allocate more energy to growth.

One unanticipated consequence of our experiment was that most delayed nestlings hatched at a time when few natural nestlings hatched. One possible explanation for this is that our disturbance at burrows before egg laying delayed egg laying. If so, experimental burrows may have been delayed by more than 5.6 days. This scenario would not affect our conclusions because the parental-quality hypothesis probably would be supported more strongly (because the mean error would be lower when using intended hatching dates). However, the lateness of the delayed group makes a comparison between natural and delayed groups less than ideal. Given the slight, but not significant, increase in nestling growth very late in the season, delayed parents may have experienced better foraging conditions than indicated by the natural seasonal trend. However, further analysis of the growth data for a different set of nestlings that were measured more frequently (high-disturbance group; Morbey and Ydenberg 1997) did not demonstrate any general increase in feeding conditions after day 150, when fast-growing delayed nestlings began their linear phase of growth. When we analyzed seasonal patterns in age-specific growth at ages 10 and 15 to enable comparisons before and after day 150, growth declined over the season and did not increase after day 150.

Some previous experimental studies of seasonal patterns in nestling growth also support the parental-quality hypothesis (Hatchwell 1991, De Forest and Gaston 1996, Nisbet et al. 1998), whereas others support the date hypothesis (Hedgren and Linnman 1979, Moreno et al. 1997, Lepage et al. 1999) or a combination of the two (Verhulst and Tinbergen 1991, Brinkhof 1997). These results suggest that other factors influence the relative importance of parental quality and feeding conditions on nestling growth. For example, if feeding conditions are generally poor, parental quality may have a greater effect on growth (Verhulst and Tinbergen 1991). Alternatively, if provisioning ability is similar among parents, variation in growth may result mostly from variation in feeding conditions.

The natural history of Cassin's Auklets is consis-

tent with the parental-quality hypothesis. Breeding age varies, older parents tend to breed earlier (Emslie et al. 1992, Knechtel 1998), and successful provisioning likely requires experience because the species feeds at sea on patchily distributed prey (mostly small crustaceans). Furthermore, the average growth in 1994 (D. Bertram pers. comm.) may have been indicative of average feeding conditions. Under such conditions, detecting seasonal variation in parental quality may be possible.

Acknowledgments.—We thank Fred Cooke and Ian Jones for helping design the experiment and Tasha Smith for field assistance. Denis Lepage and two anonymous reviewers provided excellent advice on how to improve the manuscript. Transportation to Triangle Island was provided by the Canadian Coast Guard, and permission to conduct research on the island was provided by the Ecological Reserves branch of B.C. Parks. Logistical support was provided by the Canadian Wildlife Service/Natural Sciences and Engineering Research Council of Canada (NSERC)/Simon Fraser University Research Chair in Wildlife Ecology. The research was financially supported by an Anne Vallée Ecological Scholarship to YEM and an NSERC operating grant to RCY.

LITERATURE CITED

- ASTHEIMER, L. B. 1991. Embryo metabolism and egg neglect in Cassin's Auklets. *Condor* 93:486–495.
- BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1982. The adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. *Ecology* 63: 300–306.
- BRINKHOF, M. W. G. 1997. Seasonal decline in body size of coot chicks. *Journal of Avian Biology* 28: 117–131.
- DE FOREST, L. N., AND A. J. GASTON. 1996. The effect of age on timing of breeding and reproductive success in the Thick-billed Murre. *Ecology* 77: 1501–1511.
- EMSLIE, S. D., W. J. SYDEMAN, AND P. PYLE. 1992. The importance of mate retention and experience on breeding success in Cassin's Auklet (*Ptychoramphus aleuticus*). *Behavioral Ecology* 3:189–195.
- GASTON, A. J. 1985. Development of the young in the Atlantic Alcidae. Pages 319–354 in *The Atlantic Alcidae: The evolution, distribution and biology and the auks inhabiting the Atlantic Ocean and adjacent water areas* (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, London.
- GASTON, A. J., G. CHAPDELAIN, AND D. G. NOBLE. 1983. The growth of Thick-billed Murre chicks at colonies in Hudson Strait: Inter- and intra-colony variation. *Canadian Journal of Zoology* 61: 2465–2475.
- HATCHWELL, B. J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of Common Guillemots (*Uria aalge*). *Journal of Animal Ecology* 60:721–736.
- HEDGREN, S., AND A. LINNMAN. 1979. Growth of Guillemot *Uria aalge* chicks in relation to time of hatching. *Ornis Scandinavica* 10:29–36.
- HIPFNER, J. M. 1997. The effects of parental quality and timing of breeding on the growth of nestling Thick-billed Murres. *Condor* 99:353–360.
- KNECHTEL, H. A. 1998. Effects of age, gender and condition on the reproductive effort of Cassin's Auklets (*Ptychoramphus aleuticus*) on Triangle Island, British Columbia. M.S. thesis, Simon Fraser University, Burnaby, British Columbia.
- LEPAGE, D., A. DESROCHERS, AND G. GAUTHIER. 1999. Seasonal decline of growth and fledging success in Snow Geese *Anser caerulescens*: An effect of date or parental quality? *Journal of Avian Biology* 30:72–78.
- MANUWAL, D. A. 1974. The natural history of Cassin's Auklet (*Ptychoramphus aleuticus*). *Condor* 76:421–431.
- MORBAY, Y. E., AND R. C. YDENBERG. 1997. Intraspecific variability in nestling growth and fledging behavior of Cassin's Auklets at Triangle Island, British Columbia. *Condor* 99:361–371.
- MORENO, J., A. BARBOSA, J. POTTI, S. MERINO. 1997. The effects of hatching date and parental quality on chick growth and creching age in the Chinstrap Penguin (*Pygoscelis antarctica*): A field experiment. *Auk* 114:47–54.
- NILSSON, J.-Å. 1999. Fitness consequences of timing of reproduction. Pages 234–247 in *Proceedings of the 22 International Ornithological Congress* (N. J. Adams and R. H. Slotow, Eds.). Durban, 1998. BirdLife South Africa, Johannesburg.
- NISBET, I. C. T., J. A. SPENDELOW, J. S. HATFIELD, J. M. ZINGO, AND G. A. GOUGH. 1998. Variations in growth of Roseate Tern chicks: II. Early growth as an index of parental quality. *Condor* 100:305–315.
- POWER, M. 1993. The predictive validation of ecological and environmental models. *Ecological Modelling* 68:33–50.
- VERHULST, S., AND J. M. TINBERGEN. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the Great Tit *Parus major major*. *Journal of Animal Ecology* 60:269–282.
- VERMEER, K. 1981. The importance of plankton to Cassin's Auklets during breeding. *Journal of Plankton Research* 3:315–329.

Received 16 April 1999, accepted 28 April 2000.

Associate Editor: C. Bosque