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EXPERIMENTAL EVIDENCE THAT BOTH TIMING AND PARENTAL QUALITY AFFECT BREEDING SUCCESS IN A ZOOPLANKTIVOROUS SEABIRD

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Abstract.—Avian breeding success generally declines with later laying because of seasonal reductions in food supply, late laying by less capable pairs, or both. To understand the direct fitness consequences of breeding time requires distinguishing between these two possibilities. We used egg removal and re-laying experiments to evaluate how date and parental quality affect breeding success in a zooplanktivorous seabird, Cassin's Auklet (*Ptychoramphus aleuticus*). Egg laying began at the same time in all 5 years of study at Triangle Island, British Columbia, but, compared with a cold-water year, the population laid later and less synchronously in 4 warm-water years in which prey populations peaked earlier. As a result, Cassin's Auklets were less successful in years in which they laid later. Within seasons, early-laying females whose breeding attempt we delayed did not follow the population-wide seasonal declines in hatching success. This indicates a strong role for parental quality at the egg stage, probably because early, high-quality birds maintained more constant incubation. By contrast, the experimental females followed the population-wide seasonal declines in nestling survival and fledging mass. This indicates a strong role for date at the offspring-provisioning stage, which accords well with a previous study that found that success while raising nestlings is largely determined by the degree of temporal (mis)matching with the copepod *Neocalanus cristatus*. Our results offer novel insight into the causes of seasonal declines in avian breeding success, indicating that date and parental effects can be differentially involved, depending on the stage of breeding. *Received 21 October 2008, accepted 16 May 2009.*

Key words: Cassin's Auklet, match–mismatch, parental quality, *Ptychoramphus aleuticus*, timing of breeding.

Evidencia Experimental de que el Tiempo y la Calidad Parental Afectan el Éxito Reproductivo de un Ave Marina Zooplanctívora

Resumen.—El éxito reproductivo en las aves generalmente disminuye con las puestas más tardías debido a la reducción estacional del alimento, a que las puestas tardías son generalmente de parejas de menor calidad o a ambas razones. Para entender las consecuencias directas del tiempo de reproducción sobre la adecuación es necesario distinguir estas dos posibilidades. Realizamos experimentos de remoción y re-puesta de huevos para evaluar cómo la fecha y la calidad parental afectan el éxito reproductivo en *Ptychoramphus aleuticus*, un ave marina zooplanctívora. La puesta de huevos comenzó siempre al mismo tiempo durante los cinco años de estudio en Triangle Island, British Columbia, pero, en comparación con un año de agua fría, la población comenzó la puesta más tarde y de forma menos sincrónica en cuatro años de clima cálido en los que la población de presas llegó a su máximo más temprano. En consecuencia, los individuos fueron menos exitosos en años en que la puesta fue tardía. En una misma estación, las hembras que pusieron temprano pero se les retrasó la puesta experimentalmente no presentaron las disminuciones en el éxito de eclosión observadas para toda la población. Esto indica un fuerte papel de la calidad parental en la fase de huevos, probablemente porque las aves que ponen más temprano y son de mejor calidad mantienen una incubación más constante. De modo contrastante, las hembras manipuladas experimentalmente siguieron las disminuciones en supervivencia y peso de los polluelos que se observó en toda la población. Esto indica un fuerte papel del tiempo en que sucede la fase de aprovisionamiento de los polluelos, lo que coincide bien con un estudio previo que encontró que el éxito durante la cría de los polluelos está determinado en gran parte por el grado de coincidencia temporal con el copépodo *Neocalanus cristatus*. Nuestros resultados ofrecen una nueva perspectiva sobre las causas de las disminuciones estacionales del éxito reproductivo en las aves, e indican que tanto los efectos del tiempo como de la calidad parental pueden estar involucrados de forma diferente dependiendo de la fase del ciclo reproductivo.

One of the more robust paradigms in avian ecology holds that breeding times have evolved so that the most energetically demanding phase of reproduction, usually chick rearing, is matched to the seasonal peak in food availability (Lack 1954). Within that evolutionary construct, an individual female maximizing fitness must in each year fine-tune the time at which it begins the process of forming, laying, and incubating its clutch on the basis of the anticipated timing and magnitude of that year's peak in feeding conditions (Dawson 2008).

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However, many factors can limit a female's capacity to lay its clutch on time, including gene flow between populations adapted to habitats with different prey phenologies (Thomas et al. 2001), lack of correlation between conditions on the breeding and wintering grounds for long-distance migrants (Both and Visser 2001), and anomalous advances in prey phenology that may be driven by large-scale climatic changes (Stenseth and Mysterud 2002).

More generally, nutritional constraints operating on females as they form eggs could limit their capacity to lay on time (Stevenson and Bryant 2000). These physiological constraints can affect all individuals in years of unfavorable environmental conditions, causing population-wide temporal mismatching with the prey base (Visser et al. 1998). But they also affect only a segment of the population in any year, causing some individuals to lay too late to catch the annual peak in prey availability. Late layers typically include young, inexperienced females (Forslund and Pärt 1995), individuals that are doubly disadvantaged: first, because they are behaviorally less adept and physiologically less attuned to breeding than experienced birds, and second, because they miss the annual peak in food supply. This raises an important question: to what extent are seasonal declines in avian breeding success caused by inherent differences between females that lay early and late, and to what extent by seasonal reductions in food supply?

Because they can potentially address causal mechanisms (Sheldon et al. 2003), experimental approaches have often been used to answer this question (Verhulst and Nilsson 2008). Yet important issues remain unresolved. In their recent review, Verhulst and Nilsson (2008) noted that most experimental studies were of short duration and considered only a single phase of the breeding cycle. Because the demands on parents of incubating eggs and provisioning nestlings are different, date and parental effects could play different roles during the different breeding stages. In addition, their importance could vary from year to year, depending on the prevailing environmental conditions. Thus, season-long studies over several years are needed.

The Cassin's Auklet (*Ptychoramphus aleuticus*) population breeding at Triangle Island, British Columbia, provides an ideal study system in which to address this question for several reasons. First, we can expect parental effects to operate: the timing of laying and egg size are linked to prebreeding diet (Sorenson et al. 2009), and young females tend to lay late and to produce small eggs (Knechtel 1998). Yet date effects should also be expected, especially during chick rearing: growth and survival of the single nestlings of Cassin's Auklets' are greatest when the copepod *Neocalanus cristatus* forms a large part of their diet (Hedd et al. 2002, Hipfner 2008), and this prey species is highly seasonal. Overwintering *N. cristatus* mature, mate, and spawn at great depths. In spring, early juveniles undergo a vertical ontogenetic migration to feed in near-surface waters before returning to the deep (Miller et al. 1984). Cassin's Auklets forage intensively for late-stage (C5) copepodites along the continental shelf break west of Triangle Island (Boyd et al. 2008) while they are available. Finally, we can expect date and parental effects to vary in importance from year to year: biomass of *N. cristatus* peaks earlier, and more briefly, in warm-water years than in cold-water years (Mackas et al. 2007). As a result, environmental variation causes the birds to be differentially (mis)matched with their primary prey (Hipfner 2008).

We set out to determine how parental and date effects contribute to seasonal declines in breeding success of Cassin's Auklets over a 5-year period of extreme variation in the local marine environment (Mackas et al. 2007). To achieve our goal, we (1) removed eggs from a sample of early-laying females to induce them to re-lay about 2–3 weeks later than their initial laying dates; (2) measured $\delta^{15}N$ stable isotopic values in the egg yolks to assess interannual variation in the trophic levels at which females fed; and (3) monitored the timing of laying, hatching success, fledging success, and fledging mass of control pairs and all experimental pairs that re-laid. We predicted that if date effects are more important than parental effects, the experimental pairs would follow the population-wide seasonal declines. Conversely, if parental effects are more important than date effects, the experimental pairs would be more successful than predicted from their (re-)laying date, compared with controls.

METHODS

Study site.—We conducted field work at Triangle Island (50°52′N, 129°05′W) in 2002–2006. Observations spanned the Cassin Auklets' breeding season in all 5 years (late March to early August).

Field and laboratory methods.—On a control plot, we inspected ~80 breeding burrows at 5-day intervals to determine laying dates. When an egg was found, the burrow was then left undisturbed for 35 days, to allow birds to complete their 38 days of incubation (Manual and Thoresen 1993). Burrows then were checked at 5-day intervals until a hatchling was found, whereupon we measured hatchling wing length (± 0.5 mm) and mass (± 1 g) and estimated hatching date (age 0) using a calibration of wing length against age for chicks of known age at Triangle Island (Hedd et al. 2002). We weighed and measured chicks at 5, 10, 25, and 35 days of age, then every other day until they disappeared. Fledging ages average 43 days (Manuwal and Thoresen 1993).

On an adjacent plot, we inspected burrows at 2-day intervals from the start of the season. Egg laying began at the same time (± 2 days) on the control and experimental plots. When an egg was found, we collected it for a variety of research purposes (e.g., Addison et al. 2008), then measured its length and breadth (± 0.5 mm) and mass (± 1 g) and placed it in a freezer. Samples sizes were 30 eggs in a pilot project in 2002 (Hipfner et al. 2004) and 10–11 eggs in each year from 2003 to 2006. Eggs were collected during 28 March–6 April 2002, 28–31 March 2003, 30 March–5 April 2004, 1–19 April 2005, and 1–5 April 2006. All eggs were collected before the median laying date, except for 1 egg collected 2 days after the median in 2002. Because we wanted to avoid delaying the same female, we collected eggs from different burrows in each year (but 4 burrows were used in 2002 and again in 1 other year).

In 2003–2005, we rechecked experimental burrows every 5 days beginning 10 days after eggs were removed. In 2002, burrows were rechecked 17 days after the last removal (Hipfner et al. 2004). When a replacement egg was found, we measured its length and breadth (although a few were depredated by endemic Keen's Mice [*Peromyscus keeni*]), then put it back in place. An individual female's egg shape (length:breadth ratio) is consistent (Hipfner et al. 2003), so that the shape of first and second eggs found in the same burrows will be similar if laid by the same bird (see analysis below).

On the basis of this protocol, we defined burrow occupancy as the proportion of all burrows on control plots in which eggs were laid. For both control and experimental pairs, we defined hatching success as the proportion of eggs laid that hatched, and fledging success as the proportion of chicks that survived ≥ 35 days before disappearing. Breeding success and fledging mass were defined as the proportion of eggs laid that produced fledged chicks and the last mass recorded before fledging, respectively. Re-laying intervals were defined as the period that elapsed between removal of the first egg and the appearance of the second egg in the same burrow. As a measure of egg size, we used an index of volume (length × maximum breadth^2), which is very strongly related to fresh egg mass in Cassin's Auklet ($r^2 = 0.95$; Hipfner et al. 2004).

In the laboratory, we aliquoted ~1-mL samples of yolk into Eppendorf tubes. Lipid-free prepared samples were sent to the stable-isotope facilities at the University of Saskatchewan (2002) or the University of California, Davis (2003–2006), for analysis of δ^{15}N values. Results are reported in delta notation in parts per thousand (‰) relative to air. Nitrogen stable-isotope ratios can be used to assess the trophic level at which a consumer has fed, because ^{15}N becomes systematically enriched at successive trophic levels (Peterson and Fry 1987).

Statistical approach.—We examined factors affecting (1) hatching success, (2) fledging success, and (3) breeding success, using logistic models, and (4) fledging mass, using general linear models (GLMs). As predictor variables, we used (1) year (1–5); (2) date (laying [control] or re-laying [experimental] date as a continuous variable grouped by 5-day intervals beginning in late March) for hatching and breeding success, and estimated hatching date for fledging success and fledging mass; and (3) treatment (control or experimental pair). For each breeding parameter we built the same set of seven explanatory candidate models: (1) null or equal-means model; (2) year; (3) year + date; (4) year + date + treatment; (5) year + date + treatment + (year*treatment); (6) year + date + treatment + (date*treatment); and (7) year + date + treatment + (year*treatment) + (date*treatment).

All models within each candidate set were ranked using Akaike's information criterion (AIC) corrected for small sample size (AIC$_c$), based on the difference between each model's AIC$_c$ and the lowest AIC$_c$ from among the set. In addition to the most parsimonious model ($\Delta\text{AIC}_c = 0.0$), any models with ΔAIC_c scores ≤ 2 can be considered to have received substantial support (Burnham and Anderson 2002). Other parameters of interest are Log$L$, which is an estimate of the likelihood of a particular model given the data; AIC$_c w$, which measures the weight of evidence in favor of a particular model given the data and candidate model set; and the parameter weight, which sums the weight of evidence for a particular model term across all models in the candidate set.

We fully expected that both year and date would affect all measures of success, so we were especially interested in whether treatment effects would be additive. Inclusion of the treatment term, alone or in an interaction term, in a supported model would provide evidence in favor of the parental-quality hypothesis. Conversely, the absence of treatment terms among supported models would provide evidence in favor of the date hypothesis.

RESULTS

Variation in laying dates and breeding success.—On the control plot, burrow occupancy rates were similar from 2003 to 2005, but ~40% lower in 2006 following the extremely unsuccessful 2005 season (Table 1). First eggs were laid in late March in all 5 years (Fig. 1), but despite this constancy, median laying dates varied by 3 weeks (Table 1). Years of later laying tended to be years of less synchronous laying (i.e., with smaller values for skew and kurtosis; Table 1). All four measures of breeding success varied among years, although to different degrees (Table 1), and overall success was reduced in years of later laying. Using an integrated season-long measure (percentage breeding success × mean fledging mass; Hipfner et al. 2008), median laying date explained most of the interannual variation in success ($r^2 = 0.87$, $\beta = -4.8 \pm 1.1$ g day^{-1}).

Egg size varied little among the 5 years (for year in a GLM, $r^2 < 0.01$; overall average [± SE] = 54.0 ± 1.0 cm^3 in volume index). Conversely, δ^{15}N stable-isotope values in the yolks varied among years (for year in a GLM, $r^2 = 0.62$), being highest in 2002, lower in 2003–2005, and lowest in 2006 (Fig. 2).

Parental and date effects.—As expected, there was a strong correlation between the shape index of first and second eggs found in the same burrows ($r^2 = 0.47$). For comparison, second eggs were resampled 100 times using a bootstrap function and reassigned to first eggs. The mean of the distribution of bootstrapped correlation coefficients was $r = -0.003 \pm 0.025$ (95% confidence interval [CI]). This strongly suggests that the second eggs were

Table 1. Breeding parameters for control and experimental Cassin's Auklets at Triangle Island, British Columbia, in 2002–2006.

Year	Treatment	Burrow occupancy rate (%)	Laying dates				Number hatched	Number fledged	Breeding success (%)	Fledging mass (g, mean ± SD)
			Median	Skew (mean ± SE)	Kurtosis (mean ± SE)	Number of eggs				
2002	Control	No data	31 March –4 April	2.19 ± 0.30	5.11 ± 0.60	63	41 (65%)	38 (93%)	60	160 ± 19
	Experimental	—	—	—	—	27	19 (70%)	18 (95%)	67	161 ± 16
2003	Control	82	9–13 April	0.92 ± 0.35	−0.14 ± 0.70	45	31 (69%)	27 (87%)	60	146 ± 21
	Experimental	—	—	—	—	9	7 (78%)	4 (57%)	44	143 ± 28
2004	Control	84	2–6 April	1.03 ± 0.28	0.58 ± 0.56	70	56 (80%)	49 (88%)	70	166 ± 18
	Experimental	—	—	—	—	10	7 (70%)	7 (100%)	70	152 ± 14
2005	Control	77	20-24 April	0.29 ± 0.30	−0.55 ± 0.60	63	42 (67%)	5 (12%)	8	120 ± 16
	Experimental	—	—	—	—	10	6 (60%)	0	0	—
2006	Control	44	6–10 April	1.08 ± 0.40	−0.23 ± 0.78	35	23 (66%)	19 (83%)	54	148 ± 17
	Experimental	—	—	—	—	10	9 (90%)	6 (67%)	60	134 ± 11

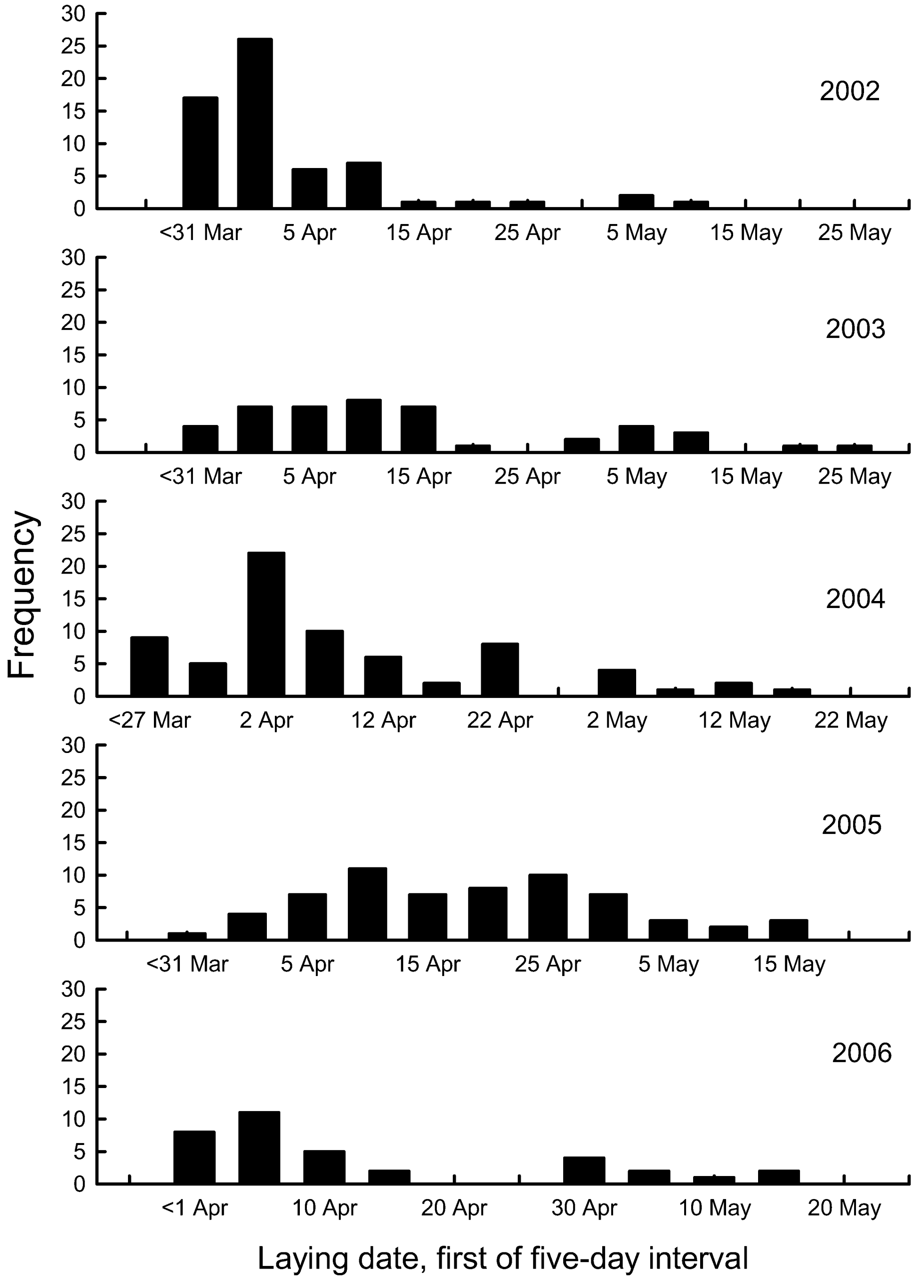

Fig. 1. Distribution of Cassin's Auklet laying dates on the control plot at Triangle Island, British Columbia, in 2002–2006.

replacements (Fig. 3), and re-laying rates were 90–100% in all 5 years. Re-laying intervals varied from 10–15 days to 40–45 days, with 82% being 10–15 to 20–25 days. As with first eggs, there was little interannual variation in the size of replacement eggs (for year in a GLM, $r^2 < 0.01$; overall average [± SE] = 52.7 ± 1.1 cm^3). The replacements averaged 2.7 ± 1.8% (95% CI) smaller than first eggs laid by the same female.

The breeding success of control and experimental pairs was strongly concordant from year to year (Table 1). As expected, the best approximating models to explain variation in all four component measures of breeding success included the year and date terms: success varied among years and declined with later laying (Table 2). However, in the experiments to distinguish between parental and date effects, results differed among the four component measures.

For hatching success (egg to hatchling) and breeding success (egg to fledgling), results best supported the parental-quality hypothesis: the best-approximating models, and the only models that received strong support ($\Delta AIC_c \leq 2$), included the treatment term in addition to year and laying date. On the basis of AIC_cw values, these models received 2.7× (for hatching success) and 6.3× (for breeding success) as much support as models that included

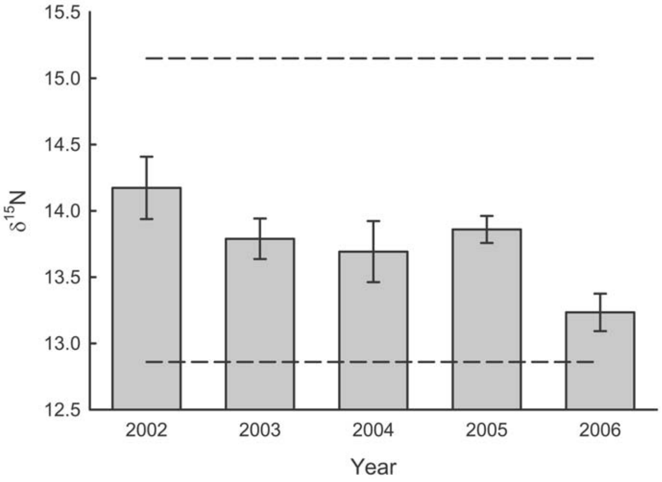

FIG. 2. Interannual variation in trophic level (mean $\delta^{15}N$ ‰ ± 95% confidence interval) in the yolks of 10 Cassin's Auklet eggs laid prior to the median laying date. Dotted lines represent $\delta^{15}N$ values that were expected if diets had consisted solely of the copepod *Neocalanus cristatus* (bottom) and the fish Pacific Sand Lance (*Ammodytes hexapterus*) (top), based on Davies et al. (2009).

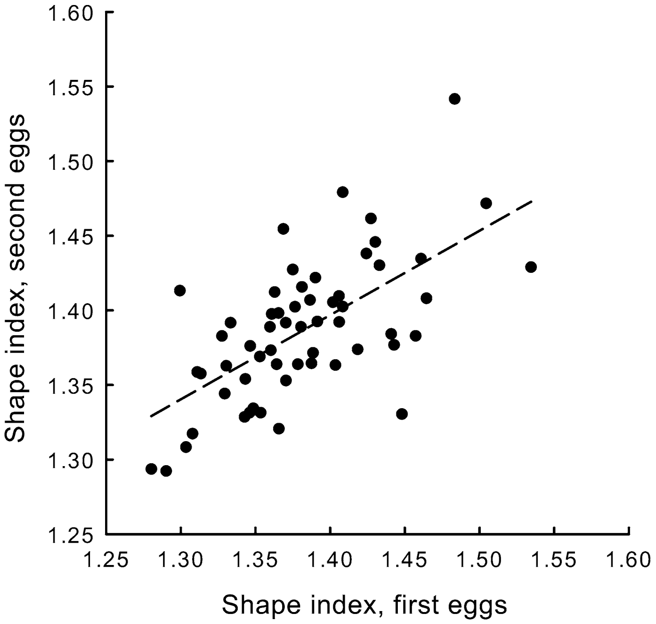

FIG. 3. Shape index (length/breadth) of replacement eggs compared with first eggs collected in the same Cassin's Auklet burrows at Triangle Island, British Columbia, in 2002–2006. The strong correlation ($r^2 = 0.47$) indicates that the second eggs were true replacements laid by the same females.

only year and date (Table 2). Parameter estimates for the treatment term in these top-ranked models were 0.45 ± 0.32 (SE) for hatching success and 0.70 ± 0.32 for breeding success (explanatory power was particularly low for hatching success; Table 2). Across all seven models, the treatment effect was well supported (parameter weight = 0.80 for hatching success, 0.93 for breeding success). Thus, for a given laying date in a given year, the experimental pairs were more likely than control pairs to hatch their eggs (Fig. 4, top) and to have their eggs result in fledged chicks.

Note that in both of these analyses, models containing the date*treatment interaction term also ranked relatively high, with ΔAIC_c values close to 2. However, in neither of these models did the Log*L* improve with the addition of the interaction term, which indicates that this term is a pretending variable (Burnham and Anderson 2002). These models are not different from the top-ranked model containing the treatment term and, thus, lend further weight of evidence to the treatment effect.

By contrast, results for both fledging success (hatchling to fledgling) and fledging mass best supported the date hypothesis: the best-approximating models included year and hatching date but not treatment (Table 2). On the basis of AIC_{cw} values, these

Table 2. Results of AIC model comparisons to explain interannual variation in Cassin's Auklet breeding parameters over the 5-year study at Triangle Island, British Columbia. The term "trt" refers to treatment group (control and experimental pairs). All candidate models with $AIC_{cw} \geq 0.05$ are included; null models received no support (all $\Delta AIC_c \geq 19$).

Parameter	Model	R^2	k	Log*L*	ΔAIC_c	AIC_{cw}
(1) Hatching success	Year + date + trt	0.08	7	−192.43	0.00	0.54
(*n* = 344)	Year + date	0.07	6	−194.48	2.01	0.20
	Year + date + trt + (date*trt)	0.08	8	−192.41	2.07	0.19
	Year + date + trt + (year*trt)	0.09	11	−190.51	4.62	0.05
(2) Fledging success	Year + date	0.53	6	−67.29	0.00	0.62
(*n* = 242)	Year + date + trt	0.54	7	−67.29	2.11	0.22
	Year + date + trt + (date*trt)	0.53	8	−67.29	4.24	0.07
(3) Breeding success	Year + date + trt	0.29	7	−168.49	0.00	0.63
(*n* = 344)	Year + date + trt + (date*trt)	0.30	8	−168.47	2.06	0.22
	Year + date	0.29	6	−171.33	3.59	0.10
(4) Fledging mass	Year + date	0.36	6	−715.14	0.00	0.40
(*n* = 168)	Year + date + trt + (date*trt)	0.37	8	−713.37	0.88	0.26
	Year + date + trt	0.36	7	−714.88	1.67	0.17
	Year + date + trt + (year*trt)	0.38	11	−710.99	2.87	0.10
	Year + date + trt + (date*trt) + (year*trt)	0.38	12	−710.45	4.12	0.05

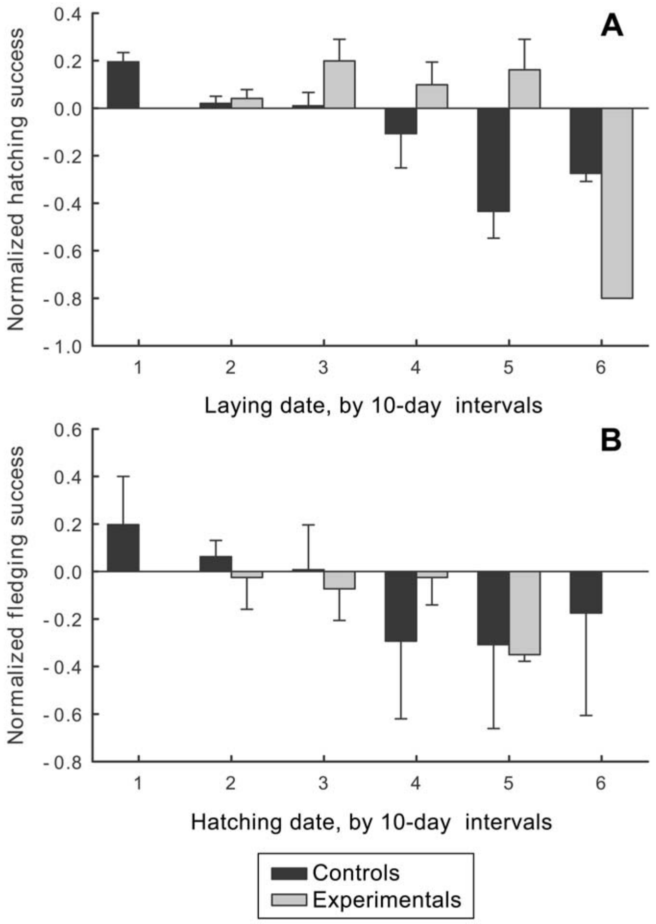

Fig. 4. (A) Hatching success and (B) fledging success (both means ± SE over 5 years) in relation to date for control and experimental Cassin's Auklets at Triangle Island, British Columbia, in 2002–2006. All measures of success varied among years, so to standardize data across years, raw data (percentage success in each 10-day laying- or hatching-date group) were converted to differences from each year's overall mean percentage success for control pairs (*y* = zero; solid line). Among controls, hatching success and fledging success declined with date. Experimental pairs did not follow the decline in hatching success (the last experimental bar represents only 1 egg) but showed a decline in fledging success.

models received 2.8× (for fledging success) and 2.4× (for fledging mass) as much support as models that also included the treatment term alone. Although models that included treatment received apparent support in both analyses ($AIC_c = \sim 2.0$), in both cases the Log*L* barely improved with the addition of the treatment term (Table 2). Furthermore, the confidence limits around the parameter estimates for the treatment term in models that included year and date bounded zero (0.48 ± 0.49 [SE] for fledging success and 2.4 ± 4.0 g day^{-1} for fledging mass), and averaged across all seven models, the treatment term was not well supported (parameter weights = 0.38 and 0.42). Thus, for a given hatching date in a given year, hatchlings raised by experimental pairs were no more likely to survive to fledging than hatchlings raised by control pairs (Fig. 4, bottom), and they fledged at similar masses (Fig. 5).

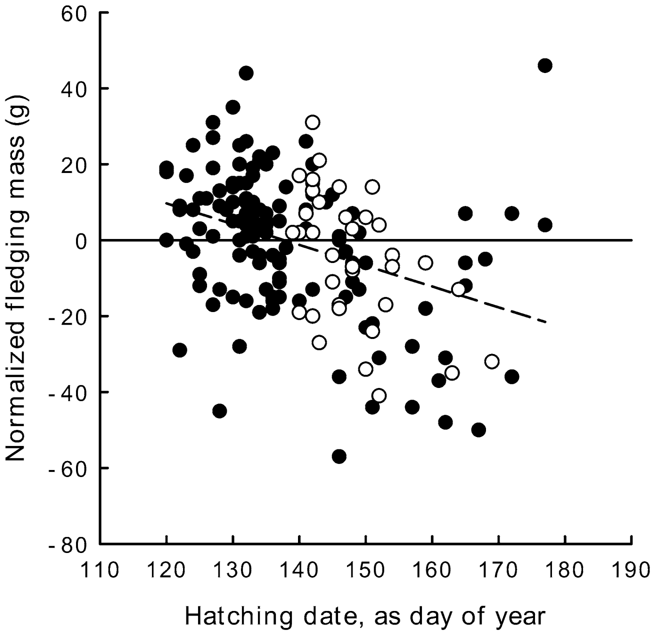

Fig. 5. Fledging mass in relation to hatching date in control (solid dots) and experimental (open dots) Cassin's Auklets at Triangle Island, British Columbia, in 2002–2006. Fledging mass varied among years, so to standardize across years, raw data were converted to the difference between a fledgling's mass and the overall mean fledging mass for control pairs in that year (*y* = zero; solid line). Among controls, fledging mass declined with hatching date (relationship shown as dotted line), and the experimental pairs tended to follow that decline.

However, the situation for fledging mass is somewhat complicated by the fact that models that included the date*treatment term also received substantial support ($\Delta AIC_c \leq 2$) and improved the Log*L* of the model appreciably (Table 2). Thus, although the weakness of the treatment effect indicates that the elevations of the lines were similar, the interaction term reflects a steeper slope of the line relating the decline in fledging mass to hatching date for experimental (–1.2 ± 0.4 g day^{-1}) than for control pairs (–0.6 ± 0.1 g day^{-1}) over a narrower range of hatching dates (Fig. 5).

Discussion

As expected, breeding success was strongly linked to laying date in Cassin's Auklets at Triangle Island in 2002–2006, both at the individual level (females that laid later bred less successfully) and at the population level (breeding was less successful in years in which laying was later and less synchronous overall). We will consider the population-level pattern first, then return to the individual patterns and the implications of our experiments to assess the relative importance of date and parental quality in driving the seasonal declines in success.

Interannual variation in laying dates.—In all 5 years, Cassin's Auklets began laying eggs in late March, which is very early in the spring at the latitude of Triangle Island. The constancy probably reflects the influence of an invariant photoperiod (Dawson 2008). Thereafter, the population proceeded to lay very synchronously in

2002, a year of cool and productive oceanic conditions (Mackas et al. 2007). In that year, zooplankton biomass peaked late—in the first week of May (Mackas et al. 2007), near the start of the Cassin's Auklets' hatching period—and early females fed at relatively high trophic levels while they formed eggs well ahead of the peak. By contrast, many females delayed laying during the warm, unproductive period from 2003 to 2006. In these years, zooplankton peaked earlier—in early to mid-April, during the Cassin's Auklets' egg production and early incubation periods—and early females fed at lower trophic levels while they formed eggs nearer the peak.

Breeding is ultimately timed in many bird species so that parents provision nestlings during the seasonal peak in food supply (Lack 1954). Although seabirds are generally thought to use environmental cues to track year-to-year variation in their prey's phenology in order to lay at the best time (Frederiksen et al. 2004), energetic constraints attributable to poor feeding conditions can limit this capacity (Daunt et al. 2006). Furthermore, previous research indicated that carry-over effects from prebreeding diet may affect a females' timing of laying in our study population (Sorenson et al. 2009). Given that more female Cassin's Auklets laid later in years in which zooplankton biomass peaked earlier (notably 2003 and 2005), we suggest that the delays were not strategic. These "mismatch" years (Hipfner 2008) featured reduced amounts of *N. cristatus* in nestling diets and, as a result, decreased nestling growth and survival (note that hatching success, which varied only between 65% and 80% through the present study, was hardly affected).

Parental and date effects.—With that as background, our experiments indicated that parental attributes and timing both affected Cassin's Auklet success but that their relative importance depended on breeding stage. Among early-laying females that were experimentally delayed by removal of their first eggs (virtually all females re-laid in all 5 years), neither hatching success nor breeding success followed the seasonal declines observed among control pairs. Thus, the quality of the pair, rather than their timing, was the major factor determining whether laid eggs successfully hatched and ultimately produced fledged chicks.

The causes of avian hatching failure often are unknown (Knappe et al. 2008). But at Triangle Island, endemic Keen's Mice eat neglected seabird eggs (Drever et al. 2000), so that incubating Cassin's Auklets face a tradeoff between the fitness costs and benefits of egg neglect: the opportunity to replenish endogenous reserves against the risk of losing eggs to mice (Ronconi and Hipfner 2009). We suggest that early pairs, which in other Alcidae tend to carry larger endogenous reserves from the start of incubation (Gaston and Hipfner 2006), were less likely than late pairs to neglect their eggs. Because they come and go from the breeding colony only at night, under cover of darkness, Cassin's Auklets' incubation shifts are long (~24 h). As a result, the decision to remain to incubate involves a considerable commitment (e.g., they lose ~10% of their body mass on a single incubation shift; Ronconi and Hipfner 2009).

By contrast, timing strongly affected events after hatching: the experimental pairs' fledging success and the fledging mass of their young tended to follow the seasonal declines among control pairs. These results indicate that even the more capable pairs in the population had little capacity to compensate for the strong seasonal declines in the availability of *N. cristatus* (Hipfner 2008). Contrary to expectation, however, there was little indication that the effect of the experimental treatment varied among years. The study period included only one cool and productive oceanic year (2002), but four warm and unproductive oceanic years (2003–2006), and it is possible that the poor balance limited our ability to detect year effects.

Most previous experimental studies involved passerine birds and found that date effects drove seasonal declines in breeding success (Verhulst and Nilsson 2008). However, seabirds form a general exception, perhaps reflecting the importance of experience for long-lived species that breed in variable environments (Daunt et al. 1999). In other species of Alcidae, for example, parental effects outweighed date effects on re-laying rates (Hipfner et al. 1999) and breeding success (De Forest and Gaston 1996); and in 1 other species, pairs that laid at the same time as their neighbors, rather than simply earlier, were most successful (Hatchwell 1991).

However, in a concurrent study on Rhinoceros Auklets (*Cerorhinca monocerata*), which are puffins rather than auklets, date effects drove seasonal declines in breeding success at Triangle Island (Hipfner et al. 2008). Although we do not know why date and parental effects should differ in importance for the 2 species breeding at the same site, the important point is that our results for Cassin's Auklets, in which both date and parental effects played roles, are intermediate to those for other auks. Furthermore, results of the two experimental studies carried out at Triangle Island stand apart for the overall strength of direct timing effects and together suggest that the marine environment around this large seabird colony is highly seasonal for species that feed offspring at both lower (Cassin's Auklet) and variably higher (Rhinoceros Auklet) trophic levels.

There are several assumptions inherent in our experimental approach (Verhulst and Nilsson 2008). The very high re-laying rates in all 5 years circumvent the issue of whether females that re-laid were representative of all early females. In addition, we (probably safely) assumed that pairs breeding on the control and experimental plots did not differ systematically in important traits such as age, experience, condition, or burrow quality. We also assumed that second eggs found in burrows were by the same females. No second eggs appeared too early to have been replacements, a great majority appeared within the expected times (11–15 to 20–25 days), and the correlation coefficients for egg shape ($r^2 = 0.47$) were similar to those in Rhinoceros Auklets ($r^2 = 0.63$; Hipfner et al. 2008) and Thick-billed Murres (*Uria lomvia*; $r^2 = 0.53$; Hipfner et al. 2003). Many of the females involved in the latter study were individually banded, and all eggs laid by the same female Thick-billed Murre can be identified by their backgound color and markings. Moreover, Cassin's Auklets tend to be nest-site-faithful (Pyle et al. 2001).

Finally, we assumed that costs associated with producing replacement eggs had little influence on the investment later made by experimental pairs. Verhulst and Nilsson (2008) considered this confounding factor unimportant, and most experimental studies on auks support the parental-quality hypothesis (De Forest and Gaston 1996, Hipfner et al. 1999) even though the bias operates in favor of the date hypothesis. Moreover, the very high re-laying rates in all 5 years (90–100%), despite dramatic variation in the re-laying females' success (0–70%), may indicate that egg production is not a particularly taxing process for Cassin's Auklets—otherwise, we would expect natural selection to act against such apparently wasted reproductive effort. In terms of adult body mass, Cassin's Auklets lay small eggs for an auk (Hipfner et al. 2004), and the percentage reduction in the size of replacement eggs compared to first eggs (2.7%) was only half that of Thick-billed Murres (5–6%; Hipfner et al. 2003). Nonetheless, the fact that the seasonal decline in fledging mass was somewhat steeper for experimental than for control pairs may indicate that females that took longer to relay provisioned less than even natural late layers. A reduction in the offspring-provisioning rate has been linked to the production of additional eggs in other seabirds (Monaghan et al. 1998).

Date and parental quality contributed to the ubiquitous seasonal declines in breeding success in this zooplanktivorous seabird, with their relative importance varying across the discrete stages of breeding. This stage-specific pattern, which has rarely been considered, deserves attention through future studies on other avian species. Combined with the results of an earlier study (Hipfner et al. 2008), our results here provide insight into the highly seasonal nature of the marine environment around Triangle Island. More generally, they suggest that a comprehensive understanding of the direct fitness consequences of avian breeding time will require additional experimental studies that integrate season-long investigations across a range of environmental conditions.

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