Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success

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Summary

1. Understanding the interactions between different periods of the annual cycle in migratory animals has been constrained by our inability to track individuals across seasons. In seabirds, virtually nothing is known about how diet quality during the non-breeding period, away from the breeding grounds, might influence subsequent reproductive success.

2. We used stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes to evaluate the effects of non-breeding diet quality on the timing of breeding and egg size in a population of Cassin's auklets (*Ptychoramphus aleuticus*) breeding on Triangle Island, British Columbia. Adult feathers are grown during two different periods of the annual cycle, which allowed us to estimate diet quality from the previous fall (October–November) and pre-breeding (February–March) period.

3. We found that the estimated proportion of energetically superior copepods (*Neocalanus* spp.) in the pre-breeding diet tended to be higher in females that bred earlier and laid larger eggs, whereas energetically poor juvenile rockfish (*Sebastes* spp.) were dominant in the pre-breeding diets of females that bred later and laid smaller eggs. We detected no effect of fall diet quality on breeding date or egg size, and no effect of pre-breeding diet quality on breeding date in males.

4. Pre-breeding diet quality was not related to body condition measured 1–2 days after laying, which suggests that females may need to attain a threshold condition before they initiate breeding and successfully rear young.

5. Our results suggest that changes in climatic conditions during the pre-breeding period may have severe consequences for reproductive success by influencing breeding date and egg size. Our work emphasizes the importance of determining how events are linked throughout the annual cycle for understanding the fitness and population dynamics of migratory animals.

Key-words: breeding date, Cassin's auklet, copepods, egg volume, seasonal interactions

Introduction

Understanding the factors that influence individual success and population dynamics of animals requires an understanding of how events in one season carry over to influence success the following season (Fretwell 1972; Norris 2005). For example, diet quality during the winter may carry over to influence reproductive success the following summer (Gill *et al*. 2001; Norris *et al*. 2004). Assessing the importance of such carry-over effects, however, has been constrained by our inability to follow individuals throughout the annual cycle (Webster *et al*.

2002). Seabirds typically spend greater than 80% of their time at sea (Hatch & Hatch 1990). However, other than a limited number of studies based on stomach contents (Baltz & Morejohn 1977; Falk, Jensen & Kampp 1992; Rowe *et al*. 2000; Lance & Thompson 2005), little information is available on diet outside of the chick-rearing period, primarily because of the difficulties associated with sampling diet and directly tracking individuals after they leave their breeding colonies. Thus, identifying the factors that influence reproduction in seabirds has been limited largely to within-season hypotheses, such as the effect of food abundance or food quality during the breeding period on chick growth rates (Vermeer 1981; Pyle, Sydeman & Hester 2001; Hedd *et al*. 2002, 2006).

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Here we examine the hypothesis that diet quality during the non-breeding period influences the timing of breeding and egg volume in Cassin's auklets (*Ptychoramphus aleuticus*), a small sized (180 g), planktivorous, burrow-nesting seabird that breeds along the western North American coast from Baja California to Alaska. Like most alcids, Cassin's auklets lay a single egg clutch and both parents share incubation and provisioning duties (Manuwal & Thoresen 1993). In British Columbia, *Neocalanus* copepods, euphausiids and small rockfish predominate food delivered to nestlings (Vermeer 1981, 1985; Burger & Powell 1990). Reproductive success is highest when copepods compose the majority of chick diet (Hedd *et al.* 2002). Considering that adults eat similar diets as those fed to nestlings (Manuwal 1974; Ainley, Spear & Allen 1996) and that copepods (in particular *Neocalanus cristatus*: 6236 cal g^{-1}) have higher energy content than rockfish (*Sebastes* spp.: 5200 cal g^{-1}; Vermeer & Cullen 1982), we consider copepods as high-quality and rockfish as low-quality prey items for adults.

Cassin's auklet pairs that breed later in the season have reduced chick growth rates and lower fledging success (Hedd *et al.* 2002, 2006). The timing of the peak in *Neocalanus* biomass favours earlier breeding because it ensures a temporal overlap between this food source and the chick provisioning period (Bertram, Mackas & Mckinnell 2001). Although there should be strong selection for early breeding, Cassin's auklets show a large variation in first egg dates (range: 55 d) and one explanation for this variation is that the timing of breeding is constrained by diet quality during the pre-breeding period. Therefore, we predict that adults feeding on high-quality prey during the non-breeding period will nest earlier in the season.

In birds, reproductive success increases with egg size (Bolton, Houston & Monaghan 1992; Bernardo 1996; Blomqvist, Johansson & Gotmark 1997) and females in better condition typically produce larger eggs (Styrsky, Dobbs & Thompson 2002; Reynolds, Schoech & Bowman 2003). In seabirds, larger eggs tend to result in larger chicks, which can buffer nestlings from food shortages early in the chick stage (Knechtel 1998). In years of poor food supply, it is not uncommon for Cassin's auklet chicks to die within 10 days of hatching (J. M. Hipfner, unpublished data), suggesting that egg size may be an important factor for reproductive success. Therefore, we also predicted that adults feeding on high-quality prey during the non-breeding period will have higher body reserves, which will allow them to produce a larger egg.

To test these predictions, we analysed stable isotopes from Cassin's auklet feathers grown during two different periods of the annual cycle (fall and pre-breeding period). Both stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotopes have been used to trace the structure of marine food webs (Hobson & Welch 1992; Kline & Pauly 1998), with δ^{15}N showing variation between trophic levels (DeNiro & Epstein 1980; Post 2002) and δ^{13}C distinguishing between pelagic and benthic prey (Hobson, Piatt & Pitocchelli 1994; France 1995). Because these feathers are retained at the beginning of the breeding season and are metabolically inert after growth, stable isotope signatures in these tissues can provide an estimate of diet quality throughout the previous year (Hobson & Wassenaar 1997).

Methods

STUDY SITE AND FIELD DATA

Our study took place on Triangle Island, British Columbia (50°52′ N, 129°05′ W), which is the outermost island of the Scott Islands Group, located 45 km off the north-western tip of Vancouver Island and situated near the northern limits of the California Current oceanographic zone. Triangle Island is home to the largest and most diverse seabird colony in British Columbia including the largest breeding colony of Cassin's auklets in the world (estimated at 547 637 pairs in 1989; Rodway 1991).

From late March to June 2007, we monitored all burrows on study plots at 2-day intervals. Lay dates were defined as the date between the day the egg was found and the day of the previous check. Once an egg was found, the incubating parent was temporarily removed from the burrow to sample feathers and blood. Because adults alternate incubation duties every 24 h, we were able to return the next day and sample the second member of the pair. Eggs ($n = 21$) were measured for length (L) and breadth (B; ±0·1 mm) using digital calipers. From these measurements we calculated an egg volume index (= $L \times B^2/1000$) as a measure of egg size (Van Noordwijk *et al.* 1981).

We sampled feathers from incubating Cassin's auklets ($n = 43$) with lay dates spread throughout the breeding period (population range = 3 April–16 May). The pre-basic molt, which overlaps with breeding, includes primaries that are grown over an extended period so that individuals are never flightless (Emslie, Henderson & Ainley 1990). Primaries are molted one at a time beginning with the first (inner) primary, which is usually molted on the breeding grounds, and ending with the ninth (outer) primary in late fall (October–November; Pyle 2008; Fig. 1). The pre-alternate molt, which occurs from mid-February to late-March just before breeding, includes most body feathers but no primary feathers (Pyle 2008; Fig. 1). To estimate diet quality from two different periods of the annual cycle, we sampled two body feathers and a clipping from the ninth primary. The ninth primary provided a signature of diet from the fall and body feathers provided a signature of diet from the pre-breeding period.

We also analysed stable isotopes from red blood cells, which represent diet assimilated from approximately 20–40 days (10–20 day half life) before sampling (Hobson & Clark 1993; Bearhop *et al.* 2002; Evans-Ogden, Hobson & Lank 2004). Because individuals were sampled over a 42-day period, signatures from red blood cells can provide information on seasonal changes in the availability of different prey types. Blood samples (100–200 µL) were drawn from the alar vein using a 1 cc syringe and a 27 gauge needle and then were placed on ice until they were centrifuged (within 4 h) for 8 min at 8000 rpm. Red blood cells were extracted and stored in 70% ethanol.

All individuals were banded with a US Fish and Wildlife Service aluminum band. As an index of body size, we used the first principal component scores (PC1) from wing chord, tarsus, and culmen (Knechtel 1998). All three variables loaded strongly on the PC1 axis with wing cord and tarsus having the largest effect (wing cord: 0·58, tarsus: 0·67, culmen: 0·46). To estimate physical condition at the time of capture, we used the linear residuals of mass (g) over body size (PC1 scores; $r^2 = 0.52$, $P < 0.0001$). Because Cassin's auklets are sexually monomorphic, individuals were sexed based on bill depth. Knechtel (1998) found that within pairs captured at burrows, female bill depth was always shallower than male bill depth (females: 9·34 ± 0·07, $n = 16$; males: 10·40 ± 0·11, $n = 16$; Knechtel 1998).
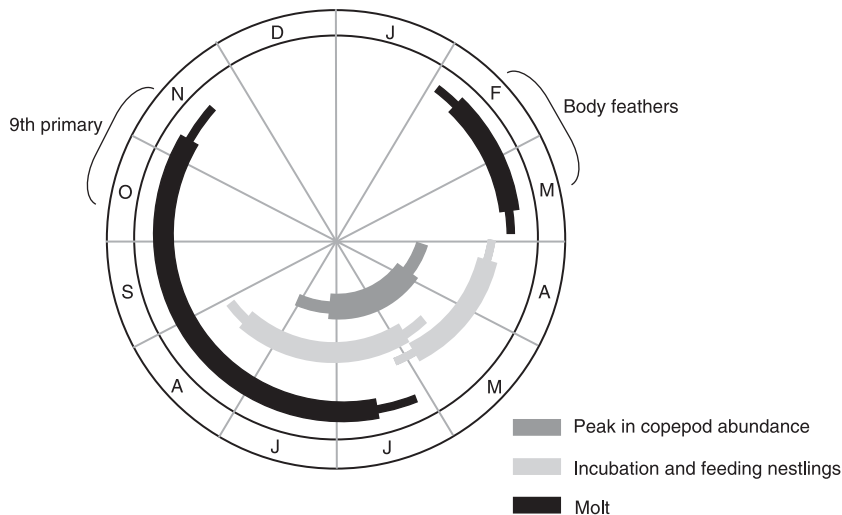
Fig. 1. Approximate timing of molt, incubation, breeding and the peak in copepod abundance for Cassin's auklets on Triangle Island, British Columbia (Mackas 1992; adapted from Manuwal & Thoresen 1993). Ninth primary and breast feathers were collected in April and May but were used to estimate previous fall and pre-breeding diet, respectively.

ISOTOPE ANALYSIS

Isotope ratios (R) are expressed in δ units where δ = [(Rsample/Rstandard)-1] × 1000. $\delta^{15}N$ is the ratio of $^{15}N/^{14}N$ relative to Air, and $\delta^{13}C$ is the ratio of $^{13}C/^{12}C$ relative to Pee Dee Belemnite. Before analysis, feathers were washed in 2:1 chloroform:methanol solution for 24 h and left to air dry for 24 h and blood samples were freeze dried. Feather (including material from the vane and rachis) and blood samples were weighed into tin capsules, then combusted and oxidized in a TC Elemental Analyser (Costech Analytical Technologies Inc., California, USA) and introduced online into a Finnigan MAT Delta Plus XL Isotope Ratio Mass Spectrometer, Bremen, Germany. During analysis, four standards were run; for carbon: the international standard NBS-21 Graphite (–27·9‰ ± 0·11 within autorun, $n = 10$) and an in-house standard UC-1 Graphite (–25·8‰ ± 0·11 within autorun, $n = 9$); for nitrogen: an international standard RM-8548 ammonium sulfate (20·0‰ ± 0·41 within autorun, $n = 9$). For both elements, we also used an in-house organic standard: domestic chicken (*Gallus gallus*) blood ($\delta^{15}N$: 4·4‰ ± 0·13 within autorun; $\delta^{13}C$: –20·3‰ ± 0·05 within autorun, $n = 5$). Samples were repeatable to within ±0·20‰ for $\delta^{15}N$ ($n = 22$) and ±0·24‰ for $\delta^{13}C$ ($n = 22$).

DIETARY MIXING MODEL

We used IsoError (Phillips & Gregg 2001), a dual-isotope ($\delta^{15}N$, $\delta^{13}C$), three-source mixing model, to estimate the relative proportion of different prey groups in Cassin's auklet diet. Because the mixing model does not estimate error from a single data point, we also compared two groups, early and late breeders, to derive error estimates. We compared these groups using a two-tailed *t*-test. All prey samples were collected in 2002 from Triangle Island (W.E. Davies, J.M. Hipfner, K.A. Hobson & R.C. Ydenberg, unpublished). Prey samples were freeze dried, subjected to lipid extraction with a methanol:chloroform:water (50:25:20 v:v) solution for at least 24 h, rinsed with distilled water, and re-dried (Thompson & Furness 1995). To remove carbonates, krill were also soaked in 1 N HCl until bubbling stopped (Thompson & Furness 1995). The three sources used for the model were juvenile rockfish (*Sebastes* spp.; $\delta^{15}N$: 13·1‰, SD ± 0·88; $\delta^{13}C$: –17·9‰, SD ± 0·43), copepods (*Neocalanus cristatus*; $\delta^{15}N$: 11·4‰, SD ± 0·72; $\delta^{13}C$: –20·1 ‰, SD ± 1·04) and euphausiids (*Euphausia pacifica*, *Thysanoessa spinifera*; $\delta^{15}N$: 11·1‰, SD ± 0·84; $\delta^{13}C$: –18·6‰, SD ± 2·04). While other prey types such as amphipod spp., flatfishes

(*Citharichthys sordidus*) and larval crabs likely contribute to the diet of Cassin's auklets, these contributions are considered small. In California, Ainley *et al.* (1996) determined from stomach contents collected in March that fish species other than juvenile rockfish contributed only 4% to overall diet composition and other invertebrate species such as amphipods and larval crabs contributed less than 7%. Unlike other copepod species that have a distinct spring peak in abundance, *N. cristatus* is available in surface waters for an extended period of time. After spawning in October–November, copepodites become available in surface waters at the beginning of February; however, the greatest abundances of C5 stage copepodites do not occur until the spring (Miller & Nielsen 1988; Kobari & Ikeda 1999). We used a diet-feather fractionation factor of +3·7‰ for $\delta^{15}N$ and +1‰ for $\delta^{13}C$, the same values estimated experimentally from a closely related species (common murres *Uria aalge*; Becker *et al.* 2007) and a tissue red blood cell fractionation factor of +2·6‰ for $\delta^{15}N$ and +1·2‰ for $\delta^{13}C$ (common murres; B. H. Becker, personal communication). In Cassin's auklet feathers, $\delta^{15}N$ explained 12% (β = –0·11, $P = 0·21$), 82% (β = 0·29, $P = 0·01$) and 36% (β = –0·18, $P = 0·01$) of the variation in copepods, rockfish and euphausiids, respectively, while $\delta^{13}C$ explained 80% (β = –0·36, $P < 0·0001$), 45% (β = 0·26, $P = 0·005$) and 6% (β = 0·09, $P = 0·36$) of the variation in copepods, rockfish and euphausiids, respectively.

Results

Body feathers (pre-breeding diet) and ninth primaries (fall diet) had significantly different $\delta^{13}C$ values (two-tailed *t*-test: $t_{84} = -5·8$, $P < 0·0001$; pre-breeding: mean = –19‰, SD ± 0·91; fall: mean = –20·5‰, SD ± 1·17; Fig. 2). There was no effect of sex on the mean difference between fall and spring diet ($t_{36} = 1·09$, $P = 0·86$). Isotopic differences between feather types suggest either that birds fed further offshore during the fall relative to the pre-breeding period or that birds molted their feathers in different geographical locations. Presumably body feathers are molted close to the breeding colony while flight feathers are molted on the wintering grounds, which are thought to be located off the coast of California (Manuwal & Thoresen 1993). $\delta^{15}N$ values were not significantly different between body feathers and the ninth primary ($t_{84} = 0·33$, $P = 0·74$; Fig. 2) and this relationship wasn't different between the sexes ($t_{36} = 0·33$, $P = 0·74$).
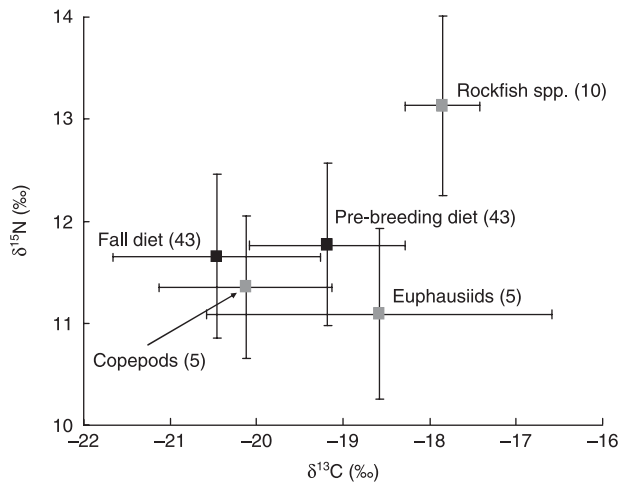
Fig. 2. Relationship between isotopic signatures of Cassin's auklet feathers and potential prey items. Mean (± SD) stable carbon ($\delta^{13}C$) and stable nitrogen ($\delta^{15}N$) isotope values of pre-breeding diet (breast feather), fall (ninth primary) feathers (subtracting an assumed diet-tissue discrimination factor of 3·7‰) and euphausiids, copepods and rockfish spp. (sample sizes in brackets). Diet items are from Triangle Island (W.E. Davies, J.M. Hipfner, K.A. Hobson & R.C. Ydenberg, unpublished).

As predicted, in females, we found a positive relationship between $\delta^{15}N$ values from the pre-breeding diet and lay date ($r^2 = 0.55$, $\beta = 10.49$, $P = 0.001$; Fig. 3) and a positive relationship between $\delta^{13}C$ and lay date ($r^2 = 0.24$, $\beta = 9.12$, $P = 0.05$; Fig. 3). Lay date was negatively related to the estimated proportion of copepods in spring diet of females ($r^2 = 0.26$, $\beta = -23.13$, $P = 0.04$; Fig. 4a) and positively related to the estimated proportion of rockfish ($r^2 = 0.61$, $\beta = 37.68$, $P = 0.0003$; Fig. 4a). Thus, females feeding on high proportions of copepods and low proportions of rockfish were more likely to breed earlier in the season. The proportion of euphausiids in pre-breeding diet was not significantly related to lay date ($r^2 = 0.05$, $\beta = -10.41$, $P = 0.38$; Fig. 4a).

For males, neither $\delta^{15}N$ or $\delta^{13}C$ signatures from the pre-breeding period were related to laying date ($\delta^{15}N$: $r^2 = 0.09$,

$\beta = 4.78$, $P = 0.19$; $\delta^{13}C$: $r^2 = 0.02$, $\beta = -1.85$, $P = 0.55$), suggesting that diet quality influenced timing of breeding only through females. Physical condition (mass given body size) was not correlated with laying date or pre-breeding diet quality in either females (lay date: $r^2 = 0.09$, $\beta = 0.31$, $P = 0.24$; pre-breeding, $\delta^{15}N$: $r^2 = 0.03$, $\beta = 2.74$, $P = 0.51$, $\delta^{13}C$: $r^2 = 0.02$, $\beta = 2.0$, $P = 0.62$) or males (lay date: $r^2 = 0.0001$, $\beta = 0.01$, $P = 0.96$; pre-breeding, $\delta^{15}N$: $r^2 = 0.09$, $\beta = 4.38$, $P = 0.22$, $\delta^{13}C$: $r^2 = 0.02$, $\beta = 2.98$, $P = 0.55$).

As predicted, we also found a significant relationship between pre-breeding diet quality and egg volume as well as laying date and egg volume. Eggs that were laid earlier in the season tended to be larger than eggs laid later in the season ($r^2 = 0.26$, $\beta = -0.25$, $P = 0.02$). However, female body size was unrelated to egg size ($r^2 = 0.04$, $\beta = -1.56$, $P = 0.47$). Females with lower $\delta^{15}N$ values in their pre-breeding diet laid larger eggs than females with higher $\delta^{15}N$ values ($r^2 = 0.36$, $\beta = -2.81$, $P = 0.03$; Fig. 3c). Females that were feeding on lower proportions of rockfish laid larger eggs than females that were feeding on higher proportions of rockfish ($r^2 = 0.31$, $\beta = -9.0$, $P = 0.04$; Fig. 4b). This suggests that females feeding on high-quality prey during the pre-breeding period were able to breed earlier and produce larger eggs. Fall diet quality was not related to lay date (females, $\delta^{15}N$: $r^2 = 0.016$, $\beta = 2.74$, $P = 0.62$; $\delta^{13}C$: $r^2 = 0.004$, $\beta = -0.82$, $P = 0.8$; males, $\delta^{15}N$: $r^2 = 0.089$, $\beta = 4.78$, $P = 0.19$; $\delta^{13}C$: $r^2 = 0.021$, $\beta = -1.85$, $P = 0.55$), egg volume (females, $\delta^{15}N$: $r^2 = 0.04$, $\beta = -1.72$, $P = 0.49$; $\delta^{13}C$: $r^2 = 0.006$, $\beta = -0.49$, $P = 0.8$) or body condition (females, $\delta^{15}N$: $r^2 = 0.01$, $\beta = 2.24$, $P = 0.66$; $\delta^{13}C$: $r^2 = 0.002$, $\beta = -0.58$, $P = 0.85$; males, $\delta^{15}N$: $r^2 < 0.001$, $\beta = 0.16$, $P = 0.95$; $\delta^{13}C$: $r^2 = 0.02$, $\beta = -1.31$, $P = 0.51$) in either males or females.

Finally, to include error associated with prey estimates, we compared early and late breeders (early breeders: rockfish SE ± 0.15, copepods SE ± 0.33, euphausiids SE ± 0.36; late breeders: rockfish SE ± 0.16, copepods SE ± 0.25, euphausiids SE ± 0.32) and found that the proportion of rockfish in pre-breeding diet was greater in late breeders than early breeders
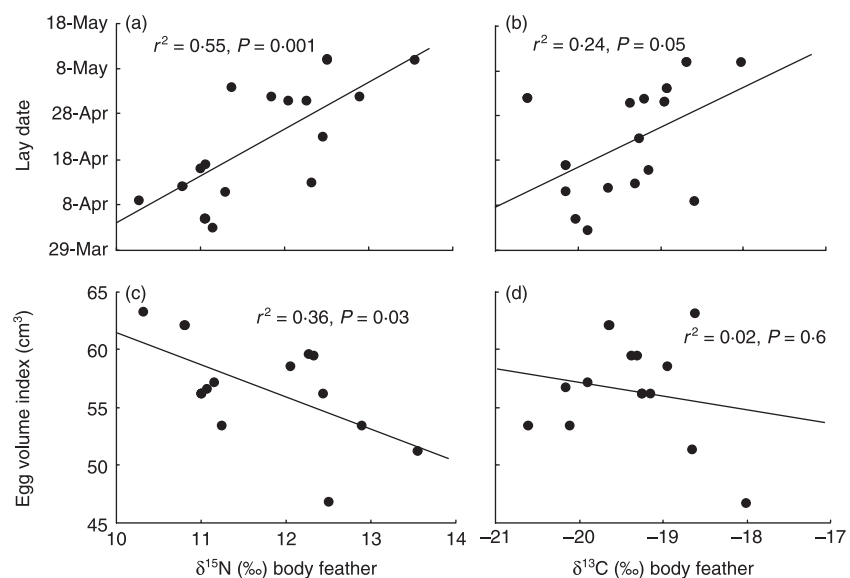
Fig. 3. Relationship between $\delta^{15}N$ and $\delta^{13}C$ values in female Cassin's auklet pre-breeding diet (breast feathers) and lay date (a, b) as well as egg volume (cm³; c, d). $\delta^{15}N$ increased with lay date and decreased with egg volume. $\delta^{13}C$ increased with lay date and remained relatively constant with egg volume.
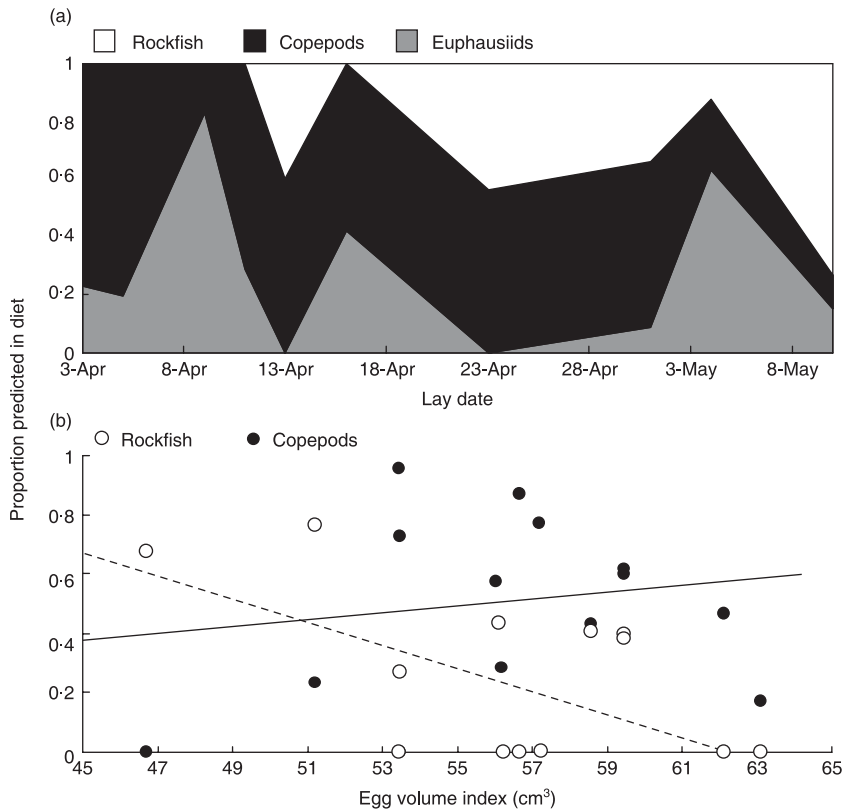
Fig. 4. Diet reconstruction of Cassin's auklet females from body feathers grown during the pre-breeding period. The proportion of rockfish, copepods, and euphausiids in auklet diet predicted from a dual isotope (δ^{15}N, δ^{13}C) mixing model (see methods). (*a*) Lay date was later with the estimated proportion of rockfish in the diet ($r^2 = 0.61$, $\beta = 37.68$, $P = 0.0003$), and earlier with the proportion of copepods ($r^2 = 0.26$, $\beta = -23.13$, $P = 0.04$), but was not related to euphausiids ($r^2 = 0.05$, $\beta = -10.41$, $P = 0.38$). (*b*) Egg volume tended to decrease with the estimated proportion of rockfish in the diet ($r^2 = 0.31$, $\beta = -9.0$, $P = 0.047$), but was not related to copepods ($r^2 = 0.03$, $\beta = 2.71$, $P = 0.57$) or euphausiids ($r^2 = 0.14$, $\beta = 5.78$, $P = 0.21$; not shown).

(two tailed *t*-test: $t_{14} = -2.07$, $P = 0.057$); however, there was no difference in copepods ($t_{14} = 0.49$, $P = 0.62$) or euphausiids ($t_{14} = 0.4$, $P = 0.69$).

Discussion

Our results support the hypothesis that the timing of breeding in Cassin's auklets is constrained by the quality of food available during the early spring pre-breeding period. We found that females with pre-breeding diets dominated by copepods (high-quality diet) bred earlier in the season and laid larger eggs than females with diets dominated by rockfish (low-quality diet). Long-term research at Triangle and the Farallon Islands, California has shown that early-breeding females raise chicks with faster growth rates and higher survival rates (Ainley & Boekelheide 1990; Bertram *et al.* 2001; Hedd *et al.* 2002; Fig. 5). The timing of breeding is, therefore, likely an important factor influencing reproductive success in Cassin's auklets.

Despite previous studies that have found strong effects of diet quality on condition (Kitaysky, Wingfield & Piatt 1999; Lanctot *et al.* 2003), we did not find a relationship between body condition and the proportion of copepods in Cassin's auklet diet. One explanation is that mass given body size was not an accurate estimate of body condition, especially if the relationship is nonlinear (Hayes & Shonkwiler 2001). Another explanation is that a threshold condition must be reached before individuals initiate breeding (Anderson, Gress & Mais 1982; Amundsen, Lorentsen & Tveraa 1996). Because we measured body condition in breeding females (1–2 days

after egg laying), individuals may have already reached the critical condition threshold required to begin laying eggs. A threshold condition would explain our finding that females feeding on low-quality prey during the pre-breeding period began laying eggs later in the season (Chastel, Weimerskirch & Jouventin 1995). We also observed a decline in δ^{15}N and δ^{13}C values in adult red blood cells over the laying period. Isotope signatures in red blood cells provided an estimate of seasonal variation in food availability between early April and mid-May. During this time, δ^{15}N values decreased by 14‰ and δ^{13}C values decreased by 9‰ (Fig. 6), matching the increase in copepod abundance known to occur over this time period (Mackas, Goldblatt & Lewis 1998). Our data suggest that, in early April 2007, adult Cassin's auklets had to rely on a mixture of prey items such as rockfish, euphausiids and copepods, but by mid-May adult diets were almost exclusively copepods. Females feeding on low-quality prey during the pre-breeding period, therefore, might have to wait for the peak in copepods before they can accumulate sufficient body reserves required for breeding.

Previous research has shown that birds use environmental cues before breeding to adjust their timing of reproduction, allowing them to match demands of parental care with peak food abundance later in the season (Frederiksen *et al.* 2004; Reed *et al.* 2006). However, our results suggest that the timing of breeding in Cassin's auklets could be constrained by the ability of females to accumulate sufficient reserves before breeding (Ainley *et al.* 1996; Daunt *et al.* 2006; Robb *et al.* 2008). We found that females feeding on higher-quality prey during the pre-breeding period not only began nesting earlier
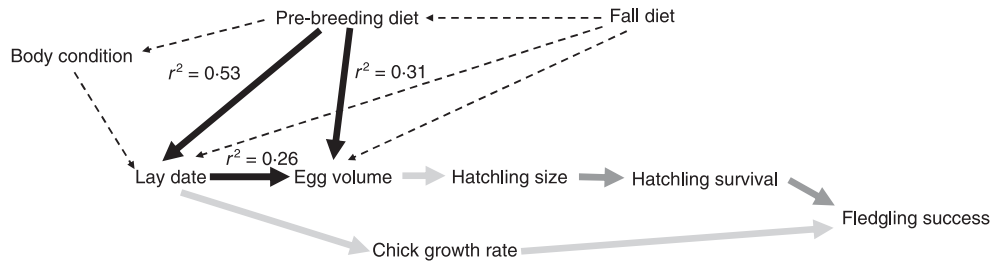
Fig. 5. Path diagram of potential pathways influencing reproductive success of Cassin's auklets on Triangle Island, British Columbia (---) indicates nonsignificant relationships, (→) indicates significant relationships (r^2 values are from linear regressions; pre-breeding diet is represented as nitrogen (δ^{15}N) isotope values), (→) indicates significant relationships from previous studies (Bertram *et al.* 2001; Styrsky *et al.* 2002), and (→) indicates the hypothesized relationship between hatchling size and reproductive success (not yet tested).
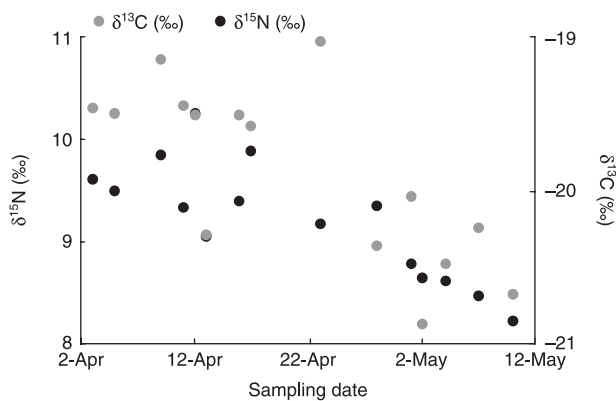
Fig. 6. Relationship between stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values of Cassin's auklet red blood cells (subtracting an assumed diet tissue discrimination factor of 2·6‰ for δ^{15}N and 1·2 ‰ for δ^{13}C) and sampling date (δ^{13}C: $r^2 = 0.49$, $\beta = -0.04$, $P = 0.001$; δ^{15}N: $r^2 = 0.69$, $\beta = -0.04$, $P < 0.0001$).

but were able to invest more energy into egg production and subsequently produce larger eggs. Knechtel (1998) also found a positive correlation between adult body reserves late in incubation and egg size in Cassin's auklets. In breeding seasons with low food availability, egg size may be particularly important for reproductive success (Fig. 5). Larger eggs produce larger nestlings which can provide young with energy reserves that might tide them over periods of food shortage post-hatching (Parsons 1970; Amundsen *et al.* 1996; Knechtel 1998). In 2005 (an El Niño year), 60% of chick mortality occurred within 10 days of hatching, suggesting that survival soon after hatch may be an important factor for overall reproductive success in warm years (J. M. Hipfner, unpublished data).

Differences in diet quality may be explained by variation in intrinsic quality, where higher-quality individuals are more efficient foragers. Daunt *et al.* (2006) found that in the European shag (*Phalacrocorax aristotelis*), individuals that had higher foraging efficiency during the pre-breeding period bred earlier in the season. They suggested that high-quality individuals were minimizing foraging costs by targeting high-quality prey patches. For Cassin's auklets, different prey types likely have different foraging costs due in large part to feeding adaptations. Cassin's auklets have wide bills and flattened palatal surfaces, which are adapted to catching slow moving soft-bodied zooplankton prey. They lack the groves and ridges that are used by fish-eating seabirds to capture hard-bodied fish (Bedard 1969). Individuals with higher intrinsic quality are, therefore, expected to exploit prey that provide the greatest return for energy expended and, thus, reach breeding condition earlier in the season.

While prey energy content is likely an important consideration for determining prey quality, prey availability and handling time are also likely to influence prey profitability (Stephens & Krebs 1986). Although the energy content of copepods is considerably higher than rockfish species (Vermeer & Cullen 1982), relative available biomass may play a role in determining prey profitability in any given year. For example, when the relative availability of rockfish is higher than copepods, rockfish may be the most profitable prey if their ease of capture outweighs the costs of finding scarce energy rich copepods. Although we assumed that copepods are the highest quality prey for Cassin's auklets, it is possible that interannual differences in prey availability could affect which is the most profitable foraging tactic in any given year.

An alternative explanation for the observed relationship between pre-breeding diet quality and the timing of breeding is that early and late breeders molted their body feathers in different locations. Geographical differences in isotopic signatures between marine regions have been documented. Schell, Barnett & Vinette (1998) found differences in isotopic signatures of zooplankton from eleven subregions in the Bering Sea and Altabet & François (1994) found that the geographical range between the Equatorial Pacific and Southern Ocean covered large gradients in both carbon and nitrogen isotopes. In our study, early breeders may have arrived at the colony earlier in the season, and molted there, while late breeders could have molted body feathers further south. Assuming no effect of sex on arrival date, this hypothesis predicts that isotope signatures would be similar between early-arriving sexes. However, we found that the relationship between the timing of breeding and pre-breeding diet quality was strong for females but not for males.

It is possible that isotopic signatures from prey collected in 2002 did not represent isotopic signatures of Cassin's auklet diet collected in 2007. Annual variation in oceanographic conditions such as the degree of vertical mixing and

the availability of nitrates may affect isotopic signatures at the base of the food web. However, Rau, Ohman & Pierrot-Bults (2003) found no significant trend in $\delta^{15}N$ or $\delta^{13}C$ signatures of zooplankton species sampled over a period of 50 years. Despite the stability of isotope signatures over time, Rau *et al*. (2003) did observe an enrichment of $\delta^{15}N$ during El Nino years. In our study, however, both 2002 and 2007 had a similar and slightly negative Southern Oscillation Index (SOI February–May average 2002: –0·4; 2007: –0·43) and Pacific Decadal Oscillation Index (PDO February–May average 2002: –0·5; 2007: –0·07).

Previous work has demonstrated that reproductive success in a number of seabird species is related to variation in climate (Aebischer & Coulson 1990; Croxall *et al*. 1990; Barbraud & Weimerskirch 2001). For Cassin's auklets, years with warm spring sea surface temperatures result in dramatically reduced hatching rates, fledging success (Bertram *et al*. 2001; Sydeman *et al*. 2006), and adult survival (Lee, Nur & Sydeman 2007). Cassin's auklet populations have been declining since the 1970s within the California Current system, with the most recent estimates showing a cumulative decline of 75% or more at the Farallon Islands, California (Lee *et al*. 2007). This population decline occurred in parallel with an 80% reduction in zooplankton biomass, which has been linked to ocean warming (Roemmich & McGowan 1995). Our results suggest that zooplankton abundance in the pre-breeding period may be an important factor influencing reproductive success by determining when females are able to lay their eggs, as well as egg size. If ocean temperatures continue to warm (IPCC 2007), only the highest quality individuals may be able to reach breeding condition at the optimal time.

Acknowledgements

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