

# Trophic responses to the hatching of offspring in a central-place foraging seabird

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**Abstract** We used  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable isotope analysis on blood drawn from adult and nestling Rhinoceros Auklets (*Cerorhinca monocerata*) in 4 years to answer two questions: (1) do adults tend to feed at higher trophic level while provisioning offspring than they did prior to breeding or while incubating eggs across a range of environmental conditions (years), and (2) do adults select prey at a similar trophic level and in similar habitats to complete the temporally overlapping tasks of self feeding and provisioning? Mean  $\delta^{15}\text{N}$  values in adult blood were higher during provisioning than prior to laying or during incubation in all 4 years. Thus, irrespective of environmental conditions, adults increased trophic level after their offspring hatched.

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Answers to the second question were more equivocal. However, there was support for models in which adult and nestling  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values did not differ, suggesting that adults did tend to take prey from similar trophic level and habitat to self-feed and load to deliver to offspring. We propose that the two behaviours are related and can be explained as a strategic response by central-place foragers: small, low trophic-level prey (zooplankton) suitable for self-feeding are not as well suited as large, high trophic-level prey (forage fish) for loading in the bill to deliver to offspring, and adults can save time by self feeding and loading in the same habitats.

**Keywords** Central-place foraging · Provisioning ·  
Seabirds · Stable isotope analysis · Trophic level

## Zusammenfassung

### Trophische Verhaltensanpassungen an den Schlupf der Jungen bei einem Seevogel mit „central place foraging“-Strategie

Durch Analyse der stabilen Isotope  $\delta^{15}\text{N}$  und  $\delta^{13}\text{C}$  in über einen Zeitraum von vier Jahren gesammelten Blutproben von Altvögeln und Nestlingen des Nashornalks (*Cerorhinca monocerata*) sollten die folgenden zwei Fragen beantwortet werden: (1) Erbeuten die Altvögel Nahrung einer höheren Trophieebene, wenn sie Junge versorgen, als vor der Brutzeit oder während der Bebrütung, und zwar unter einer Reihe verschiedener Umweltbedingungen (mehrere Jahre); und (2) suchen die Altvögel ihre Beute auf einer ähnlichen Trophieebene und in vergleichbaren Habitaten, um die zeitlich überlappenden Bedürfnisse der eigenen Ernährung und der Versorgung der Jungen zu erfüllen? Die mittleren  $\delta^{15}\text{N}$ -Werte im Blut der Altvögel waren in allen vier Jahren in der

Fütterungsphase höher als vor der Eiablage oder während der Bebrütung. Somit nutzten die Altvögel unabhängig von den Umweltbedingungen nach dem Schlupf der Jungen eine höhere Trophieebene. Die Antworten auf die zweite Frage fielen weniger eindeutig aus. Allerdings deutet das gute Abschneiden von Modellen, bei denen die Werte für  $\delta^{15}\text{N}$  und  $\delta^{13}\text{C}$  bei Altvögeln und Nestlingen nicht verschieden waren, darauf hin, dass Adulte ihre eigene Nahrung und das Futter für die Jungen in ähnlichen Habitaten auf einer vergleichbaren Trophieebene erbeuten. Wir vermuten, dass die beiden Verhaltensweisen zusammenhängen und sich als strategische Reaktion eines „central place foragers“ deuten lassen: Kleine Beutetiere niedriger Trophieebene (Zooplankton) sind zwar für die eigene Ernährung geeignet, lassen sich aber dagegen schlechter im Schnabel zum Nest transportieren als große Beutetiere einer höheren trophischen Ebene (Fische); somit können die Altvögel Zeit sparen, indem sie in denselben Habitaten Nahrung für sich selbst erbeuten und gleichzeitig Futter für die Nestlinge sammeln.

## Introduction

The foraging ecology, physiology, and body composition of parent birds all vary considerably across the discrete stages of a single breeding season (Williams et al. 2008; Rector et al. 2012). These changes can occur for a variety of reasons, including seasonal fluctuations in the availability of prey (Deguchi et al. 2010), as well as differences in the behavioural regimens, energetic expenditures, and nutritional demands of successive breeding stages (Shaffer et al. 2003).

After their nestlings hatch, adult birds that had been foraging solely to satisfy their own needs must begin to search for prey suitable for loading to deliver to offspring at the nest site, and for feeding themselves. Because the criteria that govern the selection of prey for the two tasks can differ, a single prey type might or might not be well suited to both, and if it is not, then parents will need to forage to satisfy the two requirements sequentially (Ydenberg and Davies 2010). The switch from incubating to provisioning can therefore trigger an especially pronounced change in the foraging behaviour of birds that provision offspring in the nest. For example, Cassin's Auklets (*Ptychoramphus aleuticus*), a small auk, spent 31 % less time underwater while incubating than while provisioning (Elliott et al. 2010), while the foraging trips taken by Thick-billed Murres (*Uria lomvia*), a larger auk, were only half as long during provisioning as during incubation (Ito et al. 2010).

In two species belonging to the puffin tribe Fraterculini—the Rhinoceros Auklet (*Cerorhinca monocerata*) and the Tufted Puffin (*F. cirrhata*)—adults shifted from feeding on low trophic-level prey before laying and while

incubating eggs to feeding on higher trophic-level prey while provisioning offspring (Williams et al. 2008; Ito et al. 2009). A trophic increase of similar magnitude was observed between winter moult and provisioning in the Atlantic Puffin (*F. arctica*) (Hedd et al. 2009). In Tufted Puffins and Rhinoceros Auklets, both of which are highly colonial central-place foragers (Orians and Pearson 1979), provisioning adults fed their nestlings at the same (higher) trophic level at which they fed, and in Tufted Puffins, those high trophic-level prey were caught in more benthic or pelagic habitats than were used earlier in the season (Williams et al. 2008). Yet Davoren and Burger (1999) found that Rhinoceros Auklets fed themselves on small prey items but loaded large items for delivery, and in Atlantic Puffins, adult trophic level was higher than that of nestlings (Hedd et al. 2009). Because the differences among the puffin studies suggest that the parent–offspring feeding relationship is malleable, as it is in other seabirds (Navarro and González-Solís 2009), we felt that the study of a puffin species across a range of environmental conditions might be informative.

Here, we examined the parent–offspring feeding relationship of the Rhinoceros Auklet, and its variation with environmental conditions. To do this, we collected blood from breeding adults during the prelaying, incubation, and provisioning periods of four breeding seasons, and from nestlings. We then performed  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable-isotope analyses on the blood samples to: (1) test whether the Rhinoceros Auklets tend to feed at higher trophic level while provisioning than they did prior to breeding or while incubating across a range of environmental conditions (years); and (2) test whether auklets select prey at a similar trophic level and in similar habitats to complete the temporally overlapping tasks of self-feeding and provisioning. Rhinoceros Auklets lay a single-egg clutch, have mouth parts designed to catch and hold 30 or more prey items (Bédard 1969), and each parent delivers food to offspring just once per night (Takahashi et al. 1999). Our 4-year study spanned a transition from “cool and high productivity” conditions in 2002 to “warm and low productivity” conditions in 2003 to 2005, and included a mild El Niño event in 2003, and an anomalous atmospheric blocking event in 2005 (Sydeman et al. 2006; Mackas et al. 2007). This environmental variation was linked to variation in the auklets' breeding success, as described in Borstad et al. (2011).

## Methods

### Field methods

Field work was conducted on Triangle Island, British Columbia, Canada (50°52'N, 129°05'W) in late April to

mid-August of 2002–2005. Triangle Island supports a colony of ~42,000 breeding pairs of Rhinoceros Auklet (Rodway 1990). At this site, provisioning Rhinoceros Auklets forage at up to 80 km from the colony (McFarlane-Tranquilla et al. 2005).

Rhinoceros Auklets were caught in barrier nets erected between PVC poles 4 m in length during the prelaying (late April), incubation (early June), and provisioning (late-July) periods. We assumed that all auklets caught prior to the start of egg laying would breed in that year, based on observations of other auk species (Gaston 1990), and, during incubation and provisioning, we blood-sampled only those captured individuals that had full or refeathering brood patches. Blood (0.5–1.0 ml) was drawn from the brachial vein and stored in Eppendorf tubes at  $-10^{\circ}\text{C}$ . Consecutive sampling sessions were separated by at least 25 days, to allow for turnover of isotopes in blood; expected half-lives for stable isotopes in blood are ~20 days for a bird the size of a Rhinoceros Auklet (475 g), based on an allometric relationship (Carleton and Martinez del Rio 2005). Blood samples (ca. 0.5 ml) were also collected from nestlings temporarily removed from burrows at about 6 weeks of age. By then, elements in blood derived from eggs should have been highly diluted by those in the prey.

#### Laboratory procedures

Whole blood samples were freeze-dried and powdered, and lipids extracted by successively rinsing in a 2:1 chloroform:methanol solution, then air-drying under a fume hood. Stable-carbon and nitrogen isotope assays were performed on 1-mg sub-samples of powdered material at the Department of Soil Science, University of Saskatchewan. Samples were first loaded into tin capsules and combusted in a Robo-Prep elemental analyzer at  $1,200^{\circ}\text{C}$ . The resultant  $\text{CO}_2$  and  $\text{N}_2$  gases were separated and analyzed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer, with every fifth sample separated by two (albumin) laboratory standards. Results are reported in delta notation in parts per thousand (‰) relative to Air ( $\delta^{15}\text{N}$ ) and VPDB ( $\delta^{13}\text{C}$ ). Based on replicate measurements of albumin standards, measurement precision (SD) for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were estimated to be  $\pm 0.1$  and  $\pm 0.3$  ‰, respectively.

#### Statistical analyses

To test whether Rhinoceros Auklets undergo an increase in trophic level between the early (prelaying and incubation) and late (provisioning) stages of breeding, we built a set of three candidate models for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values: (1) a null model; (2) Year (1–4); and (3) Year + Stage (1–3),

with Year and Stage as categorical variables. The dataset for these models included  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for 164 adults. To address whether provisioning adults tend to feed themselves and their offspring on prey from the same trophic level taken in the same habitats, we built a set of three candidate models for both isotopes: (1) a null model; (2) Year (1–4); and (3) Year + Age Class (2), as categorical variables. The dataset for these models included isotope values for 50 provisioning-stage adults and 54 nestlings. We expected  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values to vary among years, due to unexplained variation within the prey base (Rau et al. 2003). Our research questions thus focused on whether the Stage and Age Class terms would be additive to Year.

All models within each candidate set were ranked using Akaike's information criterion corrected for small sample size ( $\text{AIC}_c$ ), based on the difference between each model's  $\text{AIC}_c$  and the lowest  $\text{AIC}_c$  from among the candidate set. In addition to selecting a most parsimonious model ( $\Delta\text{AIC}_c = 0.0$ ), any models with  $\Delta\text{AIC}_c$  scores  $\leq 10.0$  can be considered to have received support (Burnham and Anderson 2002). We also report  $\text{AIC}_c w$ , which measures the weight of evidence in favor of a particular model on a scale from 0 to 1, given the data and candidate model set. All analyses were run using the Fit Model function in JMP.

## Results

Do adults increase their trophic level after hatching?

The top-ranked model for  $\delta^{15}\text{N}$  included both Year and Stage, had strong explanatory power, was the only model to receive support, and received all of the AIC model weight (Table 1). As predicted, mean  $\delta^{15}\text{N}$  values were significantly higher during provisioning than prior to laying or during incubation (Table 2), and that was true in all 4 years (Fig. 1).

The top-ranked model for  $\delta^{13}\text{C}$  included both Year and Stage, had only moderate explanatory power, was the only model to receive support, and received all of the AIC model weight (Table 1). Mean  $\delta^{13}\text{C}$  values were higher overall during incubation than they were prior to laying or while provisioning (Table 2), although that pattern was not observed in all 4 years (Fig. 1).

Do adults self-feed and load at the same trophic level and in the same habitats?

The top-ranked model for  $\delta^{15}\text{N}$  included both Year and Age class, had strong explanatory power, and received three times the AIC weight of the second-ranked model (Year alone). However, the model with Year alone also

**Table 1** Results of AIC model selection to explain  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Rhinoceros Auklets (*Cerorhinca monocerata*) (1) during three breeding stages (prelaying, incubation, provisioning), and (2) provisioning adults and nestlings, in 4 years

Comparison	Supported models	$\delta^{15}\text{N}$ (‰)				$\delta^{13}\text{C}$ (‰)			
		$R^2$	$\Delta\text{AIC}_c$	$\text{AIC}_{cW}$	$k$	$R^2$	$\Delta\text{AIC}_c$	$\text{AIC}_{cW}$	$k$
1. Adults at three stages	Year + stage	0.66	0.00	1.00	6	0.22	0.00	1.00	6
2. Adults versus nestlings	Year + age	0.75	0.00	0.75	5	0.42	0.00	0.97	5
	Year	0.74	2.21	0.25	4	0.37	7.14	0.03	4

Only models that received strong support ( $\Delta\text{AIC}_c < 10.0$ ) are shown

**Table 2** Parameter estimates (mean, 95 % confidence bounds) for the breeding stage and age class terms for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Cassin's Auklet (*Ptychoramphus aleuticus*) adults during three breeding stages, and in adult provisioners and their nestlings, in 4 years

Comparison	Top model	Parameter	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
			Mean (95 % CI)	Mean (95 % CI)
1. Adults at three stages	Year + stage	Prelaying	-0.43 (0.12)	-0.07 (0.15)
		Incubation	-0.44 (0.12)	0.34 (0.14)
		Provisioning	0.87 (0.13)	-0.27 (0.15)
2. Adults versus nestlings	Year	Adults	0.10 (0.09)	0.12 (0.08)

received support, and its explanatory power was almost equal to the top-ranked model (Table 1). Overall, the mean  $\delta^{15}\text{N}$  value was slightly higher in adults than in nestlings (Table 2), although that was not true in all years (Fig. 1).

Likewise, the top-ranked model for  $\delta^{13}\text{C}$  included both Year and Age Class, had moderate explanatory power, and received virtually all of the AIC weight. However, the model that included Year alone also received support (Table 2). Overall, mean  $\delta^{13}\text{C}$  values were higher in adult provisioners than in nestlings (Table 2).

## Discussion

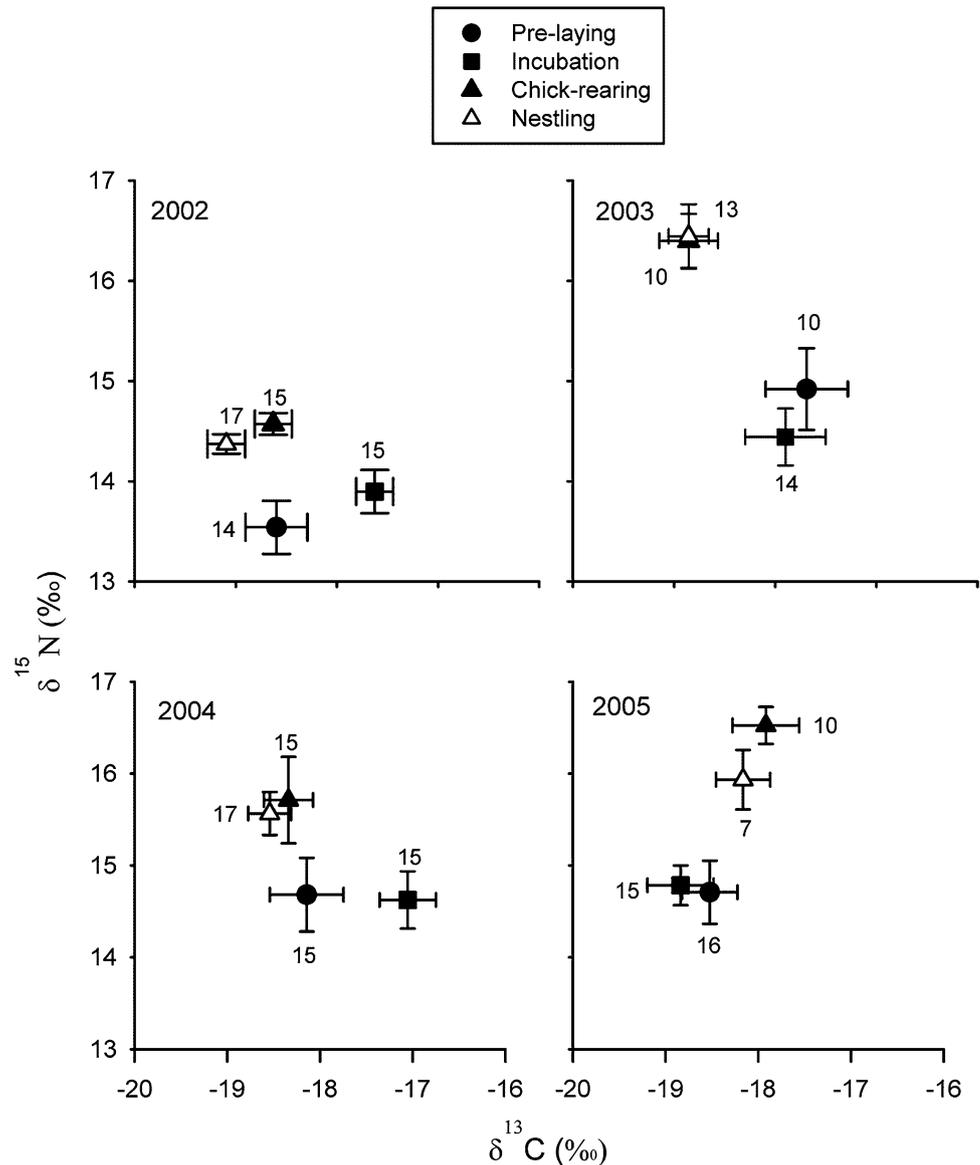
Using  $\delta^{15}\text{N}$  analyses, we found that Rhinoceros Auklets breeding on Triangle Island fed at higher trophic level while provisioning offspring than they had prior to laying and while incubating, irrespective of yearly fluctuations in environmental conditions. That result is consistent with studies of two other species of Fraterculini, the Tufted (Williams et al. 2008) and Atlantic (Hedd et al. 2009) puffins, based on  $\delta^{15}\text{N}$  analyses, and on studies of Rhinoceros Auklets at other breeding colonies, based on analyses of stable isotopes and stomach contents (Ito et al. 2009). That consistency—across species, across colonies, and across a range of environmental conditions at a single colony—suggests that a trophic increase after eggs hatch is a fixed behavioral or physiological trait in the ecology of the puffins.

Tufted Puffins foraged for prey with which to feed themselves and their offspring at similar trophic level (Williams et al. 2008), and results of our study offer

qualified support for the idea that Rhinoceros Auklets breeding at Triangle Island did the same. The differences in  $\delta^{15}\text{N}$  values between adults and nestlings were small, consistent with small differences in their diet–blood isotopic discrimination (Sears et al. 2009), and model support for differences in adult and nestling trophic level was equivocal. Although less conclusive than in Tufted Puffins (Williams et al. 2008), there was also model support for a lack of age-related differences in  $\delta^{13}\text{C}$  values in Rhinoceros Auklets, with the differences between adults and nestlings being much smaller than those among breeding stages in adult birds. Thus, our study offers weak, qualified support for the idea that Rhinoceros Auklets used similar habitats for self feeding and loading. We propose that the two behavioural tendencies—trophic increase after hatching and self feeding and loading for delivery at similar trophic level, and perhaps in similar habitats—are intertwined, and can be explained as a strategy employed by central-place foragers.

Trophic increase occurs in puffins because low trophic-level prey types suitable for self-feeding are not well suited for loading in the bill to deliver to offspring in the nest (Williams et al. 2008). Key features of prey suitable for loading include a size and shape that promote efficient packing, and high energy density (Ydenberg and Davies 2010). For puffins, which load and transport food externally in the bill, large, high trophic-level prey such as fish and squid probably meet these criteria better than zooplankton, which formed the bulk of the diets of incubating Rhinoceros Auklets in Japan (Ito et al. 2009). At Triangle Island, the rates of survival and growth of Rhinoceros Auklet nestlings were tightly linked to the amount of a

**Fig. 1** Bivariate plot representing the relative trophic position ( $\delta^{15}\text{N}$  value, mean  $\pm$  95 % confidence interval) and relative pelagic/offshore location ( $\delta^{13}\text{C}$  value, mean  $\pm$  95 % confidence interval) of the diet for adult blood drawn from Rhinoceros Auklets (*Cerorhinca monocerata*) during three reproductive stages (prelaying, incubation, provisioning), and from nestlings, in each of 4 years at Triangle Island



small forage fish, the Pacific sandlance *Ammodytes hexapterus*, that they received, which was itself tightly linked to the timing and strength of the spring phytoplankton bloom (Borstad et al. 2011).

The key assumption underlying that argument is that, at the onset of provisioning, puffin parents switch to self-feeding on prey types similar to those they load to deliver to offspring. For central-place foragers, like puffins, that switch could be a strategy that confers significant savings in time, depending on the spatial distribution of different prey types (Ydenberg and Davies 2010). Previously, Ito et al. (2009) attributed the trophic increase after hatching in Rhinoceros Auklets to seasonal patterns in the availability of alternate prey types, with zooplankton being more available early, and fish more available late. Interestingly, that hypothesis is not mutually exclusive from the hypothesis advanced here, and the two could even be

related if, consistent with Lack (1968), the auklets time their breeding so that fish is readily available at the time when they have offspring to feed in the nest.

We note that not all puffin studies have produced that same result; for example, Davoren and Burger (1999) found that Rhinoceros Auklets fed themselves on smaller prey items than they fed to nestlings, while trophic level was higher in adult than nestling Atlantic Puffins (Hedd et al. 2009). Ydenberg and Davies (2010) used modeling to assess environmental conditions under which parent seabirds might choose unimodal or bimodal foraging while provisioning, and we suggest that field tests of their model might help to explain the disparate results of the studies of the parent–offspring feeding relationship of puffins and other seabirds (Navarro and González-Solís 2009).

In summary, our study of the parent–offspring feeding relationship of Rhinoceros Auklets offers credible

explanations for behavioural patterns widely reported in three of the four species of Fraterculini. Information still is lacking for Horned Puffins (*F. corniculata*). Looking forward, we think comparative studies that incorporate some of the key life-history differences among the four puffin species—e.g., nocturnal (Rhinceros Auklet) versus diurnal (others) provisioning, and relatively slow (Rhinceros Auklet) versus relatively fast (others) offspring development (Hipfner et al. 2010)—could inform the general knowledge of auk biology, and central-place foraging theory. Studies that compare the provisioning ecology of single-prey loaders among the auks (such as murrens *Uria* spp.) to multiple-prey loaders (such as puffins), and internal versus external loaders, could also be informative.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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