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Pre-breeding diet influences ornament size in the Rhinoceros Auklet *Cerorhinca monocerata*

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Understanding the mechanisms that influence variation in sexually selected ornaments in seabirds has been challenging owing to the difficulty of capturing and sampling individuals outside of the breeding period when ornaments are usually grown. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes were used to examine the influence of pre-breeding diet composition on ornament size in the Rhinoceros Auklet *Cerorhinca monocerata*, a socially monogamous seabird that breeds in the North Pacific. We analysed stable isotopes in adult feathers grown during the pre-alternate moult, which allowed us to infer diet composition during the pre-breeding (February–March) period. Females that fed more on inshore fish had larger horns than females that fed more on euphausiids (also known as krill; Euphausiacea). Body size was a stronger predictor of horn height in males than females, suggesting that ornaments may serve as different signals for each sex. This study provides evidence that diet during the pre-breeding period can influence ornament size and emphasizes the importance of understanding individual ecology throughout the annual cycle for determining the factors that influence mate choice and fitness.

Keywords: euphausiids, krill, mutual mate choice, Sandlance, sexual selection.

Elaborate ornaments in birds are signals used in mate choice and in many cases are known to serve as reliable indicators of individual quality and condition (Evans & Hatchwell 1992, Norris 1993, Andersson 1994, Keyser & Hill 2000, Voltura *et al.* 2002, Senar *et al.* 2005). Condition-dependent ornaments may be favoured in sexual selection because they reliably link the development of the trait to the condition of the organism (Rowe & Houle 1996). The influence of diet on ornament vibrancy and size has been observed in a number of experimental studies. For example, Hill (2000) found that food-restricted male House Finches *Carpodacus mexicanus* deposited fewer carotenoid pigments into their feathers and had duller colour displays than males fed *ad libitum*. Similarly, Dark-eyed Juncos *Junco hyemalis* fed a low-quality diet grew tail feathers with smaller white patches than birds fed a high-quality diet (McGlothlin *et al.* 2007a).

Seabirds spend most of their life at sea and only a short period of time on land to choose mates and breed (Schreiber & Burger 2001). Many species have elaborate feathers or fleshy ornaments that are signals of individual quality (Velando *et al.* 2001, Childress & Bennun 2002, Daunt *et al.* 2003, Massaro *et al.* 2003) and, in some species, there is evidence of mutual mate choice based on sexually monomorphic ornamentation (Jones & Montgomerie 1992, Jones & Hunter 1993, 1999, Daunt *et al.* 2003, Veit & Jones 2003). Understanding the causes of variation in sexually selected traits of seabirds has been challenging owing to the difficulty of capturing and sampling individuals outside the breeding season when many ornaments, such as feathers and keratinous horns, are grown. The extent to which diet might influence

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the development of these traits is therefore virtually unknown.

We investigated the influence of diet composition on the ornaments of Rhinoceros Auklets *Cerorhinca monocerata*, a medium-sized (550 g) seabird that breeds in large colonies from California to the Aleutian Islands (Gaston & Dechesne 1996). Males and females display two elaborate ornaments: two long white facial plumes on either side of the head and a single keratinous horn at the base of the upper mandible. Horns are grown between February and March just prior to breeding (Gaston & Dechesne 1996), whereas facial plumes develop slowly, becoming complete by March (Pyle 2008). Although there is no information on diet during the time these tissues are grown, studies from other periods of the year suggest that adults feed primarily on fish species (juvenile rockfish *Sebastes* spp., Sandlance *Ammodytes hexapterus*, juvenile salmonids *Oncorhynchus* spp., Pacific Saury *Cololabis saira*) and to a lesser extent on euphausiids (*Euphausia pacifica*, *Thysanoessa spinifera*; Hobson *et al.* 1994, Lance & Thompson 2005). Fish and euphausiid energy densities are similar (Sandlance: 5383 cal/g; euphausiid *Thysanoessa spinifera*: 5354 cal/g; Vermeer & Cullen 1982). In many piscivorous seabirds, fish availability has been shown to strongly influence reproductive success and adult body condition (Crawford & Dyer 1995, Phillips *et al.* 1996, Kitaysky *et al.* 1999, Lanctot *et al.* 2003). For Rhinoceros Auklets, Sandlance (a small, schooling, inshore fish) has been documented as the most important prey item during the breeding season due to the strong positive relationship between breeding performance and the proportion of Sandlance in chick diets (Bertram *et al.* 2001, Hedd *et al.* 2006). This suggests that, if available, fish will be selected rather than euphausiids. Here, we use stable isotopes in feathers grown during the pre-breeding period to investigate the relationship between diet composition and ornament size and to provide the first evaluation of pre-breeding diet composition on ornament size in a seabird.

METHODS

Study site and field data

We sampled Rhinoceros Auklets 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. Triangle Island is home to the largest and most diverse seabird colony in British Columbia and includes the third largest colony of Rhinoceros Auklets (approximately 42 000 pairs; Rodway 1991).

From early April to late July 2007, we monitored all burrows on study plots at 5-day intervals and erected a soft plastic ‘pheasant’ net (approximately 20 m by 5 m) at the base of nesting slopes to capture birds as they departed from the colony during the early morning hours (02:00–05:30 h). Adults captured from the net (n = 29) or burrow (n = 19) were measured (mass, wing chord, culmen, bill depth, horn height, plume length) and sampled for feathers. The pre-alternate moult, which occurs from February to March prior to breeding, includes some breast feathers but no primary feathers (Pyle 2008). To estimate diet composition in the pre-breeding period, we sampled two grey-tipped breast feathers (February–March diet).

As an index of body size, we used the first principal component scores (PC1) from wing chord, bill depth and culmen (Reynolds *et al.* 2008). All three variables loaded positively on the first PC axis (wing cord 0.52, bill depth 0.63, culmen 0.57). Individuals were sexed based on bill depth, which is deeper in males than in females (males > 17 mm, females < 16 mm; B. Addison unpubl. data). For birds with bill depths of 16–17 mm, we used a discriminant function analysis (Brady *et al.* 2009), with wing chord, weight, culmen and bill depth, to assign birds as either male or female (males are generally larger than females; B. Addison unpubl. data). Birds that could not be assigned with a probability of 75% or higher were removed from the analysis (n = 2).

Facial plumes consist of one upper plume of white feathers extending backward from the eye to part way down the neck and a second plume that originates from the corner of the bill (Fig. 1). The horn originates at the base of the upper mandible and is paler and yellower than the orange bill. We measured the length of the straightened upper right plume (± 1 mm) using callipers (Fig. 1). Horn height was measured from the base of the lower mandible to the tip of the horn (± 0.1 mm). Bill depth was subtracted from this height to get a measurement of horn height above the bill (used in all subsequent statistical analyses; Fig. 1).

Figure 1. Measurement of Rhinoceros Auklet ornaments (see Methods). 1. Upper plume length, measured to the tip of the plume when straightened. 2. Horn, measured from the base of the lower mandible to the top of the horn. 3. Bill depth, measured from the bottom of the lower mandible to the top of the upper mandible. Horn height above the bill (horn–bill depth) was used as a measure of horn size for all statistical analyses.

Isotope analysis

We analysed stable isotopes from feathers grown during the pre-breeding period. Stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes have been used to infer the diets of marine animals (Hobson & Welch 1992, Kline & Pauly 1998), with $\delta^{15}N$, and to a lesser extent $\delta^{13}C$, increasing with trophic level (DeNiro & Epstein 1980, Fry 1988, Post 2002) and $\delta^{13}C$ also aiding in discrimination between pelagic and benthic prey, as well as inshore and offshore prey (Hobson *et al.* 1994, France 1995). Because Auklet feathers are retained at the beginning of the breeding season and are metabolically inert after growth, signatures can provide an indication of diet composition during the pre-breeding period (Chamberlain *et al.* 1997, Hobson & Wassenaar 1997). Isotope ratios (R) are expressed in δ units where $\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$. $\delta^{15}N$ 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 another 24 h. Feathers (including material from the vane and rachis) were weighed into tin capsules, then combusted and oxidized in a TC Elemental Analyzer and introduced online into a Finnigan MAT Delta Plus XL Isotope Ratio Mass Spectrometer. During analysis, four standards were run: for carbon, the international standard NBS-21 Graphite (−28.0 ± 0.08‰, $n = 7$) and an in-house standard UC-1 Graphite (−25.9 ± 0.14‰, $n = 6$); for nitrogen, an international standard RM-8548 Ammonium Sulphate (20.3 ± 0.28‰, $n = 8$). For both elements, we also used an in-house organic standard: Domestic Chicken *Gallus gallus* blood ($\delta^{15}N$: 4.4 ± 0.12‰; $\delta^{13}C$: −20.3 ± 0.12‰ within autorun, $n = 4$). Samples were repeatable to within ± 0.24‰ for $\delta^{15}N$ ($n = 16$) and ± 0.21‰ for $\delta^{13}C$ ($n = 16$).

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 Rhinoceros Auklet diets. Because IsoError cannot generate error estimates for single data points, we compared two groups, tall- and short-horned birds, to derive error estimates. All prey samples were collected in 2002 from Triangle Island (Davies *et al.* 2009). Prey samples were freeze-dried, subjected to lipid extraction with a methanol : chloroform : water (50 : 25 : 25 by vol.) solution for at least 24 h, rinsed with distilled water and redried (Thompson & Furness 1995). To remove carbonates, euphausiids were also soaked in 1 M HCl until bubbling stopped (Thompson & Furness 1995). The three sources used for the model were inshore fish (Sandlance and juvenile rockfish), offshore fish (juvenile salmonids and Pacific Saury) and euphausiids (Fig. 2). We used a tissue-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 Guillemot *Uria aalge* on a diet of Capelin *Mallotus villosus*; Becker *et al.* 2007).

For horn height and plume length we used analysis of covariance (ANCOVA) and ran separate models for each prey type (inshore fish, euphausiids, offshore fish) with sex as a factor and an interaction term between sex and the covariate. We then ran separate models for each sex. To control for the effect of body size (PC1) on ornament size we entered body size as a covariate in all ANCOVA models. Normality of residual variance was tested with Shapiro–Wilk tests ($P > 0.05$ was considered normally distributed; all of our results fell within this range). When the interaction term was significant we analysed sex categories separately, again controlling for body size. Tests were considered significant at $\alpha = 0.05$.

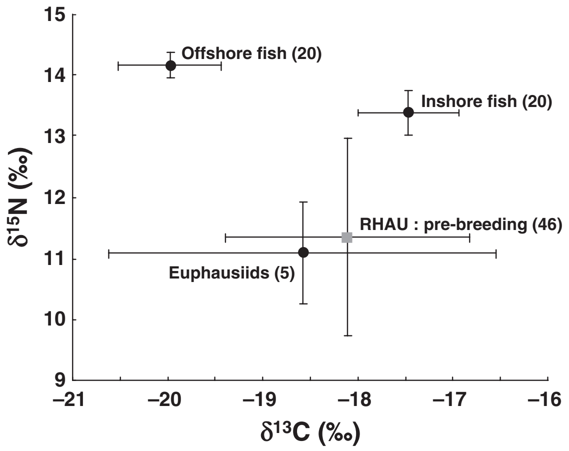

Figure 2. Relationship between isotopic signatures of Rhinoceros Auklet (RHAU) feathers and potential prey items. Mean (± sd) stable carbon ($\delta^{13}C$) and stable nitrogen ($\delta^{15}N$) isotope values of pre-breeding diet (breast feather: subtracting an assumed diet-tissue discrimination factor of 3.7‰ for $\delta^{15}N$ and 1‰ for $\delta^{13}C$; Becker *et al.* 2007) and euphausiids, inshore fish and offshore fish (sample sizes in parentheses). Diet items are from Triangle Island (Davies *et al.* 2009).

RESULTS

Males were larger than females (*t*-test: $t_{46} = -7.39$, $P \leq 0.0001$) but did not have larger horns (male mean: 9.91 mm, sd ± 1.57; female mean: 9.87 mm, sd ± 1.93, $t_{46} = -0.08$, $P = 0.93$) or longer plumes (male mean: 49.67 mm, sd ± 4.78; female mean: 49.77 mm, sd ± 3.34; $t_{28} = 0.06$, $P = 0.94$). The average estimated proportion of each diet type in the pre-breeding diet for males and females combined was 57% (95% confidence interval: 44–70%) euphausiids, 36% (23–49%) inshore fish and 7% (3–11%) offshore fish. Female diet comprised more euphausiids and fewer inshore fish than did male diet [females: 61% (45–77%) euphausiids, 30% (13–47%) inshore fish; males: 49% (26–72%) euphausiids, 47% (24–70%) inshore fish]. However, these differences were not significant (euphausiids: $t_{42} = 0.81$, $P = 0.42$; inshore fish: $t_{42} = -1.27$, $P = 0.21$). Offshore fish did not constitute a large proportion of the diet in either females [9% (3–15%)] or males [3% (0–8%)].

Horn height was significantly related to the estimated proportion of inshore fish and euphausiids in the pre-breeding diet and these relationships differed between the sexes (Table 1). In females, having accounted for body size, horn height was positively related to the proportion of inshore fish [$F_{1,25} = 15.22$, $\beta = 2.74$, $P = 0.0007$; body size (PC1): $F_{1,25} = 7.15$, $\beta = 0.33$, $P = 0.01$] and negatively related to the proportion of euphausiids ($F_{1,25} = 12.88$, $\beta = -2.65$, $P = 0.002$; PC1: $F_{1,25} = 8.21$, $\beta = 0.95$, $P = 0.009$). Thus, females feeding on more inshore fish and fewer euphausiids during the pre-breeding period were more likely to grow larger horns. There was no relationship between horn height and the proportion of offshore fish in the diet of females ($F_{1,25} = 0.33$, $\beta = -1.39$, $P = 0.57$; PC1: $F_{1,25} = 7.68$, $\beta = 1.14$, $P = 0.01$). In males, having accounted for body size, horn height was unrelated to the proportion of inshore fish ($F_{1,17} = 0.31$, $\beta = 0.42$, $P = 0.59$; PC1: $F_{1,17} =$

Table 1. Results of ANCOVA models to explain the effect of each prey type (inshore fish, euphausiids, offshore fish), in Rhinoceros Auklet pre-breeding diet, on horn height and plume length. Sex is included as a factor and body size (PC1) entered as a covariate in all models. Significant results are shown in bold type.

		Horn height			Plume length		
Prey type	Variable	*F*	β	*P*	*F*	β	*P*
Inshore fish	Sex	11.32	1.12	**0.002**	0.001	–0.05	0.98
	Body size	18.1	1.04	**0.0001**	0.0002	0.02	0.98
	Proportion in diet	8.29	1.44	**0.006**	0.13	0.76	0.72
	Proportion in diet × sex	5.44	1.22	**0.02**	0.88	1.91	0.36
Euphausiids	Sex	11.17	1.12	**0.002**	0.002	–0.06	0.97
	Body size	19.04	1.09	**0.0001**	0.001	0.04	0.97
	Proportion in diet	7.25	–1.38	**0.01**	0.22	–1.01	0.64
	Proportion in diet × sex	5.35	–1.22	**0.03**	0.94	–2.06	0.34
Offshore fish	Sex	9.86	1.2	**0.003**	0.05	0.33	0.82
	Body size	17.58	1.18	**0.0002**	0.1	0.35	0.75
	Proportion in diet	0.54	–1.83	0.47	0.005	–0.51	0.95
	Proportion in diet × sex	0.03	0.46	0.85	0.02	–0.91	0.89

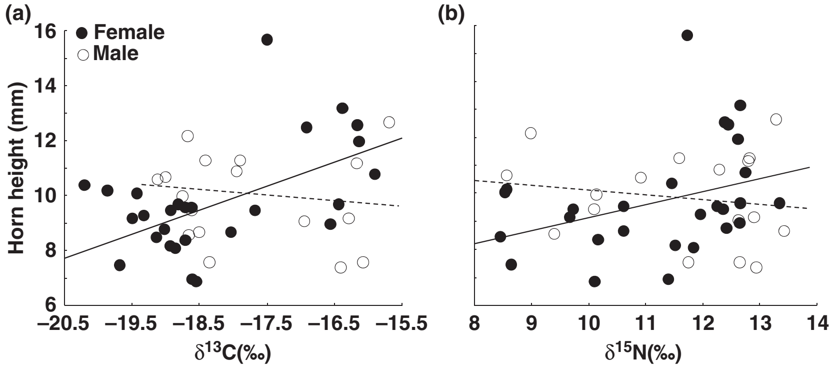

Figure 3. Relationship between horn height, $\delta^{13}C$ (a) and $\delta^{15}N$ (b) in female and male Rhinoceros Auklet pre-breeding diet (breast feathers). For females, horn height was positively related to $\delta^{13}C$ ($r^2 = 0.27$, $\beta = 0.79$, $P = 0.005$) and $\delta^{15}N$ ($r^2 = 0.13$, $\beta = 0.47$, $P = 0.06$). For males, horn height was unrelated to both $\delta^{13}C$ ($r^2 = 0.008$, $\beta = -0.12$, $P = 0.73$) and $\delta^{15}N$ ($r^2 = 0.03$, $\beta = -0.17$, $P = 0.52$).

12.79, $\beta = 1.31$, $P = 0.003$), the proportion of euphausiids ($F_{1,17} = 0.17$, $\beta = -0.31$, $P = 0.67$; PC1: $F_{1,17} = 12.24$, $\beta = 0.36$, $P = 0.004$) or the proportion of offshore fish ($F_{1,17} = 0.33$, $\beta = -2.25$ $P = 0.53$; PC1: $F_{1,17} = 12.76$, $\beta = 1.22$, $P = 0.003$) in the pre-breeding diet, suggesting that diet did not affect horn height in males. There were no significant predictors of plume length in the models (Table 1).

The relationship between horn height, $\delta^{13}C$ and $\delta^{15}N$, when accounting for body size, did not differ between the sexes ($\delta^{13}C$: $F_{1,40} = 2.33$, $\beta = 0.29$, $P = 0.13$, PC1: $F_{1,40} = 20.1$, $\beta = 1.13$, $P < 0.001$; $\delta^{15}N$: $F_{1,40} = 1.78$, $\beta = 0.21$, $P = 0.19$, PC1: $F_{1,40} = 19.9$, $\beta = 1.19$, $P < 0.001$). In univariate analyses, there was a positive relationship between $\delta^{13}C$ values from female pre-breeding diet and horn height ($r^2 = 0.27$, $\beta = 0.79$, $P = 0.005$; Fig. 3) and a positive, but marginally significant, relationship between $\delta^{15}N$ and horn height ($r^2 = 0.13$, $\beta = 0.47$, $P = 0.06$; Fig. 3). In males, horn height was unrelated to $\delta^{13}C$ ($r^2 = 0.008$, $\beta = -0.12$, $P = 0.73$) and $\delta^{15}N$ ($r^2 = 0.03$, $\beta = -0.17$, $P = 0.52$). The relationship between plume length, $\delta^{13}C$ and $\delta^{15}N$, when accounting for body size, did not differ between the sexes ($\delta^{13}C$: $F_{1,40} = 1.91$, $\beta = 0.97$, $P = 0.18$, PC1: $F_{1,40} = 0.01$, $\beta = 0.12$, $P = 0.91$; $\delta^{15}N$: $F_{1,40} = 0.97$, $\beta = 0.62$, $P = 0.33$, PC1: $F_{1,40} = 0.008$, $\beta = 0.09$, $P = 0.93$) and in univariate analyses, $\delta^{13}C$ and $\delta^{15}N$ were unrelated to plume length in both females ($\delta^{13}C$: $r^2 = 0.18$, $\beta = 1.12$, $P = 0.1$; $\delta^{15}N$: $r^2 = 0.06$, $\beta = 1.17$, $P = 0.37$) and males ($\delta^{13}C$: $r^2 = 0.05$, $\beta = -0.99$, $P = 0.45$; $\delta^{15}N$: $r^2 = 0.003$, $\beta = 0.18$, $P = 0.85$).

The relationship between body size (PC1) and horn height did not differ between the sexes ($F_{1,43} = 0.0014$, $\beta = 0.01$, $P = 0.97$), but was stronger in males than in females (Fig. 4). This difference was due to the relationship between wing chord and horn height, which differed between the sexes ($F_{1,43} = 6.68$, $\beta = -0.24$, $P = 0.01$) and exhibited a positive correlation in males ($r^2 = 0.46$, $\beta = 0.42$, $P = 0.002$) but not in females ($r^2 = 0.013$, $\beta = -0.06$, $P = 0.97$). Additionally, the relationship between weight and horn height did not differ significantly between the sexes ($F_{1,43} = 3.28$, $\beta = -0.014$, $P = 0.07$), but was stronger in males ($r^2 = 0.24$, $\beta = 0.02$, $P = 0.04$) than in females ($r^2 = 0.016$, $\beta = -0.007$, $P = 0.51$). The relationship between plume length, body size and weight did not differ between the sexes (body size: $F_{1,27} = 1.68$, $\beta = 1.47$, $P = 0.21$; weight: $F_{1,27} = 3.59$, $\beta = 0.04$, $P = 0.07$) and body size and weight were unrelated to plume length in both males (body size: $r^2 = 0.05$, $\beta = -1.73$, $P = 0.47$; weight: $r^2 = 0.02$, $\beta = 0.02$, $P = 0.49$) and females (body size: $r^2 = 0.1$, $\beta = 1.21$, $P = 0.23$; weight: $r^2 = 0.26$, $\beta = -0.06$, $P = 0.07$).

Finally, to examine error associated with predicted prey proportions, we compared females with small and large horns (small horns: inshore fish 15% ± 0.07 se, euphausiids 73% ± 0.08, offshore fish 12% ± 0.03; large horns: inshore fish 60% ± 0.15, euphausiids 37% ± 0.14, offshore fish 3% ± 0.04) and found that the estimated proportion of euphausiids was lower (two-tailed *t*-test: $t_{25} = -2.38$, $P = 0.03$) and the estimated proportion of inshore fish higher (two-tailed *t*-test: $t_{25} = -2.91$, $P = 0.007$) in large-horned females.

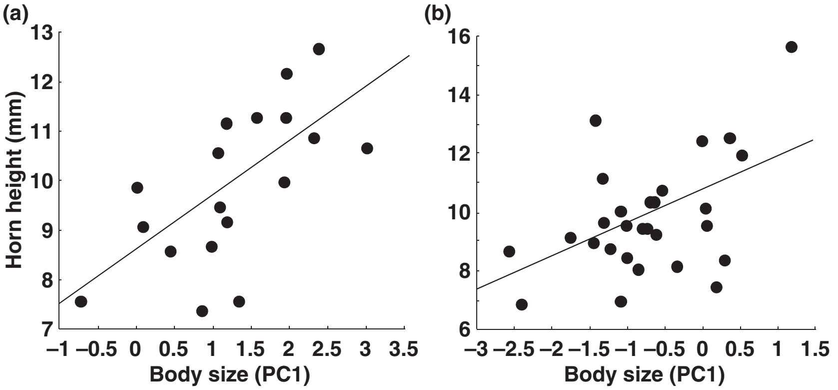

Figure 4. Relationship between body size and horn height in (a) male and (b) female Rhinoceros Auklets. In males, body size explained 43% of the variation in horn height ($r^2 = 0.43$, $\beta = 1.09$, $P = 0.003$) compared with 23% in females ($r^2 = 0.23$, $\beta = 1.13$, $P = 0.008$).

There was no significant difference between groups in the estimated proportion of offshore fish in the diet (two-tailed *t*-test: $t_{25} = 1.55$, $P = 0.14$).

DISCUSSION

Our results suggest that horn size may be constrained by production costs related to the acquisition of dietary resources during the pre-breeding period when horns are grown. Females with pre-breeding diets dominated by inshore fish had larger horns than females with pre-breeding diets dominated by euphausiids. However, for males, the proportion of inshore fish, offshore fish and euphausiids in pre-breeding diets did not affect horn size. In both sexes, plume length was not affected by the proportion of inshore fish, offshore fish and euphausiids in pre-breeding diets, which may suggest that plume length is unconstrained by diet composition. However, recent evidence (Pyle 2008) suggests that plumes develop slowly, rather than quickly in the spring, which could result in February–March diet being unrepresentative of overall diet during plume growth.

It is possible that prey samples collected in 2002 may not reflect the isotopic signatures of Rhinoceros Auklet prey in 2007. Annual variation in the availability of nitrates and degree of vertical mixing may change isotopic signatures at the base of the marine food web. However, Rau *et al.* (2003) found no significant linear trend in δ^{15}N or δ^{13}C signatures of zooplankton species sampled over a 50-year period, which suggests that long-term variability in δ^{15}N and δ^{13}C signatures should be low. Despite evidence for long-term temporal stability of isotope signatures, Rau *et al.* (2003) did observe an enrichment of δ^{15}N during El-Niño years. In our study, both 2002 and 2007 had a similar and slightly negative Pacific Decadal Oscillation Index (PDO February–May average 2002: −0.5, 2007: −0.07) and Southern Oscillation Index (SOI February–May average 2002: −0.4, 2007: −0.43).

Our results suggest that ornaments may act as different signals for each sex. For females, ornament size may signal overall physiological condition, which could be important for a female's capacity to produce a high-quality egg (Monaghan *et al.* 1998, Styrsky *et al.* 2002, Reynolds *et al.* 2003), as well as to incubate (Vleck 1981) and provision chicks (Lorentsen 1996). Females that are able to invest more in reproduction may produce larger eggs and nestlings (Knechtel 1998) with faster growth rates (Amundsen *et al.* 1997, Reed *et al.* 1999) and higher survival (Bolton 1991, Blomqvist *et al.* 1997). Interestingly, body size was a better predictor of horn height in males than in females, which suggests that horn height is a stronger indicator of overall body size in males. In dimorphic species, male ornament size or brightness is often correlated with body size (Keyser & Hill 2000, Doucet 2002, Jawor & Breitwisch 2004). Additionally, in a monomorphic subfamily of ducks (Anatidae) in which both sexes display white wing patches, wing patch size was strongly correlated with body size in males but not in females, even though wing patch size is positively related to fitness in both sexes (Hegyi *et al.* 2008). For males, large body size could provide an advantage for nest-site/mate defence and chick guarding

(Thoresen 1983, Hunter & Jones 1999). For example, McGlothlin *et al.* (2007b, 2008) found that large-ornamented male Dark-eyed Juncos were better able to defend their territories and produced larger short-term testosterone increases in response to male–male combat.

Masello *et al.* (2004) suggested that sexual ornaments could signal good parents (e.g. body condition) or good genes (e.g. body size; Andersson 1994). They found that females of the monomorphic Burrowing Parrot *Cyanoliseus patagonus* that had brighter abdominal plumage were in better condition, whereas males with brighter plumage were structurally larger. Given that in two closely related seabird species (Atlantic Puffin *Fratercula arctica* and Crested Auklet *Aethia cristatella*), females contribute more energy towards reproduction than males in terms of egg production, incubation and provisioning of chicks (Creelman & Storey 1991, Fraser *et al.* 2002), there should be strong selection for females in good condition. Thus, female ornaments may have evolved greater phenotypic plasticity to signal body condition to males. However, whether Rhinoceros Auklet horn size acts as different signals for each sex, with direct benefits for sexual selection, remains uncertain. It is also possible that Rhinoceros Auklet ornaments may signal other aspects of quality apart from body condition and size, such as immune system function (Folstad & Karter 1992), health status (Møller *et al.* 2000), parasite infection (Hamilton & Zuk 1982) or the capacity to prevent such infections (Hill & Farmer 2005, Mougeot 2008).

Contrary to previous studies which found that Rhinoceros Auklet diets were dominated by fish (Sealy 1973, Hoffman *et al.* 1981, Hobson 1994, Lance & Thompson 2005), our results suggest that there is a high proportion of euphausiids in pre-breeding diets. This indicates that there may be significant seasonal variation in diet composition, as previous studies were conducted in the summer or autumn, and that Rhinoceros Auklets are generalist feeders. Rhinoceros Auklet bill and tongue morphology is intermediate in type between fish- and zooplankton-feeding alcids (Bedard 1969), and energy densities of euphausiids and inshore fish are similar (Vermeer & Cullen 1982). This suggests that a combination of spatial and temporal prey availability and abundance determines the most profitable prey item for Rhinoceros Auklets in any given season. In our study, it may be that efficient female foragers that were able to take advantage of the greater spatial predictability of inshore prey (Thayer & Sydeman 2007), and a possible high relative abundance of inshore fish (euphausiid abundance was low in 2007; DFO 2008), grew larger horns.

This is the first study to provide evidence that seabird ornament size is constrained by production costs during the pre-breeding period when ornaments are grown. Although studies on sexual ornamentation in monomorphic seabirds have shown that ornaments are mutually sexually selected and useful predictors of reproductive success (Jones & Hunter 1993, Velando *et al.* 2001, Daunt *et al.* 2003, Massaro *et al.* 2003), the potential role of male and female Rhinoceros Auklet ornaments in mate choice remains unclear. Our work emphasizes the importance of understanding individual ecology throughout the annual cycle for understanding the factors that determine mate choice and fitness.

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