

Isotopic ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) evidence for intersexual foraging differences and temporal variation in habitat use in waved albatrosses

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Abstract: Waved albatrosses (*Phoebastria irrorata* Salvin, 1883) forage close to their breeding grounds on Isla Española, Galápagos, during the short chick-brooding stage and make long trips to the Peruvian upwelling during incubation and chick rearing. Previous studies have suggested foraging segregation by sex: females spend more time searching than males do while foraging in the Galápagos Marine Reserve (GMR), and band recoveries suggest higher bycatch vulnerability of males in the Peruvian upwelling. We used stable isotope analysis ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of whole blood of adult male and female albatrosses to test for intraspecific foraging segregation in this sexually dimorphic species. Analysis of serial blood samples revealed higher $\delta^{15}\text{N}$ values in males, suggesting consumption of prey items of higher trophic level. We also detected seasonal variation in foraging ecology, with higher $\delta^{15}\text{N}$ values at the beginning of the breeding season. Sex and regional differences in $\delta^{13}\text{C}$ values were not significant, reflecting primarily pelagic foraging sites of both sexes, both in the GMR and the Peruvian upwelling. Our results provide evidence of trophic segregation, suggestive of competitive exclusion, and novel information on marine isoscape values in the Eastern Equatorial Pacific.

Résumé : Sur l'Isla Española, Galapagos, les albatros des Galapagos (*Phoebastria irrorata* Salvin, 1883) recherchent leur nourriture près de leurs sites de reproduction durant la courte période de couvaison des petits, alors que, durant l'incubation et l'élevage des petits, ils entreprennent de longs voyages vers l'affleurement du Pérou. Des études antérieures ont suggéré qu'il y avait une ségrégation de la recherche de nourriture en fonction du sexe: les femelles passent plus de temps que les mâles à la recherche durant leur quête alimentaire dans la Réserve marine des Galapagos (« GMR ») et les retours de bandes de marquage laissent croire que les mâles sont plus susceptibles d'être capturés comme prises accessoires dans l'affleurement du Pérou. Une analyse des isotopes stables ($\delta^{15}\text{N}$ et $\delta^{13}\text{C}$) du sang entier d'albatros mâles et femelles permet de vérifier la ségrégation intraspécifique de la quête alimentaire chez cette espèce à dimorphisme sexuel. Une analyse de séries d'échantillons de sang indique des valeurs plus élevées de $\delta^{15}\text{N}$ chez les mâles, ce qui laisse croire à une consommation de proies d'un niveau trophique supérieur. Nous avons aussi décelé une variation saisonnière dans l'écologie de la recherche de nourriture, avec des valeurs plus élevées de $\delta^{15}\text{N}$ au début de la saison de reproduction. Les différences de $\delta^{13}\text{C}$ en fonction du sexe et de la saison ne sont pas significatives, ce qui indique que les sites de recherche de nourriture sont principalement pélagiques chez les deux sexes, tant dans GMR que dans l'affleurement du Pérou. Nos résultats présentent des données qui appuient l'existence d'une ségrégation trophique et laissent croire à une exclusion par compétition; ils fournissent aussi des renseignements nouveaux sur le paysage isotopique (isoscape) marin dans l'est du Pacifique équatorial.

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Introduction

Sexual size dimorphism has been associated with foraging differences between the sexes in a number of bird species (Newton 1979; Clarke et al. 1998; Cristol et al. 1999; Catry et al. 2005). More recently, technological advances in electronic data loggers and transmitters (Phillips et al. 2004, 2005; Lewis et al. 2005) and in the analysis of stable isotope ratios in tissue samples (Forero et al. 2002a, 2005; Nisbet et al. 2002; Bearhop et al. 2006) have revealed similar sex ef-

fects in seabirds, whose foraging behavior is generally difficult to observe. Such intraspecific variation in location or behavior of foraging seabirds offers important insights into their foraging ecology. For example, sex-specific foraging strategies can lead to differences in distribution, resource availability, and exposure to sources of mortality (Croxall and Prince 1990; Ryan and Boix-Hinzen 1999; González-Solís et al. 2000; DeLord et al. 2005). Identifying demographic differences in habitat use or foraging methods can therefore contribute to our understanding of population dynamics.

Breeding waved albatrosses (*Phoebastria irrorata* Salvin, 1883), essentially endemic to Isla Española, Galápagos, employ a dual foraging strategy observed in many tube-nosed seabirds, in this case making long trips to the Peruvian upwelling during incubation and chick rearing (Anderson et al. 2003) and foraging within 100 km of their breeding colony when constrained by the dietary needs of a small chick during the brood stage (Awkerman et al. 2005). Breeding

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males and females occupy the same habitat within the Galápagos Marine Reserve (GMR; Awkerman et al. 2005), and their ranges over the Peruvian continental shelf are similar also (Anderson et al. 1998). Although trip characteristics of the sexes within the GMR are similar, females spend more time in flight and less time on the water in the foraging area (Awkerman et al. 2005). This discrepancy is consistent with competitive exclusion of the smaller (in this case, female) sex, which has been observed in other procellariiforms (González-Solís et al. 2000) and can lead to male-biased adult mortality (Ryan and Boix-Hinzen 1999) if males also are more aggressive in pursuing bait set by fishing fleets. Recently we found that incidental and intentional catch of waved albatrosses at the Peruvian upwelling was indeed strongly male-biased (Awkerman et al. 2006), with important implications for population stability via the reduction in number of breeding pairs (Mills and Ryan 2005). Identifying sex differences in foraging strategies that lead to differential mortality is critical for population projections for this IUCN-vulnerable species (Croxall and Gales 1998; BirdLife International 2000). Here we test the hypothesis of sexual segregation in foraging characteristics using stable isotope ratios in blood. Stable isotope ratios have recently shown significant potential in evaluating the use of foraging areas by widely ranging seabirds whose diet is otherwise difficult to document (Hobson 1990; Bocher et al. 2000; Cherel et al. 2000; Forero et al. 2002a, 2005; Forero and Hobson 2003; Ainley et al. 2003; Quillfeldt et al. 2005), and they have been used to identify foraging segregation and trophic relationships within seabird communities (Hobson et al. 1994; Hodum and Hobson 2000).

Intraspecific differences in ratios of $^{15}\text{N}:^{14}\text{N}$ (measured as $\delta^{15}\text{N}$) and ratios of $^{13}\text{C}:^{12}\text{C}$ ($\delta^{13}\text{C}$) have revealed seasonal variability in seabird diet (Thompson and Furness 1995) and distribution (Minami et al. 1995) as well as slight demographic differences in foraging success, breeding success, and microhabitat use (Forero et al. 2002b). $\delta^{15}\text{N}$ values demonstrate a stepwise increase with trophic level (DeNiro and Epstein 1977) and are valuable in investigations of the trophodynamics of seabirds or in comparison of trophic positions within food webs (Hobson and Welch 1992). Higher $\delta^{15}\text{N}$ values in waved albatross males would provide support for the trophic segregation hypothesis, indicating access of the larger sex to preferred prey items, including bait, and corroborating evidence that males are more vulnerable to capture in fisheries. Isotopic differences (higher $\delta^{15}\text{N}$ values in males) have provided support for the trophic segregation hypothesis in other seabirds (Forero et al. 2002a; Bearhop et al. 2006).

$\delta^{13}\text{C}$ values can vary between inshore and pelagic foraging areas and are influenced by temperature (Sackett et al. 1965), latitude (Takai et al. 2000), dissolved CO_2 , and nutrient concentration (Rau et al. 1989; Goericke and Fry 1994), making them a possible indicator of the foraging region of marine predators (Hobson 1999). Regional differences in isotopic values of food webs result in marine "isoscapes" or isotopic clines (Minami and Ogi 1997; Schell et al. 1998; Sutka et al. 2004), reflecting underlying gradients in inorganic substrates or primary productivity (Rau et al. 1992; Michener and Schell 1994). Geographic isoscapes resulting from varying physical and chemical

processes between the Galápagos and Perú could contribute to demographic differences in isotopic signatures of waved albatrosses (Schell et al. 1998). Our previous work using satellite geolocation indicated that males and females occupy common foraging areas between the GMR and the Peruvian upwelling (Anderson et al. 2003; Awkerman 2006). However, the sexes could feed in different regions of their common range if, for example, females fed more than males did en route to the Peruvian upwelling and males fed more in the upwelling. Any difference of this type could be reflected in sex-specific $\delta^{13}\text{C}$ values, with males having higher $\delta^{13}\text{C}$ values due to foraging in an area of higher primary productivity (Schell 2000; Bearhop et al. 2001; Savoye et al. 2003; Hilton et al. 2006).

On the other hand, Cherel et al. (2005) found no difference between long-trip and short-trip $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, indicating that smaller sub-Antarctic procellariiforms assimilated none of the prey from short trips, employing them solely for provisioning young, and were themselves fed from long foraging trips. Because waved albatrosses also employ this dual foraging strategy, we included both non-breeders and breeders in our sampling to compare isotopic values between the two sampling periods (incubation and brooding). We expected to detect no difference in blood isotope values among non-breeders, whose time budget data suggest that the foraging regime remains similar between sampling periods and incorporates both areas (J.A. Awkerman, unpublished data), in contrast to breeders, who engaged in long trips to Perú during incubation and short trips within Galápagos while provisioning chicks.

Methods

Isotopic values can differ depending on the metabolic activity of the tissue sampled (Tieszen et al. 1983; Hobson and Clark 1993). Whole blood is metabolically active and reflects diet integrated over at least 3–4 weeks prior to sampling in large-bodied albatrosses (Rubenstein and Hobson 2004), which in this case eliminates any potential differences in assimilation due to sampling time following trips to both near and distant foraging areas. Hence, we used stable isotope analysis of whole blood to examine intraspecific temporal and spatial variation in foraging habitat throughout the breeding season.

Samples were collected at Punta Cevallos ($1^\circ 23'\text{S}$, $89^\circ 37'\text{W}$), the southeastern point of Isla Española, which is the most southeastern island of the Galápagos archipelago. Serial blood samples (0.25–0.90 mL) were taken from 37 adults (10 male non-breeders, 6 male breeders, 12 female non-breeders, and 9 female breeders) approximately 3–4 days after their return to the colony during mid-incubation (mid to late May) and again at the end of the brooding period (early July) in 2004. Whole blood was stored in 1.8 mL Eppendorf tubes with an equal volume of 70% ethanol. Prey samples were collected opportunistically from regurgitated items found at nest sites during brooding and stored in 70% ethanol. These samples are expected to represent only prey items taken within the GMR, because adults at the brooding stage forage within the GMR (Awkerman et al. 2005). Blood samples were later freeze-dried and a 1 mg subsample was taken for isotopic analysis. Subsamples were weighed

into tin cups and combusted in a Carlo Erba elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope ratio mass spectrometer at the Department of Soil Science, University of Saskatchewan. We measured a laboratory standard (albumen) for every five unknowns in sequence. Values are reported in delta notation in parts per thousand (‰) relative to PeeDee Belemnite ($\delta^{13}\text{C}$) and air ($\delta^{15}\text{N}$). Measurement error was estimated at $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ measurements and $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$.

Statistical analyses were conducted with Statistica v. 5.5 and v. 6 (Statsoft, Tulsa, Oklahoma, USA) and SPSS® v. 12 (SPSS, Chicago, Illinois, USA). Mann–Whitney U tests were used upon violation of Shapiro–Wilk’s W test of normality. Visual inspection of data within each sampling period suggested a slight decline in isotopic values with Julian date, which might imply seasonal variation in foraging habitat. To address this concern, while recognizing that foraging characteristics may differ between sexes and between breeders and non-breeders, we used a three-way repeated measures analysis to detect temporal changes in isotopic values; main effects were sampling period (incubation or brooding), sex (male or female), and breeding status (breeder or non-breeder).

Results

Temporal variation in foraging habitat

The repeated measures analysis showed that $\delta^{15}\text{N}$ values decreased between incubation (mean = 15.5‰ , SD = 0.8‰) and brooding (mean = 15.1‰ , SD = 0.5‰) periods among all adults sampled ($F_{[1,33]} = 36.26$, $P < 1 \times 10^{-6}$; Fig. 1) and were significantly higher in males (mean = 15.6‰ , SD = 0.7‰) than in females (mean = 15.0‰ , SD = 0.6‰ ; $F_{[1,33]} = 9.11$, $P = 0.005$; Fig. 2). We also found a marginally significant sampling period \times breeding status interaction ($F_{[1,33]} = 4.15$, $P = 0.05$).

$\delta^{13}\text{C}$ values (mean = -15.6‰ , SD = 0.4‰) were not significantly affected by temporal or demographic variables (all $P > 0.15$), with only a suggestive effect of breeding status ($F_{[1,33]} = 3.05$, $P = 0.09$; Fig. 1).

Prey samples

Twenty-seven prey samples were collected as regurgitated items from nest sites. Average isotopic values of prey items ($\delta^{15}\text{N}$: mean = 11.9‰ , SD = 2.9‰ ; $\delta^{13}\text{C}$: mean = -17.6‰ , SD = 1.8‰) are expected to reflect levels within the GMR. No significant differences were found between the two most common prey items, flying fish ($\delta^{15}\text{N}$: mean = 13.0‰ , SD = 1.9‰ ; $\delta^{13}\text{C}$: mean = -18.5‰ , SD = 2.3‰) and squid ($\delta^{15}\text{N}$: mean = 11.0‰ , SD = 3.5‰ , $U = 25.00$, $Z = 1.33$, $P = 0.18$; $\delta^{13}\text{C}$: mean = -17.3‰ , SD = 1.8‰ , $U = 34.00$, $Z = -0.53$, $P = 0.59$).

Discussion

Sex differences

We found no significant difference in $\delta^{13}\text{C}$ values between males and females, suggesting no spatial segregation of foraging habitat by sex. However, higher $\delta^{15}\text{N}$ values in males in both sampling periods suggested different diet and (or) foraging success, supporting the trophic segregation hy-

Fig. 1. Change in mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of adult waved albatrosses (*Phoebastria irrorata*) between the early breeding period (1) and the post-brood period (2) in both breeding (B) and non-breeding (NB) males (♂, solid arrows) and females (♀, dashed arrows).

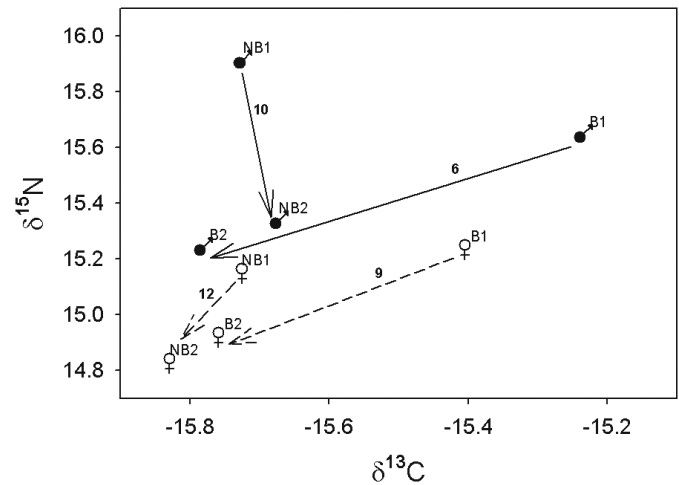
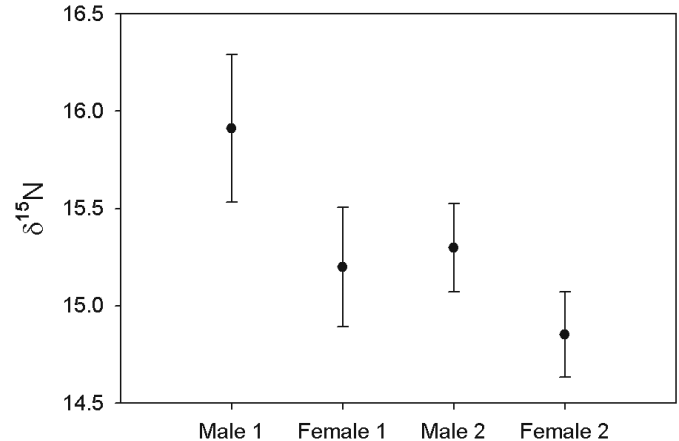


Fig. 2. $\delta^{15}\text{N}$ values (mean \pm 95% CI) of male ($N = 16$) and female ($N = 21$) waved albatrosses in two sampling periods, including both breeders and non-breeders. Samples from the first period (male 1 and female 1) were collected during the incubation period of breeding (mid-May). Samples from the second period (male 2 and female 2) were collected from the same birds following the brooding phase of breeding (early July).



pothesis and indicating that males might have better access to higher trophic level prey items or higher feeding rates (Focken 2001) within densely populated common foraging grounds. Alternatively, $\delta^{15}\text{N}$ values may reflect differences in nutritional stress between males and females; however, the same differences are present in non-breeders that are not engaged in costly provisioning behavior. Other data suggest that adult mortality has increased in recent years and that mortality is male-biased (Awkerman et al. 2006). Capture by fisheries has been implicated in this increased mortality, and our data provide a potential mechanism for sex-specific mortality due to fisheries: the competitively dominant sex in common foraging areas may have better access to fishery discards and baited hooks. Male-biased capture has great importance to management of this IUCN-vulnerable species

(Croxall and Gales 1998; BirdLife International 2000) because a biased sex ratio effectively reduces breeding population size in obligately biparental species (Mills and Ryan 2005). Waved albatrosses have now provided information suggesting that males and females occupy the same foraging areas (Anderson et al. 1998, 2003; Awkerman et al. 2005; this study), that males spend less time searching the area than females do (Awkerman et al. 2005), and that males might consume prey from a higher trophic level (this study). Competitive dominance by males, the larger sex, thus may contribute to the apparent population decline of this species.

Foraging habitat

The relatively high $\delta^{13}\text{C}$ values of waved albatrosses compared with other large procellariiform species (Cherel et al. 2000; Thompson et al. 2000; Forero et al. 2005) reflect the isotopic signatures of the eastern Pacific: $\delta^{13}\text{C}$ values in squid (Takai et al. 2000; this study) are enriched in this region compared with other areas. The $\delta^{15}\text{N}$ value of particulate organic matter is also high in this region (Saino and Hattori 1987), and a decline in $\delta^{15}\text{N}$ values between the first and the second sampling periods in all birds might reflect the incorporation of foraging trips within the GMR after the start of the breeding season, because the GMR is a resource-poor habitat compared with pre-breeding habitat near the Peruvian upwelling (Claustré and Maritorea 2003). Time budget data suggest that non-breeders engage in short and long trips throughout the breeding season and do not change their foraging strategy between sampling periods (J.A. Awkerman, unpublished data); therefore, the decline in $\delta^{15}\text{N}$ values over time for non-breeders could reflect large-scale seasonal changes in the Eastern Equatorial Pacific.

Without prey samples from the Peruvian upwelling, we were unable to compare isotopic values of prey items in the two foraging locations. Squid and flying fish samples presumed to have been collected within the GMR covered a wide range of isotopic ratios. Opportunistic catch by the artisanal gillnet and longline fisheries along the Peruvian coast makes it difficult to determine the proportions or trophic level of species that albatrosses might consume as discards or bait. In comparison with prey items such as squid and fish, discards from species such as sharks and rays, frequently targeted by these boats, would be at a very high trophic level and this regional variation in diet could contribute to the decline in $\delta^{15}\text{N}$ values. High isotopic variance among groups of prey samples from Galápagos precluded the use of a mixed modeling approach (Phillips and Koch 2002) with which we might have examined the proportion of prey sources contributing to albatross diet. Being able to collect only one type of tissue from the birds also precluded the use of a mixed model of dietary shift using tissues with different turnover rates (Phillips and Eldridge 2006).

Reproductive status

The interaction observed between breeding status and sampling period indicated a relatively greater decline in $\delta^{15}\text{N}$ values between the two sampling periods in non-breeders, which may reflect differences in foraging habitat or nutritional stress, which tends to increase $\delta^{15}\text{N}$ values (Hobson et al. 1993; Cherel et al. 2005); foraging effort by

breeders, presumably greater than that of non-breeders, is highest at the end of the brooding phase (Shaffer et al. 2003) and might result in elevated values in breeders following this period. High densities of conspecifics in a common foraging area could result in lower prey densities such that some birds might increase their foraging success by expanding their foraging range to encompass higher density patches of preferred prey items (MacArthur and Pianka 1966; Monaghan et al. 1994; Kitaysky et al. 2000). Non-breeding waved albatrosses, unrestricted by provisioning responsibilities, might evade competition within waters close to the colony by accessing a productive upwelling area at the western side of the archipelago (Houvenaghel 1984). This area, where waved albatrosses have been observed feeding (Merlen 1996), is farther and deeper than the range frequented by breeding waved albatrosses constrained to foraging close to the colony during the chick-brooding phase, which could result in relatively lower $\delta^{13}\text{C}$ values for non-breeders (Forero et al. 2002b; Forero et al. 2005) during the brooding period. $\delta^{13}\text{C}$ values of breeders and non-breeders became more similar as breeders began foraging within the GMR during the chick-brooding period, offering no evidence of intraspecific segregation within the GMR and suggesting that this area is not as enriched in ^{13}C as the productive Peruvian upwelling. Preliminary GPS tracking data also did not support the hypothesis of reduced intraspecific competition through expansion of foraging range (J.A. Awkerman, unpublished data): non-breeders appeared to forage close to the breeding colony while in the GMR. Similar habitat use by breeders and non-breeders while in the GMR supports previous results indicating the importance of shallow bathymetry in foraging habitat within the GMR (Awkerman et al. 2005).

While $\delta^{13}\text{C}$ values have been used to distinguish proximity of feeding to the colony in other species, these values generally show no or poor sensitivity to bathymetric differences within pelagic environments, so differential foraging locations would not always result in differences in $\delta^{13}\text{C}$ values (Thompson et al. 2000; cf. Cherel et al. 2000). Our results also suggested little difference in $\delta^{13}\text{C}$ values between marine locations at the macrohabitat level, i.e., between Galápagos and Perú. More documentation of isotopic values in these regions would contribute to knowledge of regional isotopic clines that could be used to further elucidate isotopic variation among other species or food webs. Isotopic differences within waved albatrosses support the competitive exclusion hypothesis, suggesting that males obtain more preferred prey items and are potentially more vulnerable to fishery interactions. Further research into male-biased waved albatross bycatch and operational sex ratio could determine the effect of these interactions on the population.

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