

CHARACTERIZING ISOTOPIC VARIATION OF A TROPICAL SEABIRD, THE WHITE TERN *GYGIS ALBA*

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SUMMARY

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Understanding a species' feeding ecology is important in understanding the impacts of disturbances to populations (e.g. pollution, declines in fisheries and climate change). Seabirds have been used as bioindicators of such disturbances, and their diets have been examined using stable isotopes throughout the Atlantic and Indian Ocean and more recently in the Pacific Ocean. In this study, carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios were examined in different feather types from a pantropical Charadriiform, the White Tern *Gygis alba* within the Hawaiian Archipelago. No difference was found within single feathers (base and tip) or between primary and breast feathers. This lack of variation among feather types within an individual indicates that either type could be used as an indicator of the status of an individual and that diet remained fairly constant throughout the year. Therefore, use of molted primary feathers for future analysis would be less invasive than capturing individuals to obtain blood or breast feather samples. Carbon and nitrogen isotope values for White Terns were similar to those of skipjack tuna *Katsuwonus pelamis* and yellowfin tuna *Thunnus albacares*, indicating that White Terns fed on prey similar to that of both species of tuna. The White Tern does not migrate, often feeding in association with predatory fish such as tuna, so that changes in its stable isotopes may reflect interannual changes in the abundance of tuna.

Key words: carbon-13, nitrogen-15, Pacific Ocean, trophic level, *Thunnus albacares*, *Katsuwonus pelamis*

INTRODUCTION

The study of stable isotopes of oxygen, carbon, nitrogen, hydrogen and sulfur can elucidate patterns in food webs, informing a broad range of ecological studies on topics such as feeding, dispersal, migratory routes and element cycling (e.g. Hobson & Clark 1992, Hobson 1999, Vanderklift & Ponsard 2003, Fry 2006). Because of predictable offsets in stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values between consumers and their diet, comparison of isotope data from predators and potential prey can provide information on nutrient sources, foraging location, migration patterns, trophic relationships and energy flow (Rubenstein & Hobson 2004, Fry 2006). The isotopic ratio of nitrogen exhibits a stepwise enrichment of about 3‰–5‰ at each trophic level in marine systems (e.g. DeNiro & Epstein 1981, Hobson & Clark 1992, Bearhop *et al.* 2002). The isotopic ratio of carbon shows an increase with trophic level by ca. 1‰ (e.g. DeNiro & Epstein 1978) and can be used to distinguish inshore (enriched in ^{13}C) versus offshore food sources (Hobson *et al.* 1994).

Stable isotopes have been particularly useful for diet studies, in which they can supplement or replace more intrusive methods such as the collection of regurgitates, stomach flushing and/or the collection of whole specimens. Such traditional approaches in avian studies require access to breeding colonies and handling of birds, which may cause the birds temporary harm or death (Duffy & Jackson 1986). Feathers, muscles and blood are the most commonly used tissues for analyzing stable isotopes in birds (Rubenstein & Hobson 2004). Because cells in different tissues turn over at different rates,

they can provide dietary information at different geographical and temporal scales (Hobson & Clark 1992, Hobson 1999, Bearhop *et al.* 2002). For example, liver, muscle, and blood have faster turnover rates compared to long-lived and inert tissues such as feathers, hair and bone, so their components may reflect different foraging environments (Tieszen *et al.* 1983; Hobson & Clark 1992; Haramis *et al.* 2001; Bearhop *et al.* 2002, 2003; Pearson *et al.* 2003). Breast feathers are often used for analysis because of their ease of collection and overall isotope average to other tissues, and they have been used to represent isotopic ratios from the individual as a whole (Thompson & Furness 1995, Smith *et al.* 2008).

Seabird diet and feeding ecology have been investigated using stable isotopes in temperate and polar waters (Thompson *et al.* 1999) as well as in the tropical Atlantic and Indian oceans (Jaquemet *et al.* 2004, Cherel *et al.* 2008). Studies have also been conducted in the North Pacific, primarily of Procellariiformes (petrels and shearwaters) and Pelecaniformes (boobies, frigatebirds and tropicbirds; Hobson *et al.* 1994, Ramos *et al.* 2002, Wiley *et al.* 2013a, b). Several isotopic studies (e.g. Bond & Diamond 2011) of Charadriiformes (specifically, terns and noddies) have been published recently (e.g. Young *et al.* 2010), but few of these studies have investigated tropical Pacific Charadriiformes.

White Terns are non-migratory pantropical seabirds (Niethammer & Patrick 1998). They are opportunistic predators, primarily taking fish and squid 10–50 mm long (Harrison *et al.* 1983, Ashmole & Ashmole 1967, Spear *et al.* 2007). They frequently feed on prey driven to the surface by predatory fish such as *Thunnus* spp. and

Katsuwonus pelamis (skipjack tuna; Dorward 1963, Harrison *et al.* 1983, Au & Pitman 1986, Harrison & Seki 1987, Spear *et al.* 2007). Within the Hawaiian Archipelago, White Terns have been observed feeding more closely with skipjack tuna than with *Thunnus albacares* (yellowfin tuna; Spear *et al.* 2007, Hebshi *et al.* 2008). However, in other areas in the Pacific Ocean, they have been observed feeding also with yellowfin tuna (Acevedo and Wursig 1991, Ballance and Pitman 1999). Tuna and other top predators in marine ecosystems have been the target of major commercial fisheries in the Pacific Ocean since the 1950s, and some stocks have been severely overexploited (Harrison 1990, Tuck & Bulman 2003) while others may be increasing and expanding their ranges because of anthropogenic climate change (Loukos *et al.* 2003, Polovina *et al.* 2011). These climatic and anthropogenic impacts may have major consequences for birds such as White Terns that feed in association with subsurface predators (Ballance & Pitman 1999, Spear *et al.* 2007).

This study establishes a baseline for stable isotopes in the White Tern *Gygis alba*. We compare nitrogen and carbon isotope variation within and among feather types (primaries and breast feather) of this species from the Hawaiian Archipelago. Because the feeding strategy of this seabird involves subsurface predators such as tuna, we compared the isotopic signatures of the White Tern with those of the yellowfin and skipjack tuna occurring in the area where tern tissues were sampled. This isotopic baseline of White Terns from the Hawaiian Archipelago will provide the necessary information to evaluate potential changes in dietary habits resulting from the continual decline of fisheries and future climate change.

STUDY AREA AND METHODS

Nine White Tern corpses were salvaged (Table 1; n = 2, Oahu; n = 3, French Frigate Shoals; n = 4, Midway Atoll) during September–

November 2006 and breast feathers, base and tips of primaries 1, 4 and 7 (primary 1 = innermost), were taken. An additional 12 molted primary feathers were collected from under nesting trees on Oahu and five from Midway Atoll for tip and base (intrafeather) comparison.

Feathers were cleaned of any external debris in an ultrasonic bath with de-ionized water, and lipids were removed using a chloroform methanol 2:1 wash (Cherel *et al.* 2005). Samples were then dried for 24–48 h at 50°C at least 24 h prior to isotopic analysis. Approximately 3 mm each from the extreme base and tip of feathers (vanes only) were used for analysis. No samples were homogenized as there was enough mass for each sample analysis. Carbon and nitrogen isotope compositions of samples (0.3–0.5 mg) were determined using an in-line carbon-nitrogen analyzer coupled with an isotope ratio mass spectrometer (Finnigan ConFlo II/Delta-Plus). Isotope values were reported in standard delta-notation relative to an international standard. Standards were V-PDB and atmospheric N₂ for carbon and nitrogen, respectively. A glycine standard was used to ensure accuracy of all isotope measurements. Several samples were measured in duplicate or triplicate, and the analytical error associated with these measurements was typically < 0.2%. Statistical analysis was done in MiniTab13.

RESULTS

There were no significant differences in nitrogen (paired *t*-test, *t* = 1.56, 22 df, *P* = 0.134) and carbon (paired *t*-test, *t* = 1.48, 22 df, *P* = 0.152) isotope values between the tips and bases of primary feathers. There was no significant difference in nitrogen values among primaries (tips only) either (Friedman test; $\chi^2_{25} = 1.37$, *P* = 0.504). However, there was a significant difference in carbon isotope values among primaries (Friedman test; $\chi^2_{25} = 8.40$, *P* = 0.015). Additionally, there was significant variation in nitrogen (paired *t*-test, *t* = 3.03, 7 df, *P* = 0.019) between primary

TABLE 1
Nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) values in a range of feathers and tissues from nine White Terns in the Hawaiian Archipelago

Tissue	1 (Oahu)	2 (Oahu)	3 (FFS)	4a (FFS)	5 (FFS)	6 (Midway)	7a (Midway)	8a (Midway)	9a (Midway)	Mean	SD
Nitrogen											
Base	9.94	10.72	10.73	9.20	9.69	10.01	16.87	15.11	11.58	11.54	2.65
Tip	8.71	9.67	9.56	8.37	9.96	10.22	16.01	16.13	10.73	11.04	2.94
Primary 1 (tip)	10.00	10.65	10.03	—	10.34	9.88	—	—	—	10.18	0.31
Primary 4 (tip)	10.00	10.93	9.89	—	9.80	9.82	—	—	—	10.09	0.48
Primary 7 (tip)	9.65	10.82	9.67	—	9.83	10.08	—	—	—	10.01	0.49
Breast feather	8.00	9.62	9.32	8.38	9.70	10.08	16.24	14.62	10.14	10.09	0.09
Carbon											
Base	-14.23	-14.96	-14.03	-16.18	-14.90	-15.14	-14.48	-14.97	-15.17	-14.90	0.63
Tip	-14.61	-14.61	-14.52	-15.95	-15.28	-15.50	-14.45	-14.82	-16.16	-15.10	0.65
Primary 1 (tip)	-14.75	-14.41	-14.54	—	-14.29	-15.33	—	—	—	-14.66	0.41
Primary 4 (tip)	-15.26	-14.43	-14.64	—	-12.58	-15.42	—	—	—	-14.47	1.13
Primary 7 (tip)	-14.30	-14.36	-14.32	—	-11.05	-15.24	—	—	—	-13.85	1.62
Breast feather	-13.98	-14.57	-14.53	-15.99	-14.96	-15.43	-14.23	-14.57	-16.08	-14.33	0.42

^aSeveral primaries were missing from these salvaged birds and were not used for comparison of primaries.
FFS = French Frigate Shoals.

(values averaged among primaries) and breast feathers. However, the differences between these two feather types did not exceed 1.8‰, with the primaries having a consistently higher value. There was no significant variation in carbon isotope values between the two feather types (paired *t*-test, $t = -0.22$, 7 df, $P = 0.836$).

DISCUSSION

Stable isotopes have been used as an indirect measure of feeding dynamics of seabird populations, providing information on diet and location of feeding areas; however, there are assumptions and caveats to the use of this method (Bond & Jones 2009). Different feather types may provide a representation of an individual's diet over different time frames. Several isotopic studies of seabirds that assessed differences among feather types have focused primarily on migratory species to determine seasonal dietary shifts and migratory patterns (e.g. Wiley *et al.* 2010, Militão *et al.* 2012). On that basis, it is crucial to assess whether feathers have different isotopic compositions to determine whether a particular feather type can represent the animal as a whole to minimize invasive sampling. For example, Jaeger *et al.* (2009) indicated that body feathers were no different than flight feathers in the Wandering Albatross *Diomedea exulans*, and therefore body feathers should be sampled, since collecting non-molted flight feathers impairs the bird's flying ability.

In general, oceanic tropical marine systems are characterized by low productivity and little seasonal variation (Longhurst & Pauly 1987), which could lead to little variation in the diets of marine predators throughout the year. The White Tern is considered non-migratory, and individuals can be found breeding at any time of the year (Niethammer & Patrick 1998). The lack of isotope variation in the primary feathers analyzed, despite full replacement occurring over several months, supports the idea that the White Tern feeds in similar food webs in the same area year-round. Additionally, White Tern breast and primary feathers had similar isotopic ratios, despite the time scale at which they are molted, so, at least in this species, both feather types can serve as an accurate representation of the isotopic measurements of individual birds. Therefore, using molted feathers for this species provides a less invasive source for isotopic analysis than collecting breast feathers and flight feathers from the live bird.

Assuming a trophic shift at 3.0‰, White Tern $\delta^{15}\text{N}$ values fell within the same trophic level as those of juvenile and adult yellowfin tuna occurring around the Hawaiian Islands (Table 1; Graham *et al.* 2007). Nitrogen isotope values of white muscle tissue from tuna < 45.0 cm standard length (SL) were reported at $6.7 \pm 0.6\text{‰}$ while those of tuna ≥ 45.0 cm SL were $10.2 \pm 1.8\text{‰}$. Carbon isotope values of tuna < 45.0 cm was reported at $-17.3 \pm 0.5\text{‰}$ and those ≥ 45.0 cm at $17.8 \pm 0.8\text{‰}$ (Graham *et al.* 2007). The isotopic signature of adult yellowfin tuna was significantly higher than that of the juveniles, probably because adults had bigger gape sizes and were faster, so they were able to pursue and consume larger prey. Although White Terns feed more closely with skipjack tuna than yellowfin tuna within the Hawaiian Archipelago (e.g. Spear *et al.* 2007, Hebshi *et al.* 2008), it has been shown that skipjack and yellowfin tuna feed within the same trophic level throughout the Pacific Ocean (Rau 1981, Cheral *et al.* 2008, Bugoni *et al.* 2010). In Hawai'i, Hobson *et al.* (2007) reported carbon isotope values of yellowfin and skipjack tuna at -16.9 and -16.6, respectively, and nitrogen values at 10.0 and 9.8, respectively.

To our knowledge, there are no isotopic studies regarding terns and noddies (Sterninae) within the Hawaiian Archipelago, and this study can serve as a comparison for future research on this group. However, in comparison with Hawaiian Procellariiformes, White Terns feed at the same trophic level as adult Bulwer's petrels and as adult and chicks of Christmas shearwaters (Bond *et al.* 2010, Spear *et al.* 2007) but forage closer to shore. Recently, based on diet and observation, it has been proposed that Newell's Shearwaters *Puffinus newelli* in Hawaiian waters may also be part of this assemblage feeding in association with yellowfin tuna (Ainley *et al.* 2014).

Changes in tuna populations because of natural or anthropogenic climate change would affect the frequency of opportunities for White Terns to forage on the prey that predatory fish drive to the surface (Spear *et al.* 2007). Regular monitoring of seabird diets would help identify changes in the abundance and distribution of tuna and other predatory fish. Use of molted feathers would allow routine sampling at a scale and frequency not always possible through other methods.

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REFERENCES

- ACEVEDO, A. & WURSIG, B. 1991. Preliminary observations on bottlenose dolphins, *Tursiops truncatus*, at Isla del Coco, Costa Rica. *Aquatic Mammals* 17: 148–151.
- AINLEY, D.G., WALKER, W.A., SPENCER, G.C. & HOLMES, N.D. 2014. The prey of Newell's Shearwater *Puffinus newelli* in Hawaiian waters. *Marine Ornithology* 42: 62–64.
- ASHMOLE, N.P. & ASHMOLE, M.J. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Museum of Natural History, Yale University, Bulletin 24. Peabody Museum of Natural History, New Haven, Connecticut, USA.
- AU, D.W. & PITMAN, R.L. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *Condor* 88: 304–317.
- BALLANCE, L.T. & PITMAN, R.L. 1999. Foraging ecology of tropical seabirds. In: Adams N.J. & Slotow, R.H. (Eds.) Proceedings of the 22nd International Ornithological Congress, Durban. Johannesburg, South Africa: Birdlife South Africa.

- BEARHOP, S., WALDRON, S., VOTIER, S.C. & FURNESS, R.W. 2002. Factors influencing assimilation and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* 75: 451–458.
- BEARHOP, S., FURNESS, R.W., HILTON, G.M., VOTIER, S.C. & WALDRON, S. 2003. A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. *Functional Ecology* 17: 270–275.
- BOND, A.L. & DIAMOND, A.W. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecological Applications* 21: 1017–1023.
- BOND, A.L., MCCLELLAND, G.T., JONES, I.L., LAVERS, J.L. & KYSER, T.K. 2010. Stable isotopes confirm community patterns in foraging among Hawaiian Procellariiformes. *Waterbirds* 33: 50–58.
- BOND, A.L. & JONES, I.L. 2009. A practical introduction to stable-isotope analysis for seabird biologists: Approaches, cautions, and caveats. *Marine Ornithology* 37: 183–188.
- BUGONI, L., MCGILL, R. A. & FURNESS, R.W. 2010. The importance of pelagic longline fishery discards for a seabird community determined through stable isotope analysis. *Journal of Experimental Marine Biology and Ecology* 391: 190–200.
- CATRY, T., RAMOS, J.A., LE CORRE, M., KOJADINOVIC, J. & BUSTAMANTE, P. 2008. The role of stable isotopes and mercury concentrations to describe seabird foraging ecology in tropical environments. *Marine Biology* 155: 637–647.
- CHEREL, Y., CORRE, M.L., JAQUEMET, S., MENARD, F., RICHARD, P. & WEIMERSKIRCH, H. 2008. Resource partitioning within a tropical seabird community: new information from stable isotopes. *Marine Ecology Progress Series* 366: 281–291.
- CHEREL, Y., HOBSON, K.A. & HASSANI, S. 2005. Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiological and Biochemical Zoology* 78.1: 106–115.
- DENIRO, M.J. & EPSTEIN, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495–506.
- DENIRO, M.J. & EPSTEIN, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45: 341–351.
- DORWARD, D.F. 1963. The Fairy Tern (*Gygis alba*) on Ascension Island. *Ibis* 103: 365–378.
- DUFFY, D.C. & JACKSON, S. 1986. Diet studies of seabird: a review of methods. *Colonial Waterbirds* 9: 1–17.
- FRY, B. 2006. *Stable Isotope Ecology*. New York, NY: Springer.
- GRAHAM, B.S., GRUBBS, D., HOLLAND, K. & POPP, B.N. 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Marine Biology* 150: 1432–1793.
- HARAMIS, G.M., JORDE, D.G., MACKO, S.A. & WALKER, J.L. 2001. Stable isotope analysis of canvasback winter diet in Upper Chesapeake Bay. *Auk* 118: 1008–1017.
- HARRISON, C.S. 1990. *Seabirds of Hawaii: natural history and conservation*. Ithaca, NY: Cornell University Press.
- HARRISON, C.S. & SEKI, M.P. 1987. Trophic relationships among tropical seabirds at the Hawaiian Islands. In: Croxall, J.P. (Ed.) *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge: Cambridge University Press. pp 305–326.
- HARRISON, C.S., HIDA, T.S. & SEKI, M.P. 1983. Hawaiian seabird feeding ecology. *Wildlife Monographs* 85: 1–71.
- HEBSHI, A.J., DUFFY, D.C. & HYRENBACH, K.D. 2008. Associations between seabirds and subsurface predators around Oahu, Hawaii. *Aquatic Biology* 4: 89–98.
- HOBSON, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120: 314–326.
- HOBSON, K.A. & CLARK, R.G. 1992. Assessing avian diets using stable isotopes I: turnover of I3C in tissues. *Condor* 94: 181–188.
- HOBSON, K.A., PIATT, J.F. & PITOCHELLI, J. 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63: 786–798.
- HOBSON, K.A., SMITH, R.J.F. & SORENSEN, P. 2007. Applications of stable isotope analysis to tracing nutrient sources to Hawaiian gobioid fishes and other stream organisms. In Evenhuis, N.L., & Fitzsimons, J.M (Eds.) *Biology of Hawaiian streams and estuaries. Bishop Museum Bulletin in Cultural and Environmental Studies* 3: 99–111.
- JAEGER, A., BLANCHARD, P., RICHARD, P. & CHEREL, Y. 2009. Using carbon and nitrogen isotopic values of body feathers to infer inter-and intra-individual variations of seabird feeding ecology during moult. *Marine Biology* 156: 1233–1240.
- JAQUEMET, S., LE CORRE, M. & WEIMERSKIRCH, H. 2004. Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FADs). *Marine Ecology Progress Series* 268: 281–292.
- JOHANNES, R.E. 1981. *Words of the lagoon: fishing and marine lore in the Palau district of Micronesia*. Berkeley, CA: University of California Press.
- LOUKOS, H., MONFRAY, P., BOPP, L. & LEHODEY, P. 2003. Potential changes in skipjack (*Katsuwonus pelamis*) habitat from a global warming scenario: modeling approach and preliminary results. *Fisheries Oceanography* 12: 474–482.
- MILITÃO, T., BOURGEOIS, K., ROSCALES, J.L. & GONZÁLEZ-SOLÍS, J. 2013. Individual migratory patterns of two threatened seabirds revealed using stable isotope and geolocation analyses. *Diversity and Distributions* 19: 317–329.
- MONTICELLI, D., RAMOS, J.A., TAVARES, P.C., BATAILLE, B., LEPOINT, G. & DEVILLERS, P. 2008. Diet and foraging ecology of Roseate Terns and Lesser Noddies Breeding sympatrically on Aride Island, Seychelles. *Waterbirds* 31: 231–240.
- NIETHHAMMER, K.R. & PATRICK-CASTILAW, L.B. 1998. White Tern (*Gygis alba*). In: Poole, A. & Gill, F. (Eds.) *The Birds of North America*, No. 371. Philadelphia, PA: The Birds of North America, Inc.
- PEARSON, S.F., LEVEY, D.J., GREENBERG, C.H. & MARTINEZ DEL RIO, C. 2003. Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Oecologia* 135: 516–523.
- POLOVINA, J.J., DUNNE, J.P., WOODWORTH, P.A. & HOWELL, E.A. 2011. Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. *ICES Journal of Marine Science* 68: 986–995.
- RAMOS, J.A., MAUL, A.M., AYRTON, V. *et al.* 2002. Influence of local and large-scale weather events and timing of breeding on tropical roseate tern reproductive parameters. *Marine Ecology Progress Series* 243: 271–279.
- RAU, G.H. 1982. The relationship between trophic level and stable isotopes of carbon and nitrogen. In: Bascom, W. (Ed.) *Coastal water research project biennial report for the years 1981–1982*. Long Beach: South California Water Research Project. pp. 143–148.
- RUBENSTEIN, D.R. & HOBSON, K.A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution* 19: 256–263.

- SMITH, A.D., DONOHOUE, K. & DUFTY A.M., JR. 2008. Intrafeather and intraindividual variation in the stable-hydrogen isotope (δD) content of raptor feathers. *Condor* 110: 500–506.
- SPEAR, L.B., AINLEY, D.G. & WALKER, W.A. 2007. Trophic relationships of seabirds in the eastern Pacific Ocean. *Studies in Avian Biology*, No. 35.
- THOMPSON, D.G. & FURNESS, R.W. 1995. Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in Northern Fulmars. *Auk* 112: 493–498.
- THOMPSON, D.R., LILLIENDAHL, K., SOLMUNDSSON, J., FURNESS, R.W., WALDRON, S. & PHILLIPS, R.A. 1999. Trophic relationships among six species of Icelandic seabirds as determined through stable isotope analysis. *Condor* 101: 898–903.
- TIESZEN, L.L., BOUTTON, T.W., TESDAHL, K.G. & SLADE, N.A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. *Oecologia* 57: 32–37.
- TUCK, G.N., POLACHECK, T. & BULMAN, C.M. 2003. Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biological Conservation* 114: 1–27.
- VANDERKLIFT, M.A. & PONSARD, S. 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. *Oecologia* 136: 169–182.
- WILEY, A.E., OSTROM, P.H., STRICKER, C.A., JAMES, H.F. & GANDHI, H. 2010. Isotopic characterization of flight feathers in two pelagic seabirds: sampling strategies for ecological studies. *Condor* 112: 337–346.
- YOUNG, H.S., MCCAULEY, D.J., DIRZO, R., DUNBAR, R.B., & SHAFFER, S.A. 2010. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. *Marine Ecology Progress Series* 416: 285–294.
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