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From ecologically equivalent individuals to contrasting colonies: quantifying isotopic niche and individual foraging specialization in an endangered oceanic seabird

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Abstract

Quantifying individual specialization and other forms of intraspecific ecological diversity can reveal variation that is critical for evolutionary or behavioral adaption of a species to changing environments. Here, the isotopic niche and degree of individual foraging specialization were quantified for an endangered seabird, the Hawaiian petrel (*Pterodroma sandwichensis*), nesting on Lāna'i (20°48′N, 156°52′W) and 72 km away on Haleakalā, Maui (20°42′N, 156°15′W; 20° 43′N, 156°14′W) between 2006 and 2011. Stable isotope values (δ^{13}C and δ^{15}N) from sequentially grown flight feathers provided time-series data that reflect the foraging habitat (relative latitude, nutrient regime of foraging location) and diet (trophic level) of individual birds across the period of molt. The two colonies differed in mean δ^{15}N and δ^{13}C throughout the period of molt, total nitrogen isotopic niche width, and extent of individual specialization with regard to δ^{15}N. It is likely that petrels from Lāna'i and Haleakalā use different feeding locations during the non-breeding season, when they are no longer tied to closely spaced breeding colonies. The loss of either colony could result in a substantial, long-term reduction in ecological diversity of the species (and perhaps, in adaptability). In contrast, comparisons of measured versus null specialization indices strongly suggest that both Lāna'i and Haleakalā populations consist of individual generalists. Individual generalization with regard to foraging habitat and diet is here predicted to be common among tropical and subtropical oceanic seabirds. Such generalization could facilitate rapid, population-level responses of seabird species to marine environmental change via individual plasticity.

Introduction

Individuals within a population may not be ecological equivalents. Instead, individuals can specialize on a subset of the resources used by their parent population, sex, or age class (Bolnick et al. 2003). The presence of such individual specialization is taxonomically widespread and can influence

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both the ecology and evolution of populations (Bolnick et al. 2003; Araújo et al. 2011; Bolnick et al. 2011). For example, individual specialists compete with fewer conspecifics than do individual generalists, and individual specialization may lead to frequency-dependent competition and phenotypic diversification (Bolnick et al. 2003).

Critically, the degree of individual specialization affects how populations respond to anthropogenic disturbance. Individual generalists tend to be behaviorally plastic and may alter their resource use in response to a changing environment, thus promoting a population-level response within a single generation. In contrast, long-term individual specialists might be less flexible and populations composed of specialists, more likely to adapt to environmental change via natural selection (Bolnick et al. 2003). Furthermore, individual specialists may be sensitive to the loss of preferred resources (Phillips et al. 2017), and prolonged specialization may require stable environments with reliably abundant resources (Svanbäck and Bolnick 2005; Ceia and Ramos 2015). Understanding the distribution of individual specialization and further exploring its relationship to environmental change could, therefore, provide predictive power about population vulnerability and adaptability, useful for the conservation of dwindling species in rapidly changing ecosystems.

Knowledge of individual specialization can inform conservation efforts by describing the distribution of intraspecific diversity. While preserving intraspecific genetic diversity is often a goal of conservation management strategies, there is also value in targeted preservation of intraspecific ecological diversity, with the aim of maintaining adaptability with regard to traits affected by changing environments (Crandall et al. 2000; Bolnick et al. 2003; González-Suárez and Revilla 2013). Describing intraspecific foraging diversity at various levels of organization—within individuals, between individuals, and between colonies or populations—is central to understanding and preserving ecological diversity.

Considerable conservation effort is focused on seabirds: a group that claims many threatened species and is a paradigm for the study of foraging niche dynamics. Globally, monitored populations of seabirds have declined by 70% between 1950 and 2010, suffering from depredation by invasive mammalian predators on land and competition from industrial fisheries at sea, among other factors (Paleczny et al. 2015). As changing oceanographic conditions and fishery collapses continue to alter seabirds' foraging environments and prey availability, numerous studies have documented consistency in individual seabirds' foraging locations, foraging strategies, and diets (Ceia and Ramos 2015; Phillips et al. 2017). However, comparatively few studies have quantified the degree of individual foraging specialization in seabird populations, and the extent of individual specialization within this group remains unknown (Woo et al. 2008; Provencher et al. 2013; Ceia and Ramos 2015; Phillips et al. 2017; Bonnet-Lebrun et al. 2018). Quantifying individual foraging specialization is particularly challenging for the most threatened group of seabirds, those with pelagic (open water) and oceanic (beyond the continental shelves) foraging habits (Croxall et al. 2012). Such quantifications require repeated measures of foraging (e.g., Jaeger et al. 2010) from birds that can range hundreds to thousands of kilometers from land.

Here, we quantify the degree of individual foraging specialization in an endangered oceanic seabird, the Hawaiian petrel (*Pterodroma sandwichensis*). While Hawaiian petrels breed exclusively on the main Hawaiian Islands, their foraging niche is broad (Fig. 1). Their at-sea range extends from the equator to near the Aleutian Islands and over a 45-degree span in longitude (Spear et al. 1995; Adams and Flora 2009; VanZandt 2012). Hawaiian petrel diet is poorly characterized, but the species is known to feed on lantern fish (Myctophidae), flying fish (Exocoetidae), ommastrephid squid (Ommastrephidae), and various other pelagic prey during solitary nocturnal flights, and diurnally, in association with subsurface predators (Pitman 1982; Simons 1985; Ostrom et al. 2017).

As in previous studies, we use stable carbon and nitrogen isotope ratios (reported as δ^{13}C and δ^{15}N values, respectively) to understand the Hawaiian petrel's foraging niche (Wiley et al. 2012, 2013; Ostrom et al. 2017; Morra et al. 2018). Because of the inverse relationship between latitude and the δ^{13}C of phytoplankton and consumers in the North Pacific, we expect Hawaiian petrel δ^{13}C data to primarily reflect foraging latitude (Goericke and Fry 1994; Wiley et al. 2012). δ^{15}N of bulk avian tissues generally increases by ca. 2–4‰ with trophic level (Hobson and Clark 1992; Hobson and Bairlein 2003; Kelly 2000; Wiley et al. 2017). However, there is also pronounced spatial variation in the δ^{15}N of nitrogen supplied to the base of Hawaiian petrel food webs (i.e., nitrate or ammonium). This variation derives from heterogeneity in the relative importance of nitrogen fixation, nitrification, denitrification, and the uptake of nitrate by phytoplankton on δ^{15}N values (Altabet and Francois 1994; Farrell et al. 1995). For example, there is a steep spatial gradient in δ^{15}N to the SE of the Hawaiian Islands (roughly 5–7‰; 0–15°N, 130–155°W), within the Hawaiian petrel's non-breeding range (Fig. 1b; Altabet and Francois 1994; Farrell et al. 1995; Graham et al. 2010; Wiley et al. 2012, 2013; Morra et al. 2019). This gradient likely results from the degree to which denitrification and phytoplankton uptake elevate the δ^{15}N of nitrate, the primary nitrogen source for phytoplankton in the region. Because the δ^{15}N of nutrients is transferred up the food web, δ^{15}N of marine consumers vary as a function of the δ^{15}N at the base of their food webs and show the isotopic gradient to the SE of the Hawaiian Islands

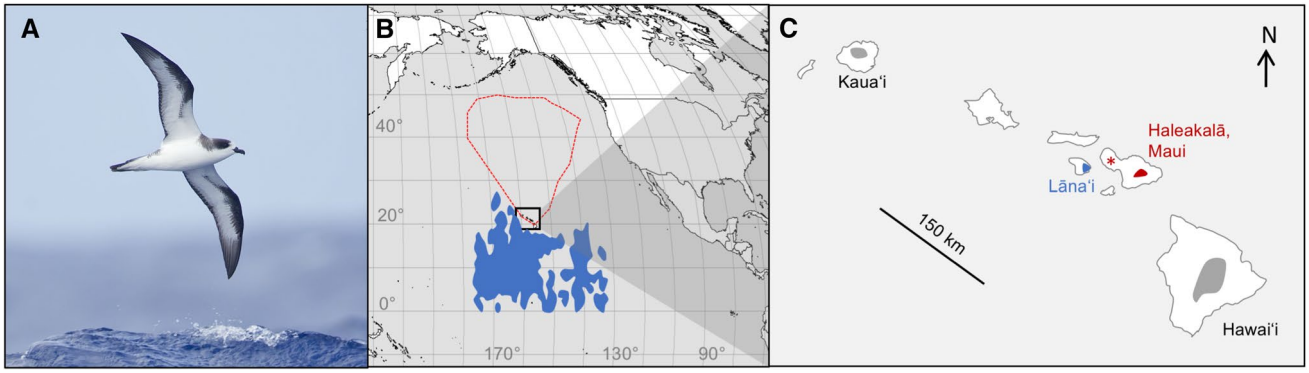

Fig. 1 A Hawaiian petrel in flight (**a**) and depictions of the at-sea (**b**) and breeding (**c**) distribution of the species. In **b**, the stippled red line indicates a single Hawaiian petrel foraging trip during the breeding season (Adams and Flora 2009), representative of the region used by 30 breeding Hawaiian petrels from across the Hawaiian Islands (J. Adams et al. unpublished data, J. Adams personal comment). The blue silhouette is the 95% utilization contour of petrels from the island of Lana'i, tracked during the non-breeding season (VanZandt 2012). Together, these regions represent the major areas where Hawaiian petrels are known to spend time at sea. Breeding distribution in C is modified from Simons and Hodges (1998); the asterisk represents a recently discovered breeding colony on West Maui. Photograph courtesy of Geoffrey Jones

(Graham et al. 2010; Wiley et al. 2012; Ostrom et al. 2017; Morra et al. 2018). The δ^{15}N of bulk petrel tissues therefore reflects both trophic level, a dietary trait, and the nutrient regime of foraging location (Wiley et al. 2012). While animals can have similar isotope values, but dissimilar foraging habits, petrels with distinct δ^{13}C or δ^{15}N values must differ in either foraging location or trophic level, or some combination thereof. To further clarify the influence of these two factors on bulk tissue δ^{15}N, we rely on previously collected amino acid-specific δ^{15}N data and tracking of Hawaiian petrels (Adams and Flora 2009; VanZandt 2012; Ostrom et al. 2017; Morra et al. 2019).

We previously developed millennial-scale stable isotope chronologies for multiple Hawaiian petrel populations. Amino acid-specific δ^{15}N chronologies supported our interpretations of bulk nitrogen isotope data and showed clear evidence of species-wide trophic decline over the past ca. 150 years: a finding that could be explained by Hawaiian petrels shifting their diet after the onset of industrialized fishing in the North Pacific Ocean (Wiley et al. 2013; Ostrom et al. 2017). We also found evidence that some Hawaiian petrel populations use distinct foraging habitats at the beginning and middle of the remige molt and of minimal gene flow between populations breeding on the islands of Lāna'i, Hawai'i, Maui, and Kaua'i (Welch et al. 2012; Wiley et al. 2012, 2013; Morra et al. 2018). Here, we collect stable isotope data from sequentially grown feathers to produce foraging chronologies for individuals (as in Quillfeldt et al. 2010; Cherel et al. 2016), and to quantify the degree of individual foraging specialization. Our primary goals are to compare individual specialization in two genetically distinct populations of Hawaiian petrel (those nesting on Haleakalā on the island of Maui, and those nesting on Lāna'i), and to examine foraging diversity within this endangered species. More broadly, we aim to shed light on the relationship between individual foraging specialization and population-level responses to shifting foraging environment, and to enable conservation plans to consider how best to preserve the Hawaiian petrel's potential to adapt to future changes in its food webs.

Materials and methods

Sample acquisition, molt, and feather sampling protocols

We acquired stable isotope data from after hatch-year (AHY) Hawaiian petrel remiges; in all cases, these petrels had gone through at least one post-fledging molt. Feathers were removed from salvaged carcasses recovered in Haleakalā National Park, Maui (henceforward, Haleakalā; 20°42′N, 156°15′W; 20° 43′N, 156°14′W), and on the island of Lāna'i (20°48′N, 156°52′W) between 2006 and 2011 (see Online Resource 1, ESM Table 1). Most birds in our study were killed by cats (*Felis catus*) or mongooses (*Herpestes javanicus*), presumably while attending their nests. Isotope data from breeding Hawaiian petrel remiges are expected to represent the 3–6 months between breeding attempts, consistent with photographic evidence from the species and the observation that most *Pterodroma* petrels molt their flight feathers during the non-breeding season (Simons 1985; Warham 1996; Pyle et al. 2011). Our examination of Hawaiian petrel carcasses and study skins at the National Museum of Natural History (NMNH) confirmed that among 56 AHY birds, the only individual with active remige molt died in

January, during the non-breeding season (catalog number USNM 643234). All petrels included in our study died during the breeding season and did not show signs of remige molt. Notably, Hawaiian petrels from Haleakalā are approximately 1 month advanced in their breeding schedule relative to petrels on Lāna‘i (Simons 1985; J. Penniman and F. Duvall, personal observations). Remige isotope data from these two colonies therefore represent overlapping, but not identical time periods.

As in other *Pterodroma* species, Hawaiian petrels are assumed to undergo a complete annual molt and to grow their primaries in descendent sequence, typically starting at P1 and ending with P10 (where P1 is the most proximal primary; Fig. 2) (Warham 1996; Pyle 2008). Secondary molt initiates following the onset of primary molt, proceeding from several loci: from S1 (proceeding proximally), from S5 (proceeding proximally), and from the innermost secondary (proceeding distally), such that S10 is among the very last feathers to be molted (Pyle 2008). Among NMNH specimens, wear on AHY Hawaiian petrel remiges is consistent with these expected molt sequences (P. Pyle, personal communication). Our examination of AHY Hawaiian petrel remiges shows that growth bars vary from roughly 3–4 mm in width. This suggests that vanes of P1 and of all secondaries (ca. 7 cm long) take approximately 18–23 days to grow (assuming formation of one growth bar day^{-1}) or 9–12 days to grow (assuming formation of two growth bars day^{-1}, as in some albatross (Langston and Rohwer 1996)).

To examine variation in the use of foraging resources, we analyzed isotope values from sequentially grown feathers. Because individual specialization indices are highly dependent on time scale, we employed two feather sampling schemes where individual samples represent foraging over different lengths of time. First, we sampled the bases of P1–P10 from 42 individuals (18 from Haleakalā and 24 from Lāna‘i). In 16 cases where one primary was missing, we collected isotope data from the nine available primaries. These samples represent a 9- or 10-point time series, where each individual sample reflects feather growth over a 2–3 day period (Fig. 2a: ten-feather protocol). Specifically, we sampled white barbs from the proximal base of the widest vane, avoiding the most plumulaceous barbs. The second feather sampling scheme was employed for a subset of 12 petrels from Lāna‘i: we sampled P1, S1, S5, and S10 to produce a 4-point time series, with each individual sample representing between 9 and 23 days of feather growth

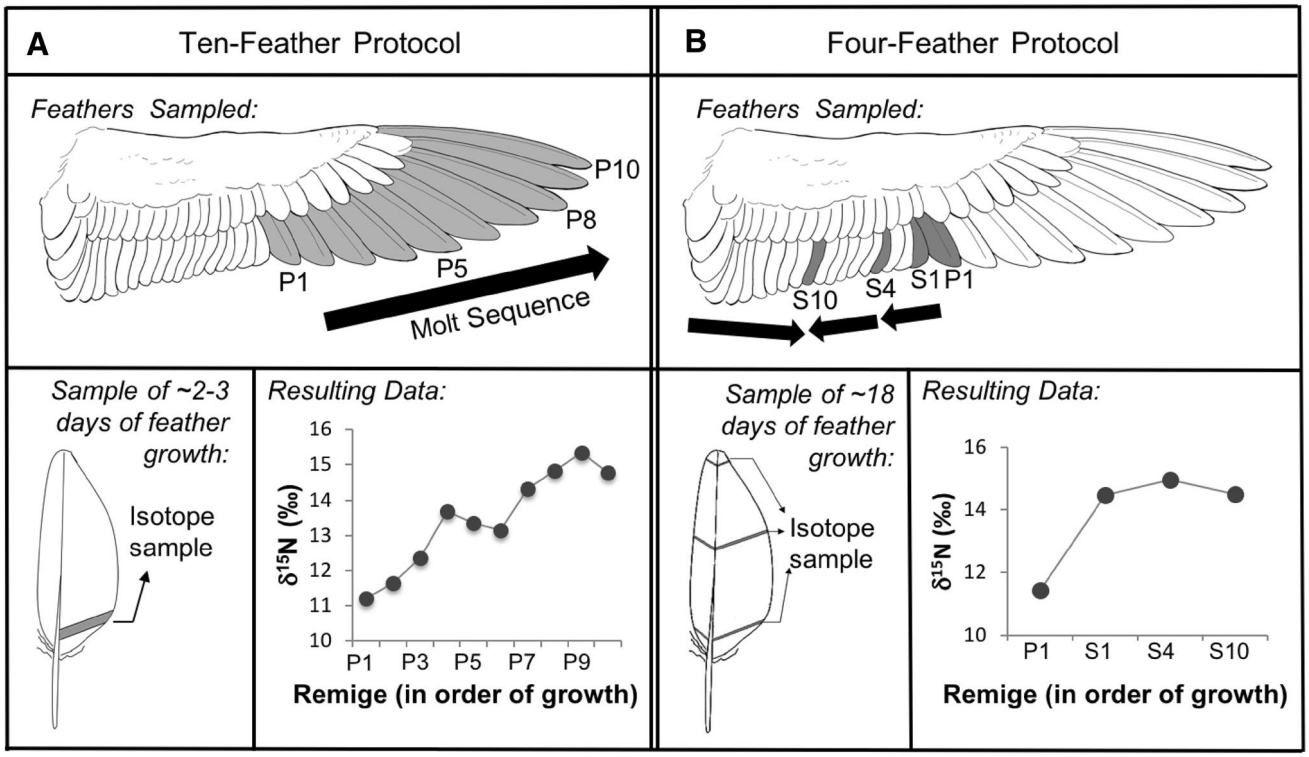

Fig. 2 Feather sampling protocols employed in this study: sampling of ten primary bases (**a**) and sampling of barbs along four primary and secondary feather vanes (**b**). In **b**, barbs are sampled strategically within each feather, so as to estimate the average isotopic composition of the entire feather vanes with minimal destruction (Wiley et al. 2010; Morra et al. 2018). In both panels, black arrows denote generalized *Pterodroma* molt sequence (see text). Example isotope data are from individual DP.35.299. The period of feather growth represented by isotope samples was estimated based on feather growth bar width in the Hawaiian petrel (*Pterodroma sandwichensis*) and the assumption that two growth bars are formed each day (see text)

(Fig. 2b: four-feather protocol). Specifically, we used the 'barb' sampling protocol developed for Hawaiian petrel P1 (as described in Wiley et al. 2010), where barbs are sampled from three locations along the feather vanes and weighted so as to represent the average isotopic composition of the entire feather vanes. In both sampling protocols, feathers were sampled from one wing only.

Finally, we tested our assumption that isotopic variation among Hawaiian petrel remiges reflects change in resource use through time. We employed the four-feather protocol on four hatch-year Hawaiian petrels, salvaged in 2007 and 2009 on the island of Kaua'i. Because hatch-year petrels grow their remiges synchronously (while in the nesting burrow), any isotopic variation among their similarly sized remiges should be a function of metabolic differences between feathers or methodological error, rather than variation in food source through time.

Stable isotope analyses

Barbs sampled for stable isotope analysis were first washed in Chloroform: Methanol 87:13, rinsed with DI water, and dried for approximately 24 h at room temperature. Barbs were next cut into ca. 5 mm lengths with a scalpel and homogenized with forceps. The majority of each feather section (ca. 1 mg) was then packed into a tin cup and analyzed for carbon and nitrogen isotope values using an elemental analyzer (EA) interfaced to a stable isotope mass spectrometer (IRMS). The majority of samples were analyzed at the Smithsonian Museum Conservation Institute (MCI) Stable Isotope Mass Spectrometry Laboratory on a Costech ECS 4010 EA interfaced to a Thermo Scientific Delta V Advantage IRMS via a Conflo IV interface. Six additional samples were analyzed on a Eurovector EA interfaced to an Isoprime 100 IRMS at Michigan State University (MSU).

Stable isotope values are reported in δ-notation, expressed in per mil (‰) according to the following equation: $\delta X = ([\text{Rsample/Rstandard}]-1) \times 1000$, where X is ^{13}C or ^{15}N, and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{15}N$. Rstandard is V-PDB and Air for $\delta^{13}C$ and $\delta^{15}N$, respectively. We analyzed laboratory standards between every 10 unknowns, with a precision of $< \pm 0.2$‰ (1σ) for both $\delta^{13}C$ and $\delta^{15}N$. Triplicate analyses of in-house MSU standards (lipid-extracted muscle powder from *Oncorhynchus kisutch* and *Steno bredanensis*) differed by no more than 0.2‰ between MCI and MSU laboratories: a difference equivalent to or less than analytical error (see Online Resource 1 for all isotope data).

Statistical Analyses

Roughgarden (1972) proposed that a population's niche, or total niche width (TNW) can be broken into the within-individual and between-individual components (WIC and BIC, respectively), such that WIC + BIC = TNW. BIC can be viewed as the variance in resource use between individuals, and WIC, the variance in resource use within an individual. The ratio WIC/TNW is widely used to characterize the degree of individual specialization or generalization (Bolnick et al. 2002, 2003). WIC/TNW values can theoretically vary between 0 and 1, reflecting the proportion of resources used by an individual relative to its parent population. Stable isotope studies have amended this approach by defining the total isotopic niche width of a population, or TINW, and using isotopic variance to describe individual resource specialization in terms of WIC/TINW (Newsome et al. 2009).

Parameters of ecological interest for populations are determined by processes that occur at the individual level. For this reason, we developed a novel hierarchical approach to examine foraging variation across both individuals and populations. The hierarchical model consists of two levels: the individual sub-model and the population sub-model. First, a multivariate normal distribution was fit to the data using a linear predictor $\hat{y}_{(k,i,j)}$ consisting of estimated carbon and nitrogen isotope values indexed by population (k), individual bird (i) and feather identity (j) with covariance matrix assumed consistent across individuals within (but not between) each population ($\Sigma_{\text{WIC}(k)}$). The linear predictor is determined in the individual sub-model by estimating an individual mean vector for the isotope values of each individual ($\alpha 0_{(k,i)}$) and the linear influence of which feather is being sampled estimated for each individual in the dataset ($\alpha 1_{(k,i)} \times \text{feather}_{(j)}$). Feathers were assigned ordinal values from one to ten based on progression of molt, which were then standardized for computational expediency. The population-level model is hierarchical using the estimated individual level parameters of mean ($\alpha 0_{(k,i)}$) and slope with respect to feather ($\alpha 1_{(k,i)}$) to estimate population-level parameters of population mean vector (consisting of $\delta^{13}C$ and $\delta^{15}N$ means) ($\mu_{\text{pop}(k)}$, $\Sigma_{\text{BIC}(k)}$).

Niche estimates (WIC, BIC, and TINW) were calculated in the same method as R^2 statistics (also similar to Newsome et al. 2009). To understand factors influencing within-individual isotopic variation, we partitioned WIC into $\text{WIC}_{\text{directional}}$ and $\text{WIC}_{\text{non-directional}}$. $\text{WIC}_{\text{directional}}$ was calculated based on the sequential change in isotope values within an individual during the period of molt (from P1 to P10 for the ten-feather protocol; from P1 to S10 for the four-feather protocol). $\text{WIC}_{\text{non-directional}}$ quantified the remaining within-individual variation: variation that was not associated with a directional trend. We also calculated two WIC/TINW estimates: a traditional WIC/TINW that we term WIC/TINW (sum), and WIC/TINW(adjusted). The latter discounts the influence of $\text{WIC}_{\text{directional}}$ to both WIC and TINW. The model is summarized as follows:

The Data

$$y[k,i,j] \sim \text{mvnorm}\left(\hat{y}_{(k,i,j)}, \Sigma_{\text{WIC}(k)}\right)$$

The Individual Model

$$\hat{y}_{(k,i,j)} = \alpha 0_{(k,i)} + \alpha 1_{(k,i)} \times \text{feather}_{(j)}$$

The Population Model

$$\alpha 0_{(k,i)} \sim \text{mvnorm}\left(\mu_{\text{pop}(k)}, \Sigma_{\text{BIC}(k)}\right)$$

$$\alpha 1_{(k,i)} \sim \text{mvnorm}\left(\mu_{\text{slope}(k)}, \Sigma_{\text{slope}(k)}\right)$$

Estimates of Specialization

$$\text{TINW} = \sum \left(y_{(k,i,j)} - \mu_{\text{pop}(k)}\right)^2$$

$$\text{BIC} = \sum \left(y_{(k,i,j)} - \alpha 0_{(k,i)}\right)^2$$

$$\text{WIC}_{\text{directional}} = \sum \left(y_{(k,i,j)} - \left(\mu_{\text{pop}(k)} + \alpha 1_{(k,i)} \times \text{feather}_j\right)\right)^2$$

$$\text{WIC}_{\text{non - directional}} = \text{TINW} - \text{BIC} - \text{WIC}_{\text{directional}}.$$

The model was fit in a Bayesian framework using the program JAGS (Plummer 2003) interfaced to R (Development Core Team 2013) using a Markov Chain Monte Carlo for 10,000 iterations with a 55,000 iteration burn in and three chains. The posterior distributions were thinned at a rate of saving of one iteration in every 25. Convergence was ensured through monitoring trace plots and Rhat values (Gelman and Hill 2007). Full model code with data can be found in Online Resource 2.

Because the WIC metric is derived from an R^2 value, with potential for over fitting in small data sets, we were interested in the potential of the model to estimate WIC in a scenario where between individual variation did not exist, i.e., a null WIC/TINW value. Studies of individual diet specialization calculate null distributions in a variety of ways (Bolnick et al. 2002; Araújo et al. 2011). We generated null WIC/TINW values for our two focal petrel populations by simulating 500 data sets where isotope values within our focal populations were randomly reassigned to different individuals. For instance, the P1 isotope values for individual 1 may have been randomly reassigned to P1 from individual 8. We then generated WIC/TINW values for the populations to determine what values would be observed if no individual specialization occurred.

Our hierarchical approach provides a powerful means to partition variation in isotope values as it provides a mechanistic framework to derive population level parameters from processes occurring at the individual level. Moreover, because Bayesian analysis estimates uncertainty in all parameters, this method provides a means of hypothesis testing for differences in the degree of specialization between populations that is not always possible using more traditional, frequentist ANOVA-based methods.

Results

Population mean δ^{15}N and δ^{13}C

We generated stable carbon and nitrogen isotope data from a total of 43 Hawaiian petrels using the ten-feather protocol. δ^{15}N values ranged from +8.7 to + 17.9‰ and δ^{13}C values, from − 16.0 to – 13.4‰. Haleakalā and Lāna‘i colonies differed in both mean δ^{15}N (P[Lāna‘i > Haleakalā] > 0.999) and δ^{13}C values (P[Haleakalā < Lāna‘i] > 0.999)(Fig. 3; Table 1).

The four-feather protocol used on a subset of 12 Lāna‘i individuals yielded similar δ^{15}N results as the ten-feather protocol (Fig. 3a, Table 1). However, grand mean δ^{13}C

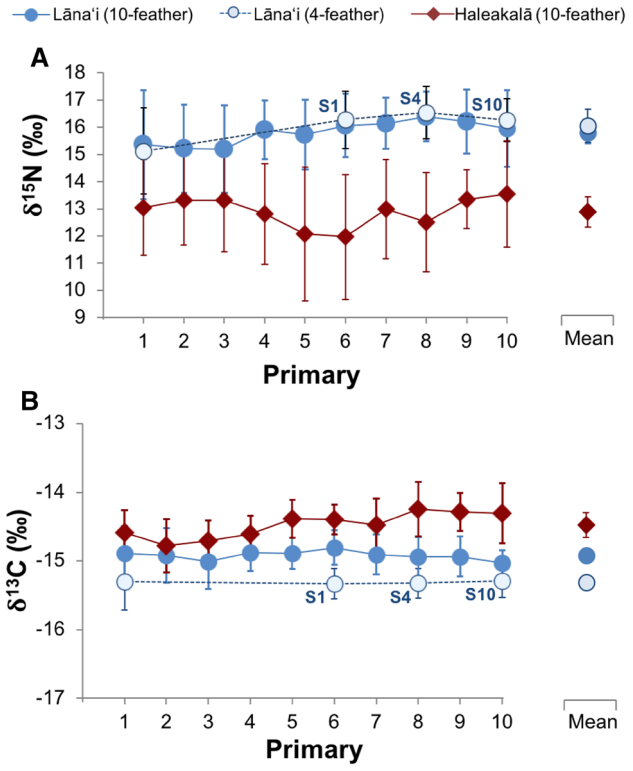

Fig. 3 Stable nitrogen (**a**) and carbon (**b**) isotope values through the period of remige molt in the Hawaiian petrel. Means and standard deviations are shown for each feather, along with the grand mean and grand standard deviations at the far right. The precise timing of S1, S4, and S10 molt relative to primary molt is unknown for the Hawaiian petrel; the position of S1, S4, and S10 data on the *x* axis is therefore approximate. For Lāna‘i, isotope data are shown from both the ten-feather and four-feather protocols (depicted in Fig. 2)

Table 1 Estimated population mean δ^{13}C and δ^{15}N and 95% confidence intervals, calculated for Hawaiian petrels from the Haleakalā and Lāna'i populations using either the ten or four-feather sampling protocol. Sample sizes, *N*, are noted as number of individuals (number of feathers)

	N	δ^{13}C (‰)			δ^{15}N (‰)		
		Mean	2.5%	97.5%	Mean	2.5%	97.5%
Haleakalā (10-feather)	18 (174)	− 14.5	− 14.7	− 14.4	12.8	12.3	13.2
Lāna'i (10-feather)	24 (227)	− 14.9	− 15.1	− 14.8	15.8	15.4	16.1
Lāna'i (4-feather)	12 (48)	− 15.3	− 15.5	− 15.1	16.1	15.5	16.7

calculated from the four-feather protocol was significantly lower than the grand mean δ^{13}C from the ten-feather protocol (Fig. 3b, Table 1). The offset was small in magnitude and expected, because the two sampling strategies differed in where barbs were taken from within individual feathers (Fig. 2). Previous research shows that δ^{13}C values increase from the tip to base of Hawaiian petrel remiges (Wiley et al. 2010; Morra et al. 2018).

Isotopic niche width and degree of individual specialization

Based on δ^{15}N data collected using the ten-feather protocol, we calculated total isotopic niche width (TINW) and the within and between-individual components of isotopic niche width (WIC and BIC, respectively; Fig. 4). The TINW for the Lāna'i petrels was 59% smaller compared to that of the Haleakalā petrels. The populations further differed in that WIC accounted for 67% of TINW in Lāna'i, as compared to 82% in Haleakalā (Table 2).

We divided WIC into two components: $WIC_{directional}$ and $WIC_{non\text{-}directional}$. $WIC_{directional}$, or the mean shift in δ^{15}N through the period of molt, accounted for a minor portion of WIC within both populations (Table 2, Fig. 4). For both populations and sampling strategies, WIC/TINW (sum) values were similar to their corresponding WIC/TINW (adjusted) values, which removes the influence of $WIC_{directional}$ to WIC and TINW (Table 2). Using WIC/TINW (sum), we could not reject the null hypothesis that individuals are equivalent for the Haleakalā population (i.e., the estimated CIs overlapped with those of the null values; Table 2). In contrast, WIC/TINW (sum) from the ten-feather protocol was lower than the associated null value for Lāna'i (Table 2). Thus, individual petrels from Lāna'i were significantly differentiated from one another in δ^{15}N. The four-feather protocol produced a WIC/TINW estimate for Lāna'i that was similar in mean value to the 10-feather estimate, but less precise (i.e., with larger 95% CIs; Table 2).

For δ^{13}C, the variance among simultaneously grown hatch-year remiges was similar to the variance among sequentially grown adult remiges (0.16 vs. 0.13‰) and to our instrumental precision of 0.2‰. We, therefore, did not estimate niche width parameters based on δ^{13}C variance within individuals.

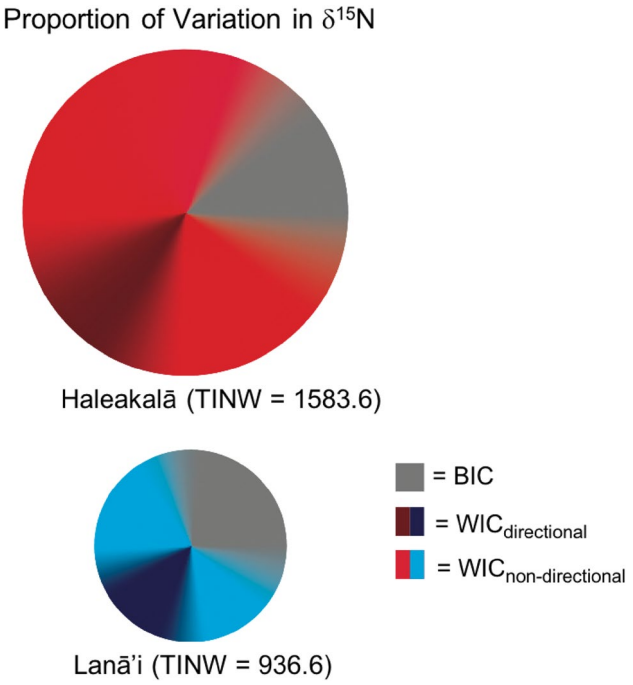

Fig. 4 Estimates of niche component size, based on δ^{15}N data, for Hawaiian petrel populations breeding on Lāna'i and Haleakalā, Maui. The relative size of niche components is represented by the relative area in pie charts; color gradients represent the 95% CIs. TINW is the total isotopic niche width. BIC and WIC are the between-individual and within-individual niche components, respectively

Discussion

Our study used approximately 900 stable carbon and nitrogen isotope measurements to investigate Hawaiian petrel foraging habitat and diet (specifically, these data can reflect consumption of prey from isotopically distinct locations and trophic levels). Our results show that diversity in these foraging attributes lies primarily within individuals and between populations. These findings are visualized in Fig. 5, which shows that Bayesian ellipses for Hawaiian petrel populations from Haleakalā and Lāna'i are largely distinct, but

Table 2 Isotopic niche width estimates from Hawaiian petrel δ^{15}N data, calculated for petrels from Haleakalā and Lāna'i using either the ten or four-feather protocol

Population (protocol)	$WIC_{directional}$/TINW	$WIC_{non\text{-}directional}$/TINW	WIC/TINW (null)	WIC/TINW (sum)	WIC/TINW (adjusted)
Haleakalā (10-feather)	0.13 (0.05–0.25)	0.69 (0.54–0.81)	0.91 (0.85–0.96)	0.82 (0.68–0.92)	0.79 (0.64–0.90)
Lāna'i (10-feather)	0.18 (0.10–0.27)	0.49 (0.38–0.59)	0.91 (0.85–0.95)	0.67 (0.54–0.77)	0.60 (0.46–0.71)
Lāna'i (4-feather)	0.12 (0.03–0.28)	0.44 (0.23–0.69)	0.79 (0.62–0.91)	0.56 (0.30–0.81)	0.51 (0.25–0.78)
Hatch-years (4-feather)	0.29 (0.04–0.76)	0.11 (0.02–0.32)	0.75 (0.32–0.98)	0.41 (0.07–0.83)	0.17 (0.02–0.48)

Mean values are reported with 95% confidence intervals in parentheses. WIC/TINW (sum) refers to the total WIC ($WIC_{directional}$ + $WIC_{non\text{-}directional}$) divided by TINW. WIC/TINW (adjusted) estimates remove the influence of $WIC_{directional}$ from both WIC and TINW

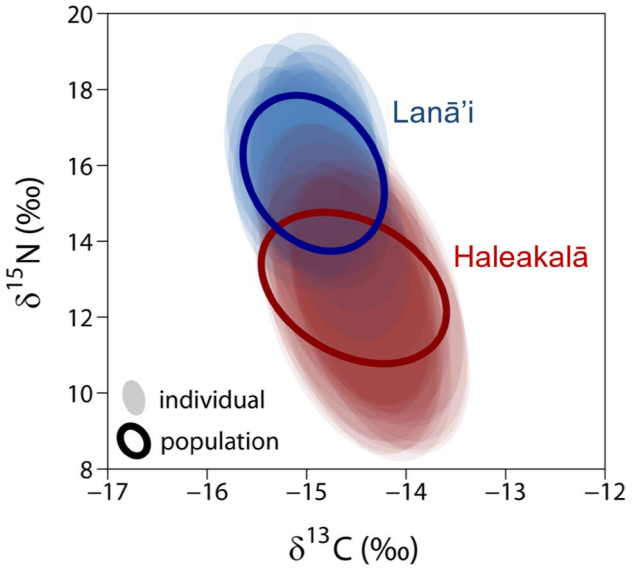

Fig. 5 Isotopic niches of Hawaiian petrels from Haleakalā, Maui and Lāna'i populations, represented by Bayesian ellipses. Filled, transparent ellipses represent individual birds; open ellipses represent populations

that within each population, ellipses representing individuals overlap considerably. We discuss these results in detail, below.

Interpretations of population mean isotope data

We found a marked segregation in foraging habits between Hawaiian petrels that breed on Lāna'i versus Haleakalā, Maui. We know that inter-colony differences in δ^{15}N and δD are characteristic of the Hawaiian petrel; however, previous feather isotope studies report isotopic segregation between colonies during a portion of the non-breeding season (Wiley et al. 2012, 2013; Ostrom et al. 2014, 2017; Morra et al. 2018). Our current data extend this view of foraging segregation by providing a more complete representation of the non-breeding season and showing a striking inter-colony segregation in δ^{15}N throughout the entire period of primary molt (Fig. 3a; mean δ^{15}N differs by 3‰). They also show a small, but significant difference in δ^{13}C values between the two colonies (Fig. 3b).

Carbon isotope values vary inversely with latitude in the Pacific Ocean (Goericke and Fry 1994), and as first noted by Wiley et al. (2012), a comparison of δ^{13}C between adult Hawaiian petrels and other pelagic seabirds of the North Pacific suggests that Hawaiian petrels molt in or near the tropics. This interpretation is now supported by tracking data, which show that Hawaiian petrels from the island of Lāna'i focus their time between 0 and 25°N during the non-breeding season (Fig. 1b; VanZandt 2012). The small disparity in δ^{13}C between Lāna'i and Haleakalā colonies, observed here, suggests that petrels from the two populations might segregate their foraging habits latitudinally.

The observation that Haleakalā petrels have a consistently lower δ^{15}N than their Lāna'i counterparts has three potential explanations: Haleakalā birds might forage at a lower trophic level, in a location with a different nutrient regime, or a combination thereof. Amino acid-specific δ^{15}N data can help to disentangle the effects of trophic level and nutrient regime because the δ^{15}N of phenylalanine ($\delta^{15}N_{Phe}$) primarily reflects the δ^{15}N at the base of an organism's food web and the δ^{15}N of glutamic acid minus the δ^{15}N of phenylalanine ($\delta^{15}N_{Glu-Phe}$) is a proxy for trophic level (Ohkouchi et al. 2017; Morra et al. 2019). Previously published amino acid-specific data show that Haleakalā petrels likely forage at a higher trophic level (i.e., have a higher $\delta^{15}N_{Glu-Phe}$) and in a region of lower δ^{15}N (i.e., have a lower $\delta^{15}N_{Phe}$) than other Hawaiian petrels at the scale of years (Ostrom et al. 2017; Morra et al. 2019). Therefore, the relatively low bulk-feather δ^{15}N values of Haleakalā birds observed here (and in Wiley et al. 2012, 2013; Morra et al. 2018) are most likely driven by foraging location. Potentially, Haleakalā petrels forage in an area more heavily influenced by nitrogen fixation.

Overall, our δ^{13}C and δ^{15}N data suggest that a significant component of the foraging segregation between Lāna'i and Haleakalā petrels during the non-breeding season is spatial. Tracking data during the non-breeding season only exist for the Lāna'i population of Hawaiian petrels. However, tracking of 30 Hawaiian petrels from Lāna'i, Haleakalā, Hawai'i, and Kaua'i populations reveals that during the breeding

season, individuals performed similar and spatially overlapping foraging trips throughout the northeastern Pacific (Adams and Flora 2009; VanZandt 2012, J. Adams et al. unpublished data, J. Adams personal communication). Taken together, isotope and tracking data suggest that spatial foraging segregation between populations occurs primarily during the non-breeding season, when petrels are no longer central-place foragers tied to closely spaced breeding sites. The isotopic divergence between Lāna'i and Haleakalā colonies previously observed in ancient bone collagen shows that this segregation has likely persisted through centuries and even millennia (Wiley et al. 2013).

Isotopic niche width and degree of individual specialization

We employed the widely used metric, WIC/TINW, to quantify individual specialization in the Hawaiian petrel. WIC/T(I)NW values must be viewed in the context of the time period being studied as individuals are most likely to appear specialized over shorter time scales (Weimerskirch 2007; Woo et al. 2008). Araújo et al. (2011) report an average WIC/TNW of 0.66 ± 0.22 for 78 species (largely vertebrates) based on studies covering time scales ranging from days to years. Our δ^{15}N data from Hawaiian petrels reflect a short to intermediate time-scale of approximately three months and yielded mean WIC/TINW values of 0.67 and 0.82 for Hawaiian petrels from Lāna'i and Haleakalā, respectively. Importantly, the ten and four-feather protocols yielded similar WIC/TINW estimates, showing that this result was not highly dependent on sampling protocol or the length of time integrated by each feather sample (Figs. 1, 2, Table 2). Comparisons between our estimated and null WIC/TINW strongly suggest that Hawaiian petrels are individual generalists. Haleakalā WIC/TINW was not significantly lower than its corresponding null value, while Lāna'i WIC/TINW showed only a marginal offset from the associated null (Table 2). Secondarily, our niche width estimates highlight differences between petrel populations. Lāna'i petrels showed a significantly lower WIC/TINW than Haleakalā and therefore, a higher degree of individual specialization. Lāna'i petrels also had a significantly smaller total isotopic niche width, meaning that both Lāna'i individuals and the population as a whole use a smaller range of isotopically distinct foraging locations and prey during the period of molt compared with petrels from Haleakalā (Fig. 4).

The difference in isotopic niche size between Hawaiian petrel populations has two potential explanations. Individual petrels from Haleakalā may show a broader range of behaviors; they may feed over a larger spatial scale and/or be more variable in their trophic level during primary molt, compared with petrels from Lāna'i. Alternatively, the Haleakalā population might forage in a region with steeper nitrogen isotope gradients. In the latter case, birds from Haleakalā could exhibit identical foraging behaviors as birds from Lāna'i, but they would feed on more isotopically variable prey and therefore, show more δ^{15}N variation among their flight feathers. While we cannot fully dismiss the second explanation, it would not explain the observed difference in WIC/TINW between colonies and it is less likely because tracking shows that Lāna'i petrels forage in a region of steep nitrogen isotope gradients during their molt, approximately 140–180°W and 0–20°N (Graham et al. 2010; Wiley et al. 2012; VanZandt 2012).

Notably, our method of quantifying isotopic niche allowed for the estimation of two sub-components of WIC. $WIC_{directional}$ reflects the population mean shift in δ^{15}N from the beginning to end of primary feather molt. A large $WIC_{directional}$ relative to $WIC_{non\text{-}directional}$ would imply that much of the variation within individuals is driven by large-scale phenomena experienced by the population as a whole, such as seasonal or intra-seasonal shifts in prey availability or even by temporal shifts in δ^{15}N at the base of a regional food web. In our models, however, $WIC_{directional}$ accounts for a minor portion of the WIC in either Hawaiian petrel population and does not have a large influence on our WIC/TINW estimates (Table 2, Fig. 4). Therefore, population-level directional trends cannot account for our relatively large WIC and WIC/TINW estimates.

Many studies have found seabirds, including procellariiforms, to repeatedly use the same foraging habitats and prey types (reviewed by Ceia and Ramos 2015; Phillips et al. 2017). However, comparatively few studies quantify within- versus between-individual niche width for seabirds (Woo et al. 2008; Provencher et al. 2013; Bond et al. 2016; Pontón-Cevallos et al. 2017). The most comparable data derive from an isotopic investigation of habitat use and diet in the light-mantled sooty albatross (*Phoebetria palpebrata*) in the Southern Ocean (Jaeger et al. 2010). Jeager et al. 2010 report WIC/TINW of 0.7 and 0.6 for δ^{13}C and δ^{15}N, based on multiple body contour feathers molted over a timespan of approximately 1 year; this longer time frame would presumably inflate WIC/TINW values compared with those in our study. To the extent that comparison is possible, our data suggest that individual Hawaiian petrels may use a similar or slightly larger portion of their population's niche (i.e., are more generalized) than light-mantled sooty albatross.

More broadly, marine predators can display strikingly high levels of individual specialization in habitat use and diet. Vander Zanden et al. (2010, 2013) estimated population mean WIC/TINW values lower than 0.1 in loggerhead (*Caretta caretta*) and green sea turtles (*Chelonia mydas*) at the scale of years, using stable isotope analysis. Their data suggest that within a given life stage, individual turtles from the Caribbean and Western Atlantic consistently use the same foraging areas and diets. Similarly, Rossman et al.

(2015) estimated mean female bottlenose dolphin (*Tursiops truncatus)* WIC/TINW to be 0.4 and 0.12 using δ^{15}N and δ^{13}C, respectively, revealing high levels of individual specialization within a single shallow Florida estuary, again at the scale of years. Indeed, the growing number of niche quantifications in marine mammals suggest that individuals frequently use less than 50% of the isotopic niche of their parent population (Newsome et al. 2009; Hückstädt et al. 2012; Newsome et al. 2015). While further studies are needed for any taxon-level conclusions, the aforementioned marine reptile and mammal studies provide a marked contrast to the high degree of individual generalization we observed among Hawaiian petrels.

Overall, our results show that Hawaiian petrels, especially those from Haleakalā, fall on the extreme individual generalist end of the specialist–generalist spectrum, and that individual birds use a large range of nutrient regimes and trophic levels over the course of molt, as compared with their parent populations. Individual specialization may require relatively stable environments and disappear if the resources on which individuals are specialized become scarce or unpredictable (Svanbäck and Bolnick 2005; Ceia and Ramos 2015). Indeed, the abundance and predictability of seabird prey is likely very low in the tropical, oceanic ecosystems where Hawaiian petrels molt (Weimerskirch et al. 2005, 2007). Selection in such environments probably favors individual generalists with highly flexible foraging behavior. Hawaiian petrels certainly feed on a wide diversity of prey (Simons 1985) and presumably, they use multiple foraging strategies, including diurnal foraging with subsurface predators, scavenging, and solitary nocturnal foraging (Pitman 1982; Simons 1985; Ostrom et al. 2017). In addition, Hawaiian petrels are among the most mobile marine predators (Adams and Flora 2009; Van Zandt 2012): a trait that implies generalization with regard to foraging location.

In contrast, marine predators that show high degrees or high incidence of individual specialization are typically less mobile and either forage at higher latitudes or coastally, where prey are more abundant and predictable. Some also forage in highly heterogeneous regions, for example, benthic habitats with local topographic features that can be memorized to improve foraging success (e.g., cormorants and shags; Phillips et al. 2017), or in a diversity of habitat types on which individuals might become specialized (e.g., seagrass vs. open water habitats available to estuarine bottlenose dolphins; Rossman et al. 2015).

Most published studies addressing individual specialization in seabirds report that individuals consistently use the same foraging resources, commonly within seasons and between years (Ceia and Ramos 2015; Phillips et al. 2017). However, Ceia and Ramos (2015) suggest that there may be publication bias towards reporting evidence of individual specialization, and furthermore, relatively few studies focus on tropical and subtropical species, quantify the degree of individual specialization, or test the null hypothesis of individual equivalency (Ceia and Ramos 2015; Phillips et al. 2017). A paucity of comparable data makes it challenging to relate the incidence of individual specialization to seabird phylogeny, but Phillips et al. (2017) note that among seabird studies, those focusing on albatrosses and petrels most commonly fail to find evidence of resource use consistency.

For future studies of individual specialization, we offer a testable prediction. We predict that most oceanic tropical and subtropical seabirds, including many procellariiforms, are individual generalists with regard to foraging habitat and diet. Notably, our method of quantifying individual specialization with isotope data from sequentially grown flight feathers could be repeated for many other seabirds and, especially if used for other North Pacific species, presents the opportunity to create highly comparable individual specialization estimates that could be used to test our prediction.

Implications of inter-colony foraging differences

It is striking that, despite the prevalence of individual generalists in both Hawaiian petrel populations, we found a suite of isotopic niche differences between them during the period remige molt, including differences in mean δ^{15}N and δ^{13}C, total nitrogen isotopic niche width, and extent of individual specialization with regard to δ^{15}N. These inter-colony differences are robust, despite the high mobility of individual petrels (e.g., foraging trips in excess of 10,000 km, Adams and Flora 2009) and the fact that Hawaiian petrel populations on Haleakalā and Lāna‘i breed less than 100 km apart. For oceanic seabirds, prey aggregations are most predictable at the scale of 100–1000 s of kilometers (Weimerskirch et al. 2005; Weimerskirch 2007), and thus, Hawaiian petrel populations may be adapted to exploit distinct, large-scale regions of reliably enhanced prey availability. This difference may be heritable in the genetically distinct Hawaiian petrel populations nesting on Haleakalā and Lāna‘i (Welch et al. 2012). Indeed, seabirds migrate for the first time without their parents, leading Phillips et al. (2017) to speculate that, like other birds, they respond to genetically based cues for dispersal direction and even migratory distance. Population-level differences in prey searching behavior (and associated differences in foraging habitat) could also be transferred between generations via olfactory cues, which are known to play an important role in locating both burrows and prey for burrow-nesting procellariiforms (Nevitt 2008; Cunningham and Nevitt 2011).

Our findings have implications for the conservation of the endangered Hawaiian petrel. Notably, Hawaiian petrels and other North Pacific seabirds are declining in trophic level (Wiley et al. 2013; Ostrom et al. 2017; Gagne et al. 2018), a trend that likely reflects widespread shifts in prey availability

and emphasizes the importance of preserving foraging diversity and adaptability of foraging habits within dwindling seabird populations. Based on our results, this goal would be best advanced through conservation of multiple Hawaiian petrel populations, even at the cost of less extensive conservation efforts within individual breeding colonies. The loss of Hawaiian petrels on a single island would likely result in a substantial and persistent reduction in ecological diversity at the species level; a reduction that could not be regained through reintroduction. Our data further suggest that Hawaiian populations might respond differently to future changes in prey availability, given that they rely on different foraging resources and because the Lānaʻi population is potentially more specialized in the foraging location and trophic niche dimensions.

Historical perspectives on individual specialization

Prior studies showed that multiple Hawaiian petrel populations declined in trophic level during the past 100–150 years: a period encompassing 15 or fewer generations (Simons 1984; Wiley et al. 2013; Ostrom et al. 2017). Our current work stresses that this change occurred in populations that are highly distinct in their isotopic foraging niches, and in populations composed of individual generalists. This generalization may account for the species' ability to change foraging habits relatively rapidly, as individual generalists might be more likely to exhibit behavioral plasticity in foraging that enables within-generation shifts in prey base (Bolnick et al. 2003).

As a caveat to the points above, we note that the degree of individual specialization can change within a generation and be affected by food availability, resource diversity, and competition (Svanbäck and Bolnick 2005; Darimont et al. 2009; Semmens et al. 2009, Araújo et al. 2011), all of which might have shifted for the Hawaiian petrel and other seabirds during the past century. We, therefore, emphasize that this and other studies of individual specialization may not represent historical levels of individual specialization. Instead, our estimates of Hawaiian petrel foraging specialization can be used as a starting point and meter stick for future measures of specialization in the species, as well as reconstructions of historical levels of specialization. Given the extensive isotope work already conducted on the Hawaiian petrel and availability of historical specimens, this species may be an exemplar for continued study of foraging niche dynamics. More broadly, isotope studies that use inert tissues such as feathers and whiskers to study individual specialization can be repeated with historical specimens and may therefore be uniquely situated to reveal how foraging specialization changes at the scales of decades and in response to environmental perturbation.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. Salvaged seabird carcasses were collected under the Endangered Species Act permit TE-145562 and the cooperative agreement between the Hawaii Department of Land and Natural Resources and the US Fish and Wildlife Service. Funding was provided by National Museum of Natural History, Smithsonian Institution.

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