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Enhancing dietary specialization metrics in observational studies of wild animal populations

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Abstract. Studies of intraspecific dietary variation can greatly enrich our view of a species' niche and role in the ecosystem, particularly when species with broad diets are found to be composed of generalist and specialist individuals. However, the current framework for quantifying dietary specialization leaves certain standards unformalized and is susceptible to overestimating specialization when there are few repeated observations per individual, as is often the case in observational studies of wild populations. Here, we use the hihi (*Notiomystis cincta*), a threatened New Zealand passerine, as a case study for demonstrating how existing statistical tools can be applied to strengthen the dietary specialization framework. First, we assess whether the reliability of common dietary measures can be improved through Bayesian adjustments and by using rarefaction to compare uncertainty levels of metrics calculated from different sample sizes. As diet links closely to environmental factors, we also demonstrate how adding phenological data and habitat assessments to standard protocols can help validate our dietary measures as evidence for resource selection rather than random foraging. Finally, in light of our finding that diet predicts survival in hihi, we discuss the utility of dietary specialization for elucidating broader behavioral syndromes.

Key words: dietary specialization; ecological niche; foraging; individual differences; intraspecific behavioral variation; niche differentiation; proportional similarity index; resource partitioning.

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INTRODUCTION

Among behavioral ecologists, there is a growing interest in measuring behavioral variation within species (Sih et al. 2004, Dall et al. 2012, Brommer and Class 2017). Diet is one trait that has been found to vary individually in many taxa, enhancing our view of species' niches and roles in the ecosystem (Bolnick et al. 2003, Araújo et al. 2011, Troxell-Smith and Mella 2017). Most studies quantify dietary variation using the proportional similarity index (PS_i: Bolnick et al. 2002), which measures individuals' dietary similarity to the population as a whole. Specialists on a single food receive a PS_i equal to that food's proportional representation in the population diet; meanwhile, extreme generalists consume all foods in the same proportions as the population as a whole and receive a PS_i of 1. However, even within this widely applied framework, certain standards remain unformalized: namely, (1) how many observations per individual are needed to achieve reliable measures of diet; (2) how to ensure the validity of these metrics as evidence for dietary preferences; and (3) how to account for measurement uncertainty when evaluating diet's utility as an ecologically informative trait. Addressing these limitations will help to ensure that our shared dietary framework yields comparable measures across studies.

Advocates of PS_i caution that it can overestimate specialization in individuals with few repeated observations (Bolnick et al. 2002, Araújo et al. 2011). But without a formal criterion, sample sizes vary widely throughout the literature. Often, the largest datasets come from studies conducted in captivity or using advanced technologies such as stable isotope analysis or remote tracking. For example, Tinker et al. (2012) used radio telemetry to track southern sea otters (*Enhydra lutris nereis*) over six years, recording more than 60,000 feeding dives across 74 individuals. However, these methods are not suitable for all species. Direct observation remains a valuable method for collecting detailed foraging records but often yields small sample sizes in species that are challenging to observe in the field. Nevertheless, measuring specialization could be important even when these data are difficult to collect, as dietary variation can be used to predict a population's viability (Bolnick et al. 2003, Colles et al. 2009, Clavel et al. 2011) and model its effects on ecosystem health (Bolnick et al. 2011, Raffard et al. 2017).

These benefits make it worth asking whether we can quantify or even correct for uncertainty in dietary estimates derived from small sample sizes. Currently, some studies exclude individuals falling below an arbitrary sample size cutoff (e.g., 6 in De León et al. 2012, 8 in Szigeti et al. 2018), but this can significantly reduce statistical power, particularly in field studies where sample sizes may already be limited (Garamszegi 2016). Existing statistical tools may enable us to retain more individuals. Coblentz et al. (2017) propose a Bayesian hierarchical method that shifts individuals' PS_is toward the population mean by an amount inversely proportional to their sample size; this helps to account for the uncertainty in inferring true diets from a small number of observations. To measure the reliability of these Bayesian PS_is, they suggest recalculating the PS_is of the most frequently observed individuals across a range of simulated sample sizes. Using this rarefaction procedure, Coblentz et al. demonstrate that the Bayesian method estimates diet reliably even at their lowest simulated sample size of five foods, while unadjusted PS_is consistently overestimate specialization below 50 foods. However, this reliability test was used only on simulated data. Applying it to real-world data is an important next step toward integrating Bayesian methods into the dietary specialization framework.

Once we are confident in the reliability of our behavioral measure, we still need to ensure that it truly captures our trait of interest (i.e., is valid; Martin and Bateson 1993). This is especially key for traits like diet that are closely linked to extrinsic factors. PS_is are often interpreted as reflecting individuals' intrinsic preferences when dietary variation could also arise from unequal access to resources (Bolnick et al. 2003, Araújo et al. 2011). In heterogeneous environments, individuals may be exposed to different resources through their ranging patterns (Buskirk and Millspaugh 2006, Cunningham et al. 2018, Coblentz 2020). This effect can be compounded by phenological changes. For example, Szigeti et al. (2018) found that pairs of Apollo butterflies (*Parnassius mnemosyne*) had more similar diets the closer in time they were observed to one another, suggesting that phenology at the time of observation can significantly influence diet scores. Yet, studies of dietary variation rarely include detailed habitat or phenology assessments. In a review of 87 resource selection studies, only 26% measured resource availability at the individual level (Thomas and Taylor 2006). These data could be important for validating our dietary metrics, allowing us to determine whether individuals have dietary preferences or are merely sampling foods randomly in proportion to their availability.

Finally, a crucial step in placing dietary variation in a wider context is evaluating its utility as an ecologically informative trait. This could be particularly beneficial for species of conservation concern. Many threats are so urgent that even traits predicting fitness in the short term could help conservation biologists tailor their management interventions to individuals' needs (see Arcese 2003 for an opposing view). Because diet underlies some of the most fundamental ecological interactions, variation can also scale up to affect other species through competition, predation, and mutualisms (Bolnick et al. 2011, Dupont et al. 2011, Dall et al. 2012, Phillips et al.

2017, Raffard et al. 2017); thus, diet studies could also inform strategies for ecosystem restoration. However, just as studies quantifying dietary variation should account for uncertainty, so, too, should studies examining the potential consequences of diet. This could be especially important in survival analyses, as factors driving uncertainty in dietary metrics may be confounded with individual health. For example, diseased individuals may be easier or more difficult to observe depending on how their illness affects their mobility or conspicuousness. As small sample sizes can lead to overestimates of specialization (Bolnick et al. 2002, Araújo et al. 2011), this could lead to a false correlation between diet and survival if uncertainty is not accounted for.

In this study, we use the hihi (*Notiomystis cincta*), a threatened passerine endemic to New Zealand, as a case study to demonstrate how some of the current limitations to the dietary specialization framework can be addressed using existing analytical tools. Hihi have a broad species-level diet including fruit, nectar, and invertebrates (Rasch and Craig 1988), but early researchers hypothesized that individual diets may vary (Craig 1985), and there is some evidence that the sexes exhibit seasonal differences in resource use (Walker et al. 2014). Hihi also meet many criteria predicted to drive specialization (Bolnick et al. 2003, Araújo et al. 2011): their physiological needs change with age, they exhibit inter- and intraspecific dominance hierarchies, and their territories vary in quality (Thorogood et al. 2013). Because of their conservation status, hihi are closely monitored, making it possible to study individual behavioral differences and track long-term survival. Here, we begin by showing that individuals vary in their diets. We then go on to test (1) what dietary metrics and sample sizes yield reliable estimates; (2) whether dietary differences reflect individual preferences; and (3) whether diet predicts survival.

Methods

Study site and population

Tiritiri Matangi Island (36°36′00.7″ S 174°53′21.7″ E) is a 220-hectare nature reserve located 3.5 km off the coast of New Zealand's North Island. After being cleared for pastureland and farmed for over a century, the island was extensively replanted in the 1980s. Today, the vegetation consists of regenerating native bush with small patches of remnant mature forest. The island has been free of introduced mammalian predators since 1993, and hihi were reintroduced from Te Hauturu ō Toi (Little Barrier Island Nature Reserve) two years later. During our study, the population numbered ~170 adults. Every breeding individual nests in an intensively monitored nest box, so all chicks are of known age. Individuals are classed as juveniles after fledging in summer until they become adults in the following spring breeding season. At 21 d old, each nestling is given a unique combination of colored leg bands to facilitate individual identification after fledging, and sex is determined based on early signs of sexually dimorphic plumage (Smith et al. 2015). While the population's productivity is enhanced by the provision of sugar water (Armstrong and Ewen 2001), hihi preferentially select natural foods when they are sufficiently available. Therefore, we chose to focus on natural foraging behaviors for the purposes of this study.

Foraging observations

Foraging observations were conducted by a single observer (CA) from 24th January to 18th March 2017 (215 h) and from 4th February to 21st March 2018 (230 h), coinciding with the end of the hihi breeding season. The observer walked transects which were evenly distributed across the island (Fig. 1a) and included areas of high hihi presence (14 km; walked three times weekly) and low hihi presence (6 km; walked once weekly), as determined from regular population monitoring. Morning (c. 8:00–12:30) and afternoon (c. 12:30–16:30) sessions were balanced for each transect.

During each session, the observer walked at a constant rate until a hihi was seen or heard within 10 meters of the transect. If the bird could be located within 10 min, the observer noted the individual's band combination, recorded the local habitat type (from eight predefined, visually distinct categories; Appendix S1: Table S1), and began a focal follow of the individual. Feeding events were recorded ad libitum, with each food classified as a fruit, nectar, or invertebrate (Fig. 1b–d); while plant foods were identified to

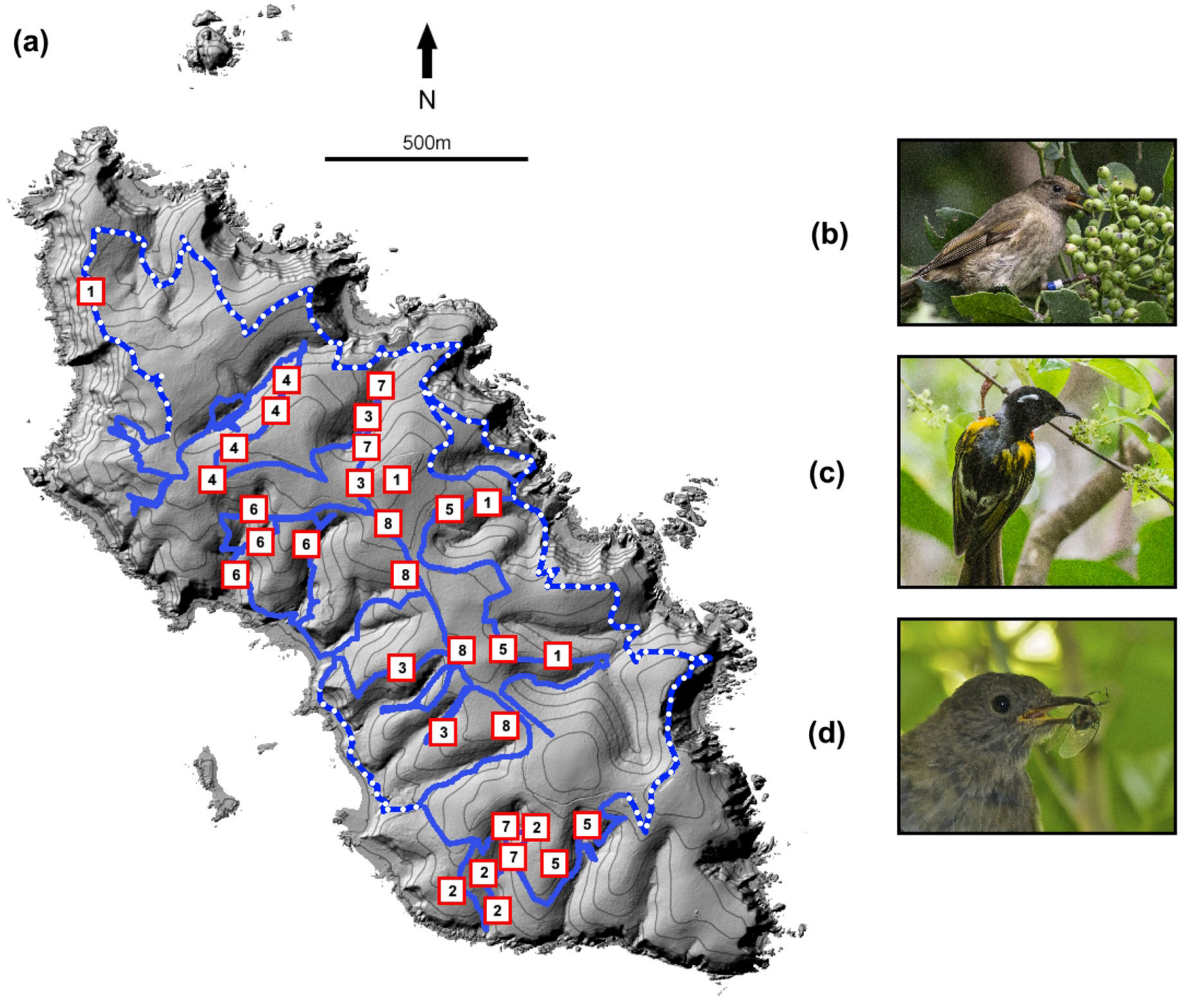

Fig. 1. (a) Contour map of Tiritiri Matangi Island (from data obtained and modified from L*and* I*nformation* N*ew* Z*ealand* Data Service on 1 July 2019) with foraging transects marked with blue lines (solid = high hihi presence; dotted = low hihi presence). Boxes indicate the locations of habitat assessment plots, with numbers corresponding to the habitat types in Appendix S1: Table S1. Hihi photos show examples of (b) a female foraging on houpara (*Pseudopanax lessonii*) fruit (photo by Martin Sanders), (c) a male foraging on hangehange (*Geniostoma ligustrifolium*) nectar (photo by Martin Sanders), and (d) a juvenile eating a cicada (Hemiptera: *Cicadidae*; photo by Steve Attwood).

species level, invertebrates could not be classified more precisely because of their small size and the distance between the observer and focal birds. When multiple birds were in view, the group was scanned to capture as many foods eaten as possible. Focal individuals were abandoned if they moved too quickly to follow through the dense understory, or if they became inactive (preening or resting) or moved out of sight for five minutes.

Habitat assessments and phenology

To assess the abundance of each known hihi food plant expected to have fruits or flowers available during the study period (determined from Perrott and Armstrong 2000 and personal communications with site managers; Appendix S1: Table S2), we conducted habitat assessments and phenological surveys. For each of the eight habitat types, we selected four representative plots distributed as evenly across the island as possible (Fig. 1a). In each plot, we designated five 25-m sampling lines radiating evenly from a central point. Every 5 m along each line, we counted and identified (to species level) all plants of reproductive size within a 1 m radius. This resulted in 25 sampling points per plot, or 100 per habitat type. The counts for each species were then summed across these 100 sampling points to arrive at a measure of abundance for each food plant within each habitat type. Next, 15 specimens (or fewer if unavailable) were selected for each food plant species and as evenly distributed along the foraging transects as possible. Once every two weeks, we estimated the numbers of fruits and flowers on each plant (following the methods of Perrott and Armstrong 2000) and averaged these values across all monitored specimens of that species. We multiplied this number by our species counts within each habitat type to calculate an absolute abundance for each food item in each habitat type for a given two-week period. We converted this to a relative abundance by dividing by the total number of food items of all types available in that habitat type and time period.

Population surveys

Ongoing management of the Tiritiri Matangi hihi population includes biannual, constant-effort (about 40 h in five days) surveys in September and February, in which an experienced observer attempts to sight as many individuals as possible. For the purposes of this study, two additional surveys of about 40 h each were completed in April and May.

Data analysis

All analyses were conducted in R (version 3.5.1; R Development Core Team 2018) unless noted otherwise. When means are reported, they are accompanied by their standard errors.

*Foraging variation.—*Within each season, we tallied foods eaten by type and calculated two dietary specialization metrics for each bird we observed. First, we used the R package RInSp (version 1.2.3; Zaccarelli et al. 2013) to calculate a proportional similarity index ("unadjusted PS_i") for each individual (Bolnick et al. 2002). When calculating the population diet, we avoided giving greater weight to birds that were observed eating more foods by using the averaging method proposed by Zaccarelli et al. (2013). This method first calculates each individual's proportional use of the various food types and then averages these proportions across all individuals to arrive at the population diet. Each individual's diet is then compared to the population diet to assign the individual a PS_i, calculated as: $1–0.5\Sigma_j|p_{ij}–q_j|$, where p_{ij} is the proportional use of food type j by individual i and q_j is the proportional use of food type j by the average population member (Bolnick et al. 2002). We also calculated an adjusted "Bayesian PS_i" for each individual following the methods of Coblentz et al. (2017). We modified this method to match the population diet averaging technique described above, as the original version was less suited to populations with highly variable sample sizes per individual (Zaccarelli et al. 2013).

To assess the degree of variation in the population, we calculated the means and standard errors for unadjusted and Bayesian PS_i scores in each year. The RInSp package tests the significance of specialization by comparing these means to 10,000 means calculated through a Monte Carlo resampling procedure in which all foods eaten by the population are randomly redistributed across individuals. We also compared PS_i distributions between years and methods using Student's *t*-tests where distributions were normal and variances were equal, and Welch's *t*-tests where distributions were normal but variances unequal.

Because our classification of invertebrates as a single food type could affect the accuracy of our dietary estimates, we recalculated Bayesian PS_is using only plant foods for individuals that ate some (but not only) invertebrates. These were highly correlated ($r = 0.94$, $P < 0.001$) to the PS_is including invertebrates. Combined with the fact that invertebrates comprised only a small portion of foods eaten in each year (about 12%; result not presented), this suggested that retaining individuals with invertebrates in their diets would not affect further analyses. However, because we could not check this correlation for individuals that only ate invertebrates, we excluded these individuals ($n_{2017} = 11$, $n_{2018} = 19$) from all remaining analyses.

*Reliability.—*To determine how many foods are needed to achieve reliable measures of diet, we carried out a rarefaction procedure (similarly to Coblentz et al. 2017) with the 47 birds from our

2018 dataset that had been observed eating at least 20 food items (we did not use 2017 data, as only one bird met this criterion). For every $x \leq 20$, we randomly resampled x foods from each bird's observed diet and used these simulated diets to recalculate their unadjusted $\mathrm{PS_i}$s. We chose not to update the population diet in these recalculations, because we made the simplifying assumption that our observed population diet was an accurate representation of the true population diet. We repeated the resampling procedure 100 times and then conducted a paired *t*-test comparing each individual's mean simulated $\mathrm{PS_i}$ with their original $\mathrm{PS_i}$. We repeated the entire rarefaction procedure using the Bayesian $\mathrm{PS_i}$ method.

We assessed the reliability of our dietary measures using two criteria. For Criterion 1, we examined the P values from the paired *t*-tests and accepted sample sizes yielding simulated $\mathrm{PS_i}$s that, on average, did not differ significantly ($P \geq 0.05$) from the original $\mathrm{PS_i}$s. However, an average difference of zero says nothing about the magnitude of these differences. Therefore, for Criterion 2, we quantified the magnitude percent difference between each individual's simulated $\mathrm{PS_i}$ and original $\mathrm{PS_i}$, calculated as:

$$\left|\frac{\text{simulated}\,\mathrm{PS_i} - \text{original}\,\mathrm{PS_i}}{\text{original}\,\mathrm{PS_i}}\right| \times 100$$

and calculated the mean across individuals for each simulated sample size. To reduce the likelihood that individuals' original sample sizes would significantly impact their $\mathrm{PS_i}$ rank relative to other individuals, we a priori designated a maximum acceptable threshold of 18.15%, which represented half of the average between-individual difference in original $\mathrm{PS_i}$ scores (36.30%; result not presented). Thus, all simulated sample sizes with a mean magnitude percent difference no greater than 18.15% were considered to have satisfied Criterion 2. After applying both reliability criteria, we repeated our assessment of population-level specialization in each year as before and compared our new mean $\mathrm{PS_i}$ estimates to our previous estimates using *t*-tests.

Validity.—We investigated whether the observed dietary variation was a reflection of individual preferences or random sampling of available foods. In other words, birds could vary in their visitation rates to different habitat types but indiscriminately eat the foods they encounter in them. If so, we would expect birds' diets to match the resource availability that they uniquely experience based on their use of different habitats and the phenology at the time they visit.

Because phenology data were only available for fruits and flowers, we excluded invertebrates from these analyses. From the remaining observations, we noted the habitat type that each feeding event occurred in. For each bird that met our reliability cutoff (five foods eaten; see Results), we tallied their use of each habitat type within each two-week period. We multiplied these values by the proportional availability of each food in each habitat type during that period (from our phenology data) and summed across all periods to arrive at an experienced abundance of each food item for each bird. This represented their expected diets if they were randomly eating foods in proportion to their availability. Note, any food types that were not detected in phenology assessments during a two-week period were given an arbitrarily low proportional availability (10^{-6}) to avoid calculation errors due to values of 0.

In the adehabitatHS package (version 0.3.14; Calenge 2006), the compana function uses a Wilks' lambda to assess whether a population exhibits habitat selection. Here, we adapted it for resource selection by comparing individuals' observed diets to their expected diets if they were foraging randomly. As our dataset follows the structure of a Design III resource selection model (i.e., resource use and availability measured at the individual level; Manly et al. 1993), we also used the widesIII function as an additional, χ^2-based measure of population-wide resource selection and a test for resource selection at the individual level.

Utility.—We tested whether dietary specialization could be used to predict survival in hihi. As dominance of different age–sex classes may influence the effects of dietary specialization on survival (Whitten 1983, Langen and Rabenold 1994, Dennehy 2001), we conducted a preliminary analysis (using Akaike information criterion model selection: Symonds and Moussalli 2011, Mazerolle 2017) to assess whether $\mathrm{PS_i}$ varied by age or sex. As we found only weak evidence (a model containing an interaction between age and sex was within 2 AIC_c units of the null model; Appendix S1: Table S3), we did not consider age or sex in any further analyses.

For each bird that met our reliability cutoff ($n_{2017} = 25$; $n_{2018} = 82$) and that remained in the population following conservation translocations to other populations (21 birds observed were removed in 2017, 33 in 2018; Franks et al. 2019), we used our population survey data to construct an encounter history. We analyzed the two years separately, with any birds seen in both years appearing as two separate entries: one associated with their 2017 PS_i and one associated with their 2018 PS_i. Birds were noted present in February of the year they were observed and either present (1) or absent (0) in the following April, May, September, and February surveys.

Using a live-recaptures model (Cormack-Jolly Seber, CJS) in Program MARK (version 6.2; White and Burnham 1999), we tested the dietary and time dependence of monthly survival probability (ϕ; for each inter-survey interval) and resighting probability (ρ; for each sampling occasion). Our global model explaining individuals' encounter histories was $\phi(PS_i \times time)\rho(PS_i \times time)$, which we compared to successively reduced models using Akaike information criterion (AIC_c) values. AIC_cs for the 2017 model selection were corrected for a small degree of overdispersion ($\hat{c} = 1.10$) using quasi-likelihood AIC_cs ($QAIC_c$s). Goodness-of-fit testing indicated underdispersion ($\hat{c} < 1$) for the 2018 model selection, so we did not apply any corrections, following common practice for Program MARK. When two or more models emerged as equally well-supported ($\Delta(Q)AIC_c < 2$), we used model averaging to examine the relationship between PS_i and monthly survival during the first three inter-survey intervals; otherwise, we extracted estimates from the single top model. Using these monthly estimates, we calculated seven-month (February–September) survival estimates for each study year. 95% confidence intervals (restricted between 0 and 1) were derived in R by applying the delta method (Powell 2007) to the confidence intervals of the monthly estimates using the msm package (Jackson 2011, version 1.6.2).

To account for the uncertainty inherent to the Bayesian PS_i method, we repeated our survival analyses using modified PS_i scores. Each PS_i was randomly increased or decreased by a percentage within the 95% confidence interval of the mean magnitude percent difference for the individual's sample size of foods eaten (see *Results*). For individuals with sample sizes greater than 20 (the maximum tested in our rarefaction procedure), the 95% confidence interval for a sample size of 20 was used. This procedure represents a more conservative estimate of the relationship between survival and PS_i.

RESULTS

Foraging variation

In 2017, 127 individuals (45 females, 82 males; 75 juveniles, 52 adults) were observed eating 538 food items of 15 types (Appendix S1: Table S2) over 364 discrete encounters (totaling 22 h). In 2018, 164 hihi (69 females, 95 males; 84 juveniles, 80 adults) were observed eating 2362 food items of 23 types (Appendix S1: Table S2) over 838 discrete encounters (totaling 66 h). The number of foods eaten per individual varied widely in each year (1–30 in 2017, 1–88 in 2018), with most falling toward the lower ends of these distributions ($\bar{x}_{2017} = 4.24 \pm 0.41$; $\bar{x}_{2018} = 14.40 \pm 1.11$; Fig. 2). The number of discrete encounters per bird was also highly variable, ranging from 1 to 14 in 2017 ($\bar{x} = 2.87 \pm 0.20$) and 1 to 17 in 2018 ($\bar{x} = 5.11 \pm 0.32$).

In both years, dietary variation differed significantly from what would be expected by chance (Monte Carlo $P < 0.001$), regardless of the method used to calculate PS_i. Individuals were somewhat specialized ($PS_i < 0.5$) on average, with a mean unadjusted PS_i of 0.22 ± 0.012 in 2017 and 0.30 ± 0.011 in 2018, and mean Bayesian PS_i of 0.45 ± 0.0050 in 2017 and 0.42 ± 0.0085 in 2018 (Fig. 3). The population was significantly more specialized in 2017 than in 2018 whether unadjusted PS_is (Student's *t*-test, $t = -4.64$, df = 289, $P < 0.001$) or Bayesian PS_is (Welch's *t*-test, $t = 3.17$, df = 255.49, $P = 0.0017$) were used. The Bayesian method consistently yielded less specialized estimates (higher PS_is) than the unadjusted method in both 2017 (Welch's *t*-test, $t = 17.22$, df = 168.76, $P < 0.001$) and 2018 (Welch's *t*-test, $t = 8.02$, df = 301.38, $P < 0.001$).

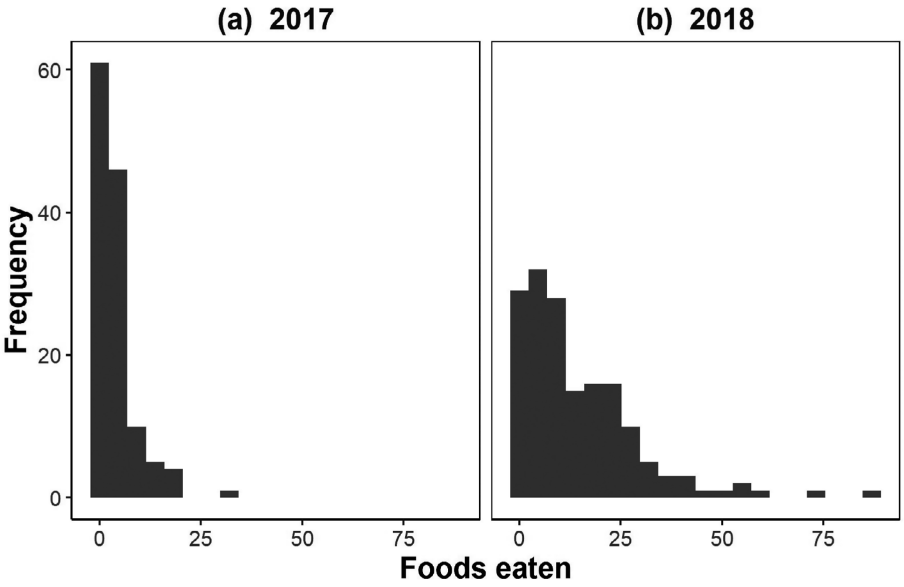

Fig. 2. Distribution of the number of foods eaten per individual in (a) 2017 and (b) 2018.

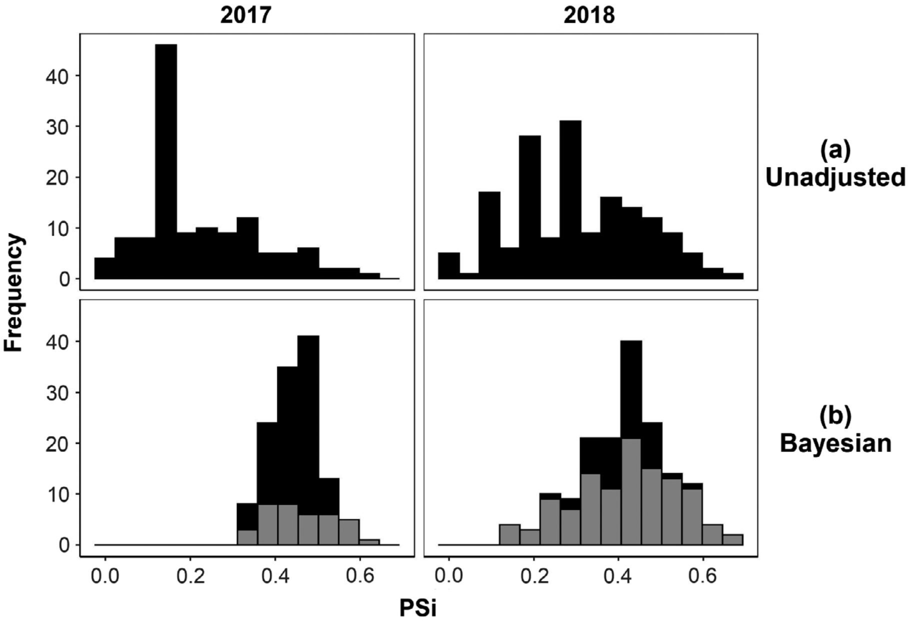

Fig. 3. Distribution of dietary specialization scores in 2017 and 2018 calculated as (a) unadjusted PS_is and (b) Bayesian PS_is. In (b), distributions show PS_is before (black bars) and after (gray bars) the reliable sample size cutoff of five foods eaten was applied.

Reliability

The unadjusted PS_i method consistently overestimated specialization (underestimated PS_i) at all simulated sample sizes ($\bar{x}_{\text{simulated}} < \bar{x}_{\text{original}}$, $P < 0.05$ for all paired *t*-tests; Fig. 4). In contrast, while the Bayesian method underestimated the range of PS_is in the population at low sample sizes, it satisfied Criterion 1 at all sample sizes by

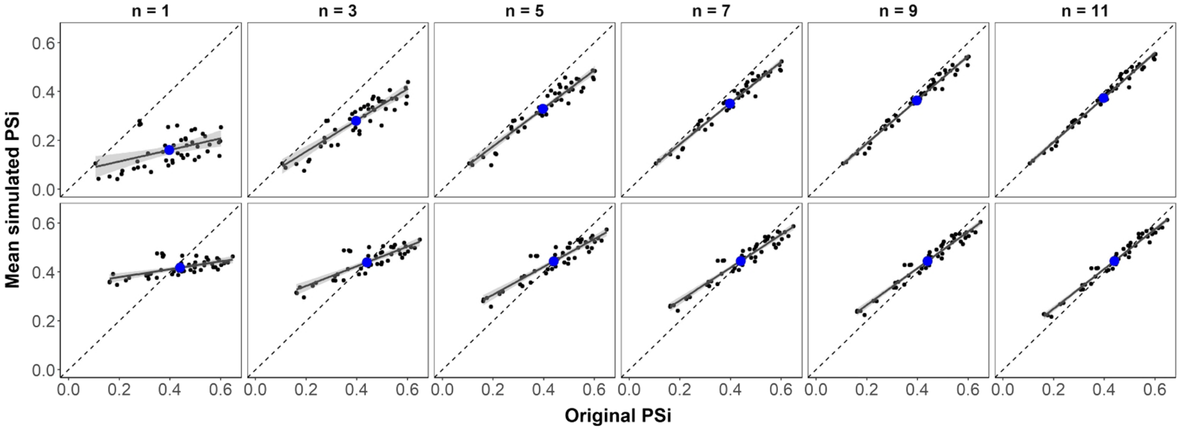

Fig. 4. Relationship between the original PS_is (calculated from the full dataset) and mean simulated PS_is (calculated from simulated diets of *n* foods eaten) using (top row) the unadjusted PS_i method and (bottom row) the Bayesian PS_i method. Dotted lines indicate equality between the original PS_i and simulated PS_i values. Solid lines are regression lines with standard errors shaded in gray. Blue dots represent population means.

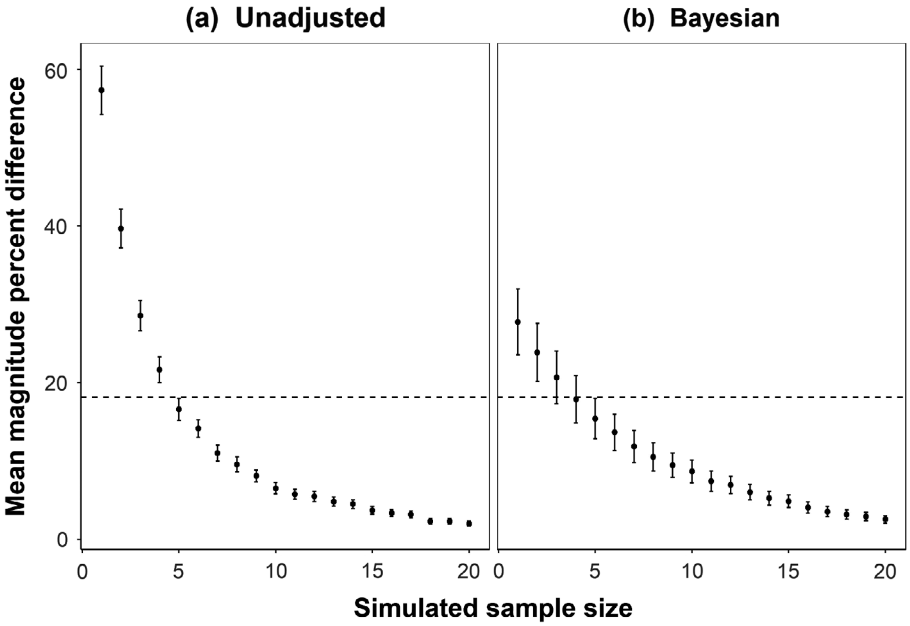

Fig. 5. Mean magnitude percent difference between original PSis and (a) unadjusted PS_is or (b) Bayesian PS_is at each simulated sample size (foods eaten per individual). Dotted horizontal line represents our designated acceptable difference of 18.15%.

accurately estimating the population mean ($P > 0.05$ for all paired *t*-tests; Fig. 4). For both methods, sample sizes of five or more foods satisfied Criterion 2 by yielding PS_i scores that were on average less than 18.15% different from their corresponding original PS_is (Fig. 5). However, as only the Bayesian method met Criterion 1, we applied a cutoff of five foods eaten and used only Bayesian PS_is in further analyses. Thirty-seven individuals met the reliability cutoff in 2017 and

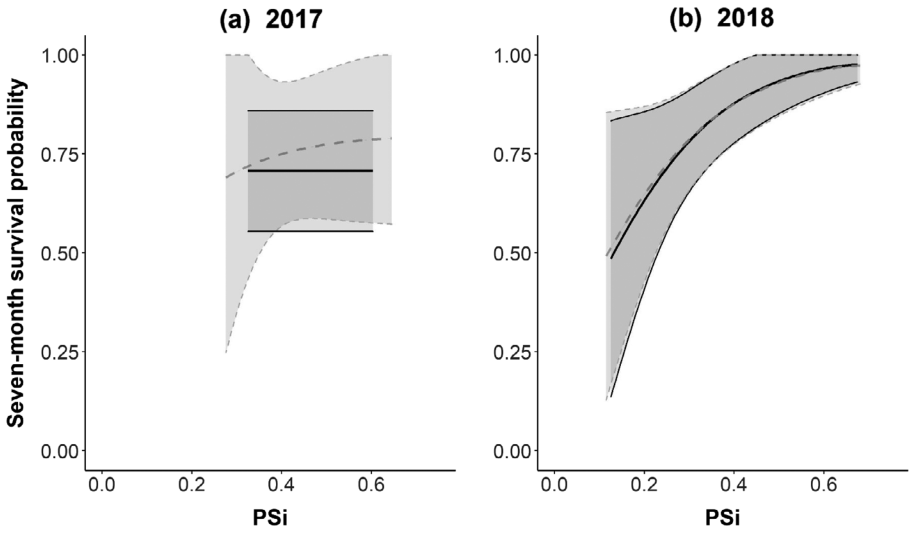

Fig. 6. Estimates of seven-month (February–September) survival probability as a function of dietary specialization (PS_i) in (a) 2017 and (b) 2018. Solid black curves are estimates derived from our Bayesian PS_is. Dashed gray curves are more conservative estimates derived from Bayesian PS_is that were randomly corrected to account for the uncertainty inherent to each individual's sample size of foods eaten. 95% confidence intervals (restricted between 0 and 1) are shaded in gray.

114 individuals in 2018. Applying this cutoff did not change the mean Bayesian PS_i significantly in 2017 (Welch's *t*-test, $t = -0.78$, df = 47.72, $P = 0.44$) or 2018 (Student's *t*-test, $t = 0.035$, df = 276, $P = 0.97$; Fig. 3b), but it raised the mean number of discrete encounters per bird to 4.78 ± 0.46 in 2017 and 6.13 ± 0.34 in 2018.

Validity

Both methods for quantifying resource selection found evidence for significant resource selection in 2017 (Wilks' $\lambda = 0.0056$, $P = 0.0020$; $\chi^2 = 1082$, df = 73, $P < 0.001$) and 2018 (Wilks' $\lambda = 0.0025$, $P = 0.0020$; $\chi^2 = 5810$, df = 173, $P < 0.001$). Resource selection was evident in 95% of individuals in 2017 (35/37) and 96% in 2018 (110/114), while the remaining individuals appeared to be randomly eating foods in proportion to their availability.

Utility

In both study years, the survival analyses indicated a possible relationship between diet and monthly survival (ϕ). In 2017, this relationship was weak. Our initial model selection did not find PS_i to be a significant predictor of survival (Appendix S1: Table S4a), and all individuals were predicted to have a 71% (95% CI = 55–86%) chance of survival over a seven-month period, regardless of diet (Fig. 6a). However, when rerun with uncertainty-corrected PS_is, a model containing PS_i appeared in the top model set alongside four others (Appendix S1: Table S4b). After averaging these models, seven-month survival ranged from 69% (95% CI = 25–100%) for the most specialist individuals ($PS_i = 0.28$) to 79% (95% CI = 57–100%) for the most generalist individuals ($PS_i = 0.65$), but uncertainty was high (Fig. 6 a).

In 2018, a larger dataset enabled us to estimate survival with more certainty and for a wider range of PS_is. A strong relationship between PS_i and survival emerged, as the two top models both included PS_i in the survival term (Appendix S1: Table S5a). Seven-month survival ranged from 48% (95% CI = 14–83%) in the most specialist individuals ($PS_i = 0.13$) to 98% (95% CI = 93–100%) in the most generalist individuals ($PS_i = 0.67$) and began to plateau as PS_i approached 0.70 (Fig. 6b). A second model selection using uncertainty-corrected PS_is identified the same two top models (Appendix S1: Table S5b) and found a similar range in seven-month survival probabilities, from 49% (95%

CI = 13–85%) in the most specialist individuals (PS_i = 0.11) to 98% (95% CI = 93–100%) in the most generalist individuals (PS_i = 0.68; Fig. 6b).

Discussion

While diet has historically been treated as uniform within species, many populations have now been found to contain a diverse array of specialists and generalists (Bolnick et al. 2003, Araújo et al. 2011). In our study, we demonstrated how the current dietary specialization framework could be enhanced and made more amenable to a range of sample sizes using the hihi, a threatened New Zealand passerine, as a case study. We first demonstrated that individual hihi vary in their use of foods within the broad species diet. Next, by applying a Bayesian adjustment (adapted from Coblentz et al. 2017) to the proportional similarity index (PS_i), we improved the reliability of our dietary estimates, particularly for individuals with the fewest repeated observations. We also showed that dietary variation did not arise from individuals randomly selecting foods in proportion to their availability, ensuring the validity of PS_i as a measure of individual preferences. Finally, a rarefaction procedure helped us decide which individuals to exclude from further analyses while providing a measure of uncertainty for the PS_is we retained. Even after accounting for this uncertainty, we found that diet predicted survival in at least one of our study years, highlighting the utility of diet as an ecologically informative trait.

Having a common dietary metric is crucial if we are to compare results across studies. Over the past two decades, PS_i has become the most widely used metric, but it may be vulnerable to overestimating specialization when sample sizes are small (Araújo et al. 2011). Our rarefaction procedure supported these concerns. However, a Bayesian adjustment enabled us to correct this error and expand upon the findings of Coblentz et al. (2017) by showing that this method can estimate a population's mean PS_i reliably even below sample sizes of five foods. While judging reliability is still somewhat subjective, there are two ways that this method improves upon the current practice of using an arbitrary sample size cutoff (or none at all). First, to maximize objectivity, an uncertainty threshold can be set a priori, informed by the variability in one's PS_i data. Second, the procedure enables uncertainty to be quantified and considered in further work, as we did in our survival analyses. Thus, future studies could benefit from using Bayesian PS_is, but they will need to exercise caution when comparing results to previous studies. In our case, comparing our mean Bayesian PS_is (0.42–0.45) to the mean of 0.47 reported in a review of 142 studies (Araújo et al. 2011) may have led us to conclude that hihi are similarly specialized to other taxa. However, if the Bayesian adjustment were applied consistently, the PS_is in these past studies could shift higher and hihi could lie at the specialist end of the spectrum.

Despite the benefits of the Bayesian method, it does have limitations which may be important to consider depending on the aims of a study. Studies vary widely in their reasons for exploring dietary variation. Some calculate individual-level specialization but focus their discussion on population or species means; for example, Araújo et al. (2007) compared mean PS_i values across four Brazilian frog species, finding that individuals are more specialized in species with broader diets. Other studies use dietary differences among individuals to explain variation in other traits; for example, in the spectacled salamander (*Salamandrina perspicillata*), Costa et al. (2015) showed that specialists exhibit better body condition than generalists. In our analyses, the Bayesian method always estimated the population's mean PS_i accurately but tended to underestimate the range of PS_is in the population at low sample sizes. Therefore, while Bayesian PS_is may be well-suited to questions relating to higher ecological levels (e.g., populations or species), studies attempting to explain individual differences may need to consider that these differences could be underestimated. Nevertheless, the accuracy with which the Bayesian method calculates population means still makes it the most useful method currently available.

Regardless of the ecological level they examine, many studies interpret PS_is as indicators of intrinsic dietary preferences without controlling for extrinsic factors such as environmental heterogeneity (Bolnick et al. 2003, Coblentz 2020). Some circumvent the need for this control by limiting their analyses to certain individuals. For example, Lowrey et al. (2016) focused their analysis of cougar (*Puma concolor*) diets on seven individuals with significantly overlapping home ranges so that resource availability could be assumed to be equal for all. Similarly, in a comparison of two sea otter (*Enhydra lutris nereis*) populations, Tinker et al. (2008) selected focal individuals so that each group had approximately equal spatial concurrence; this helped to ensure that an equal amount of dietary variation could be attributed to environmental variability in each population. In both examples, the number of individuals had to be limited to control for environmental heterogeneity. While phenology and habitat assessments can be time-consuming, adding these data (when feasible) could provide greater control over environmental effects and allow more individuals to be examined. In our study, we were able to demonstrate that very few hihi foraged randomly, and instead, most seemed to select foods based on individual preferences. Because our method provides a measure of the relative strengths of these preferences, it could enable us to explore the factors driving individual selectivity in future work.

Linking behavioral variation to fitness can provide key insights into ecological and evolutionary dynamics (Dingemanse and Réale 2005, Smith and Blumstein 2008). In at least one study year, we found that generalists survived significantly better than specialists over a seven-month period including winter, a resource-limited time for hihi (Armstrong and Ewen 2001) and many other animals. These results align with a broader trend at the species level, where generalist species tend to survive better than specialists in the face of climate change (Clavel et al. 2011, but see Colles et al. 2009). Generalization in other traits, such as habitat use, has also been shown to give species an advantage in anthropogenically disturbed landscapes (Devictor et al. 2008, Börschig et al. 2013). The most common explanation for this generalist advantage is that generalists are better equipped than specialists to respond flexibly to changing resource availabilities (Beever et al. 2017). However, it is difficult to determine the direction of causality between diet and survival based on an observational study like ours. In the case of hihi, a generalist diet could increase one's chance of survival, or individuals could shift toward more specialist diets when they are old or diseased, as they may be less able to forage efficiently or compete successfully for preferred resources. Similarly, in the wandering albatross (*Diomedea exulans*), foraging behavior is considered a key indicator of senescence; after a foraging trip, older males exhibit increased corticosterone, likely reflective of decreased foraging efficiency (Lecomte et al. 2010).

Alternatively, diet and survival may not be related causally but could be linked as part of a broader behavioral syndrome (Réale et al. 2007, Sih et al. 2012, Raffard et al. 2017). Dietary specialization could have wide-reaching effects by shaping an individual's developmental trajectory (Dall et al. 2012), predation risk (Toscano et al. 2016), or mate choice (Merrick and Koprowski 2017). Réale et al. (2007) also suggest that foraging behavior may be one of several component traits within a broader syndrome of boldness; instead of directly impacting fitness itself, foraging could act as an indicator of an individual's boldness, which influences fitness via effects on dominance, dispersal, or antipredator behaviors (see Fig. 2 in Réale et al. 2007). In fact, Richardson et al. (2019) recently found that bold hihi are more likely to survive to adulthood than shy hihi, suggesting that boldness may confer an advantage when individuals compete to establish territories or exploit risky food sources. To better understand the mechanisms linking diet to fitness, future work should examine possible correlations between diet and other traits, such as boldness, and examine whether generalists survive better in all environments.

To conclude, by applying statistical enhancements to the existing dietary specialization framework, we have outlined a path forward that could enable more taxa and methodologies to be assessed with greater accuracy. We have also identified a new case of dietary variation within a generalist species—adding to the growing literature on this phenomenon—and found evidence that dietary specialization can be used to predict survival. This highlights the value of dietary specialization as an ecologically meaningful trait that is worthy of greater consideration in the broader literature on behavioral variation.

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