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Estimating nestling diet with cameras: quantifying uncertainty from unidentified food items

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Cameras at nest sites are becoming a common means for quantifying nestling diet, but there are two problems associated with this method: food items delivered to nestlings often cannot be identified, and quantification of error around diet estimates for individual nests is problematic. We present a novel method of incorporating unidentified food items into diet estimates and quantifying error around these estimates for individual nests. In our method, unidentified food items are accounted for by considering all of the possible ways in which they could be allocated among previously defined food categories (possible outcomes). We then calculate the probability of each possible outcome by assuming the probability that an unidentified food item belongs to any given category is equal to the proportion of identified items from that category. All possible outcomes, along with the probability of each, represent a probability space. We allocate the unidentified food items to each category according to the most probable outcome in the probability space when estimating the contribution of each food category to nestling diets. Confidence intervals around diet estimates for each food category are estimated by simulating many samples from this probability space and using kernel density estimation. We demonstrate the implementation of our method with data from motion-sensitive cameras monitoring Arctic peregrine falcon *Falco peregrinus tundrius* nests in Nunavut, Canada.

Quantification of diet is an important aspect of avian ecology, particularly during the breeding season when demand for food is greatest. The quantity and composition of nestling diet influence growth rate, immunological development and, ultimately, survival and fitness (Birkhead et al. 1999, Naef-Daenzer and Keller 1999, Schwagmeyer and Mock 2008, Navarro-López et al. 2014, Resano-Mayor et al. 2014). There are many methods for determining nestling diet including stable isotope analysis (Moreno et al. 2010, Pokrovsky 2012), direct observation (Real 1996, Schwagmeyer and Mock 1997, Margalida et al. 2007), faecal analysis (Michalski et al. 2011, Orlowski et al. 2014) and, for birds of prey, prey remains and pellets analysis (Simmons et al. 1991, Symondson 2002).

However, one of the most cost effective and accurate methods of determining diet with minimal disturbance to the study organism is through direct observation of provisioning at the nest; observations can be made by observers with optical equipment or cameras installed at nest sites (Wille and Kampp 1983, Marti 1987, Franzreb and Hanula 1995, Margalida et al. 2005, Tornberg and Reif 2007, Sanchez et al. 2008, Zarybnicka et al. 2011). Camera systems for monitoring both cliff- and tree-nesting birds first emerged in the early 1980s and have become widely adopted as cameras have become smaller, cheaper and more advanced. A wide variety of surveillance techniques have been utilized including motion-sensitive and preprogramed cameras, time-lapse photography and video cameras (Delaney et al. 1998, Booms and Fuller 2003, Margalida et al. 2006, Tornberg and Reif 2007). Nest cameras can document food deliveries to nestlings while simultaneously collecting a host of other important data (e.g. phenology, behaviour and causes of mortality). One common problem in most diet studies employing nest cameras is the inability to identify all food items to fine-scale taxonomic levels or other categories. The percentage of unidentified food item can vary depending on the specific observation method used and whether prey deliveries by parents or prey remains at the nest are being identified (Margalida et al. 2007). Unidentified or broadly classified food items often constitute upwards of 20–40% of all observed deliveries (Rogers et al. 2006, Takagi and Akatani 2011, Schroeder et al. 2013).

As the proportion of unidentified food items increases, so too does the uncertainty around estimates of diet composition. Unidentified food items are particularly problematic if the proportional contribution of each food source to the total biomass consumed is required. Techniques have been developed to assign biomass estimates to unidentified food items (Miller et al. 2014), but attempts to quantify the amount of uncertainty around estimates of diet composition are lacking. Variance around diet estimates can be reported for the population (e.g. standard deviation or error), but this

does not account for the uncertainty related to unidentified food items, nor does it allow for measures of uncertainty for individual nests.

In this paper we develop and apply a method of incorporating unidentified food items into estimates of diet composition for individual broods, while also quantifying uncertainty around these estimates. Our method allows for the proportional contribution of each food source to overall diet to be estimated in both frequency of deliveries and biomass. We demonstrate our method using data collected with motion-sensitive cameras monitoring Arctic peregrine falcon *Falco peregrinus tundrius* nests in Nunavut, Canada.

Methods

Study area and nest monitoring

The study took place in a tundra ecosystem in the eastern Canadian Arctic near the community of Igloolik, Nunavut (69°53′45″N, 82°50′70″W). Spring thaw begins in early June and the majority of terrestrial snow cover has melted by early July. The area experiences short, cool summers with temperatures ranging from 2 to 7°C and rainfall accumulation averaging 86 mm from June to August (Robinson et al. 2014). Cliffs along coastlines and the shores of inland lakes provide nesting habitat for peregrine falcons, rough-legged hawks *Buteo lagopus*, common ravens *Corvus corax*, glaucous gulls *Larus hyperboreus*, Thayer's gulls *L. thayeri*, Canada geese *Branta canadensis* and common eiders *Somateria mollissima*. Black guillemot *Cepphus grylle* colonies occur on small rocky islands throughout the study area. Inland areas consist of raised beaches, dry tundra, sedge meadows, wetlands and lakes which provide breeding habitat for a diverse community of song and shorebirds such as Lapland longspurs *Calcarius lapponicus*, snow buntings *Plectrophenax nivalis*, American golden plovers *Pluvialis dominica*, semipalmated plovers *Charadrius semipalmatus*, phalaropes *Phalaropus* spp. and sandpipers *Calidris* spp., all of which are potential prey items for the peregrine falcon. Collared lemmings *Lemmus trimucronatus* and brown lemmings *Dicrostonyx groenlandicus* are abundant, but cyclical prey for peregrine falcons in the study area.

Once peregrines laid eggs and began incubating (13–20 June), we secured a motion-sensitive camera (PC85 Rapidfire or PC8000 Hyperfire) to a large rock 1–1.8 m from each nest. The infrared motion detector and lens of each camera was aimed ~0.15 m above the nest cup using a laser pointer. Cameras were programmed to take an image when motion was detected at a maximum rate of 1 image / 2 seconds (e.g. Supplementary material Appendix 1 Fig. A1). Cameras had infrared illuminators allowing images to be taken in low light. Each camera was in place until all nestlings had fledged from the nest (20–25 August). Nests were visited once per week to replenish the cameras' memory cards and batteries. Because we were interested in nestling diet, we only analyzed prey deliveries while nestlings were 1–14 days old. Once nestlings were > 14 days old, they started moving around the nest cliff, so some prey deliveries occurred outside of the camera's field of view.

Estimating diet along with uncertainty

Prey items delivered to nests were identified to the finest taxonomic level possible and then assigned to one of five ecologically meaningful prey categories: insectivorous birds (songbirds and shorebirds; Passeriformes, Scolopacidae and Charadriidae), gulls (Laridae, Sternidae and Stercorariidae), ducks (Anatidae), black guillemots, or lemmings (e.g. Supplementary material Appendix 1 Fig. A1). Prey items that could not be identified due to low lighting, poor camera focus or a blocked field of view were assigned to one of two possible categories: unidentified or unidentified avian (Table 1 provides example datasets from four separate nests).

We then determined all of the possible ways in which unidentified prey items could be allocated among the different categories. Because we had multiple, nested, categories, which is common in this type of study, we first allocated prey items from the broadest unidentified category. In our example, a prey item in the unidentified category could have been either a lemming or one of the avian prey categories. We therefore determined all of the possible ways in which the unidentified prey items could be allocated to the lemming and the unidentified avian categories (possible outcomes; e.g. Table 2) using the 'compositions' function in the 'partitions' package (Hankin 2006) for the R statistical environment (<www.r-project.org>) (Supplementary material Appendix 2).

Next, we calculated the probability of each possible outcome j (Po_j) occurring by using probability theory:

$$Po_j = \frac{\prod\left(p_i^{N_{ij}}\right)\left(\sum N_{ij}\right)!}{\prod\left(N_{ij}!\right)}$$

where P_i is the probability of an unidentified prey item being the ith category, and N_{ij} is the number of unidentified prey items assigned to category i in outcome j. The P_i values can be determined based on knowledge of the specific system being studied. For example, unidentified prey items could be considered to have an equal probability of being in each prey category, or probabilities could be based on the relative availability of prey from each category within the study system (e.g. prey surveys). The latter strategy assumes the consumer being studied is a generalist that consumes each prey type in proportion it its availability. Alternatively, P_i's could be based on the total number of identified prey items in each category. Using the proportion of identified prey items to estimate P_i could be biased if some prey categories are more easily identified than others; for example, small prey items may be

Table 1. Data from four nest cameras monitoring peregrine falcon nestlings in Nunavut, Canada, showing the frequency of prey items within each category delivered to nestlings during the observation period.

Nest site	Year	Unid.	Unid. avian	Insect. bird	Duck	Gull	Black guillemot	Lemming
1	2010	2	3	55	0	0	0	1
2	2010	7	4	68	5	0	1	1
8	2011	45	3	72	0	0	0	12
14	2011	16	1	19	1	2	0	24

Table 2. All of the possible outcomes (j) of allocating the 7 unidentified prey items from nest site 2 in 2010 (Table 1) to either the unidentified avian or lemming categories, along with the probability of each outcome occurring (Po_j).

Outcome j	Unid. avian	Lemming	Po_j
1	7	0	0.906
2	6	1	0.090
3	5	2	0.004
4	4	3	<0.001
5	3	4	<0.001
6	2	5	<0.001
7	1	6	<0.001
8	0	7	<0.001

harder to identify relative to larger prey. In our system avian prey deliveries were identified as the smallest prey category (insectivorous birds) more frequently than the larger-bodied prey categories (ducks, gulls and black guillemots), and lemmings, which were not commonly identified, are roughly the same size as insectivorous birds. We, therefore, did not feel that prey category had any influence on our ability to identify prey deliveries, so we assumed P_i was equal to the proportion of all identified prey items that were assigned to category i across all nests in a given year (Table 3). We estimated P_i separately for each year because lemming populations fluctuated throughout this study (Robinson et al. 2014) and Arctic peregrine falcons increase their consumption of lemmings when lemming populations peak (Court et al. 1988, Robinson 2015). Although estimates of prey density were available for our study area (Robinson et al. 2014), evidence suggests Arctic peregrine falcons are selective and do not consume prey in proportion to availability (Burnham and Mattox 1984, Rosenfield et al. 1995, Robinson 2015). We could have estimated P_i for each nest individually, but for nests with a high proportion of unidentified prey (e.g. Table 1, site 8), these proportions may not accurately represent true probabilities.

Using the above equation and the N_{ij} and P_i values from Table 2 and 3, respectively, we estimated the probability of each possible outcome, which produced a probability space (Table 2). Although the first possible outcome is the most probable, the possibility of the other outcomes occurring can be accounted for and used to estimate uncertainty around diet estimates. We simulated 100 samples from the probability space using the 'sim' function from the 'partitions' package (Hankin 2006) in R (Supplementary material Appendix 2). We then added the number of prey assigned to the unidentified avian and lemming categories in each of the 100 simulated samples to the number of identified prey deliveries in each of these categories (Table 4). If we were concerned only with the proportion of avian versus lemming prey within the diet of peregrine nestlings, we could stop here and calculate these proportions for each of the simulated samples and calculate measures of central tendency (e.g. mode) and dispersion (e.g. 95% confidence intervals) across the 100 simulated samples. But, because we were interested in estimates of diet composition with a finer taxonomic resolution, we repeated this process again.

Table 3. The probability of an unidentified prey item being within each prey category for each year. Probabilities are based on the proportion of identified prey items within each prey category across all nests for a given year.

	Unidentified		Unidentified avian			
Year	Lemming	Unid. avian	Insect. bird	Duck	Gull	Black guillemot
2010	0.014	0.986	0.953	0.039	0.000	0.008
2011	0.269	0.731	0.968	0.010	0.021	0.000

This time, we determined all of the possible outcomes of allocating the updated unidentified avian prey items from each of the 100 simulated samples among the four avian categories. The additional prey categories resulted in a larger number of possible outcomes, particularly if there were a large number of unidentified avian prey. For example, sample 1 in Table 4 had 364 possible outcomes for which the 11 unidentified avian prey could be allocated to the four avian categories. As before, we used the above equation to calculate the probability of each possible outcome to produce a probability space, assuming P_i was equal to the relative proportion of each identified avian prey item for a given year (Table 3). We then simulated another 100 samples from each of the 100 probability spaces, resulting in 10 000 samples.

For each sample, the proportional contribution of each prey category can be calculated either in frequency of deliveries or total biomass of deliveries. We transformed the frequency of deliveries into biomass using prey weights from the literature and adjusting them based on the average size of prey items relative to adult and nestling peregrines within camera images. We assumed lemmings, insectivorous birds, ducks, gulls and black guillemots weighed 40, 30, 50, 150 and 300 g, respectively (Starck and Ricklefs 1998, Butler and Buckley 2002, Lindström et al. 2002, Montgomerie and Lyon 2011, Savoca et al. 2011, Legagneux et al. 2012).

Treating each prey category separately, we then used kernel density estimation across the distribution of 10 000 proportions to determine the most probable proportion (mode). We estimated 50, 75 and 95% confidence intervals around the most probable proportion by calculating the highest density regions within the probability distribution created from the kernel density estimation (Hyndman 1996). We used the 'hdr' function within the 'hdrcde' package (Hyndman 2013) for R to conduct the kernel density estimation and calculate the highest density regions (Supplementary material Appendix 2). Because we used kernel density estimation separately for each prey category, the modes of the proportions did not necessarily sum to one. If proportions that sum to one are required, they can be calculated based on the most probable allocation of unidentified prey items (possible outcomes), and the 10 000 samples can be used only for calculating confidence intervals. We have provided an example dataset and R code to carry out the above analysis in Supplementary material Appendix 2.

Results

Peregrine falcon diet varied across nests and years. In 2010, diet was dominated by insectivorous birds with a small component of ducks and marine birds in one nest (Fig. 1a–b). In 2011, the lemming component of diets increased, but

Table 4. An example of 10 samples of possible outcomes simulated from the probability space shown in Table 2, demonstrating how the frequency of identified prey items in each prey category (site 2, 2010, in Table 1) were modified by allocating the unidentified items according to each sampled outcome.

	Unidentified		Unidentified allocated to other categories					
Sample no.	Unid. avian	Lemming	Unid. avian	Insect. bird	Duck	Gull	Black guillemot	Lemming
1	7	0	4 + 7 = 11	68	5	0	1	1 + 0 = 0
2	6	1	4 + 6 = 10	68	5	0	1	1 + 1 = 2
3	7	0	4 + 7 = 11	68	5	0	1	1 + 0 = 0
4	7	0	4 + 7 = 11	68	5	0	1	1 + 0 = 0
5	7	0	4 + 7 = 11	68	5	0	1	1 + 0 = 0
6	7	0	4 + 7 = 11	68	5	0	1	1 + 0 = 0
7	7	0	4 + 7 = 11	68	5	0	1	1 + 0 = 0
8	7	0	4 + 7 = 11	68	5	0	1	1 + 0 = 0
9	6	1	4 + 6 = 10	68	5	0	1	1 + 1 = 2
10	7	0	4 + 7 = 11	68	5	0	1	1 + 0 = 0

there was still a substantial contribution of insectivorous birds (Fig. 1c–d). The width of the 95% confidence intervals around estimates of the proportional contribution of each prey category to the diet increased with the number of unidentified prey deliveries (Table 1, Fig.1).

Discussion

The method presented offers a means of incorporating unidentified food items into diet estimates, while quantifying uncertainty around these estimates. A convenient aspect of this method is that it allows for nested unidentified categories at multiple taxonomic levels, which is common among studies of nestling diet using nest cameras (Behney et al. 2010, Miller et al. 2014). When a high proportion of food deliveries are unidentified, diet estimates become uncertain and it is difficult to estimate the relative contribution of each food source to the overall biomass of food consumed. We overcome this limitation by considering every possible way in which unidentified food items can be allocated to each food category and assigning a probability to each possible outcome.

Another advantage of our method is that the probabilities of possible outcomes can be based on previous knowledge of the system being studied, such as data on prey availability, diet

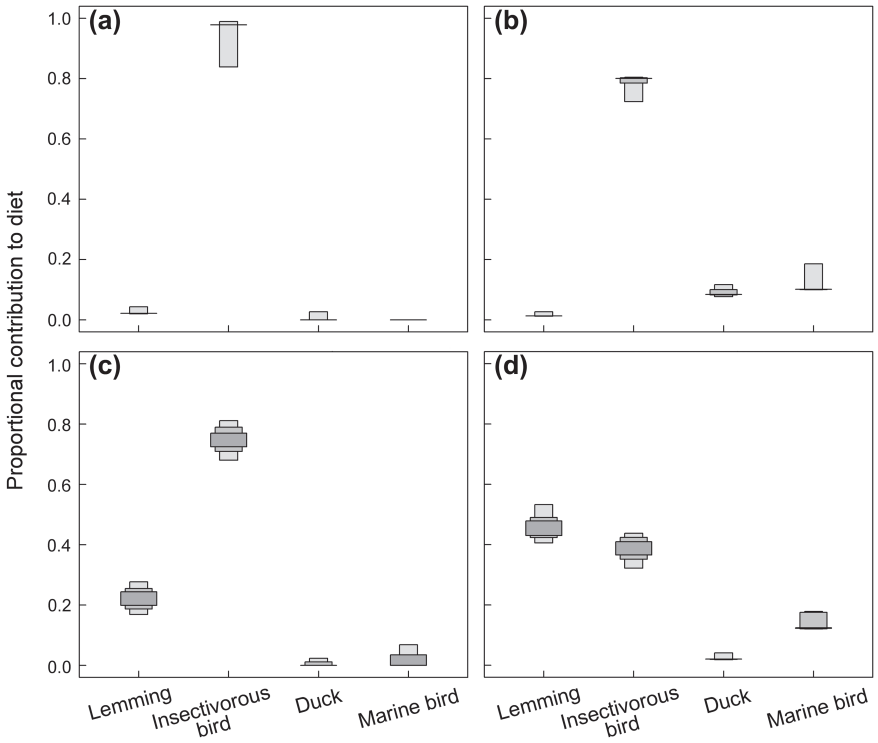

Figure 1. Highest density regions of kernel density estimates from the distributions of the proportional contribution of each prey category (gulls and black guillemots have been combined into marine birds) to the diet of nestling Arctic peregrine falcons in Nunavut, Canada. The 50, 75 and 95% regions are shown; boxes decrease in thickness and darkness from 50 to 95%. Nests shown are site 1, 2010 (a), site 2, 2010 (b), site 8, 2011 (c), and site 14, 2011 (d).

estimated from other methods, or the identified food items documented. In our example, we assumed there was a higher probability of an unidentified prey item (P_i) being an insectivorous bird than any other prey type, because insectivorous birds were more common among the known deliveries. As a result, the probabilities were skewed toward those possible outcomes with many insectivorous birds, so there was a small range of possible outcomes drawn from the probability spaces leading to narrow 95% confidence intervals around our diet estimates. Had we assumed there was an equal probability of an unidentified item being within each prey category, confidence intervals would have been wider because there would be a greater range of possible outcomes drawn from the probability spaces (Supplementary material Appendix 3 Fig. A2). When estimating diet in terms of biomass, changes in P_i values for larger-bodied prey categories will have greater influence on the resulting diet estimates. For example, changing P_i from 0.00 to 0.50 for gulls (the heaviest prey category) changed the estimate of their proportional contribution to the diet (mode) of nestlings at site 1, 2010, from 0.00 to 0.14 (Fig. 1a, Supplementary material Appendix 3 Fig. A2a). A small change in the number of unidentified prey assigned to gulls resulted in a large change in their biomass contribution. We recommend that users of this method use care and have adequate justification when choosing a method to assign P_i values because these probabilities will inevitably influence diet estimates and the amount of error around them (Supplementary material Appendix 3 Fig. A2).

Our method provides a novel means of estimating error around diet estimates for individual nests, rather than just the population. Estimating error around individual nests is particularly useful if diet estimates are to be used in further statistical analysis. For example, the use of Bayesian mixing models to estimate diets based on stable isotopes is becoming common (Phillips et al. 2014), and a major advantage of the Bayesian statistical framework is that informative prior hypotheses about the diet can be incorporated into the analysis (Moore and Semmens 2008). These priors are entered as estimates of the mean proportional contribution of each food source to the diet, but a measure of standard error around the mean of one food source is also required (Parnell et al. 2010). Nest cameras provide a way to estimate prior hypotheses for Bayesian mixing models, and our method demonstrates a way of quantifying standard error around these priors.

Although studies estimating nestling diets with nest cameras are somewhat biased toward large-bodied birds, such as raptors (Delaney et al. 1998, Booms and Fuller 2003, Margalida et al. 2006), the method has been used on species as small as blue tits *Parus caeruleus* (Tremblay et al. 2005) and ladder-backed woodpeckers *Picoides scalaris* (Schroeder et al. 2013). As the technology improves and cameras become smaller and higher in resolution, studies using nest cameras to estimate nestling diet will likely proliferate. Our method provides a way to quantify the uncertainty associated with unidentified food deliveries, which are inevitable in any study using nest cameras.

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Supplementary material (Appendix wlb.00114 at <www.wildlifebiology.org/readers/appendix>). Appendix 1–3.