

CHAPTER 5

Quantifying diet

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5.1 Introduction

Dietary studies of raptors and other predators help us to understand their ecological role (Newton 1979, Marti et al. 2007). Raptors are important actors in ecology and evolution, because their predatory habits facilitate the development of life history traits (Valkonen et al. 2012, McGraw and Berger 2013) that maintain healthy ecosystem function and promote biodiversity (Sergio et al. 2008). Additionally, the individual and population health of raptors can indicate the health of their system (Sergio et al. 2008, Barraquand et al. 2014) where changes to reproductive output of pairs may signal ecosystem disruption (Steenhof et al. 1997). Thus, studying raptor diet provides an understanding of ecological relationships, mechanisms involved in ecosystem functions, a measure of system health, and critical information for conservation (Newton 1979, Nyström et al. 2006, Sergio et al. 2008, Dawson et al. 2011, Pokrovsky et al. 2014).

Gyrfalcon diet has been studied across its circumpolar range through a variety of methods including indirect analyses by the collection of pellets and prey remains, and direct observations at nest sites and frequently used locations during the nonbreeding season (Bengtson 1971, Muir and Bird 1984, Poole and Boag 1988, Nielsen and Cade 1990, Dekker 2003). Most recently the direct method of nest observations through photography has greatly improved our understanding of Gyrfalcon prey use and diet during the breeding season (Booms and Fuller 2003b, Robinson 2016). This chap-

ter summarizes techniques to quantify Gyrfalcon diet, and presents guidelines to conduct a study and analyze diet data obtained through cameras deployed at nests.

5.2 Pellet and prey remains

The use of indirect methods such as pellet and prey remains analysis has provided much insight into Gyrfalcon diet (Cade 1960, Nielsen and Cade 1990). Most descriptions of Gyrfalcon diet are based on some combination of analysis of pellets and prey remains (Dementiev and Gortchakovskaya 1945, Hagen 1952, Cade 1960, Bengtson 1971, Roseneau 1972, Summers and Green 1974, Langvatn 1977, Kalyakin and Vinogradov 1981, Poole and Boag 1988, Huhtala et al. 1996, Nielsen 1999, Booms and Fuller 2003a, Nyström et al. 2005).

Pellets and prey remains can be collected in nests, below nests, and at accessible perch sites at and around occupied cliffs. The timing that collections are made determines the period of the Gyrfalcon life cycle for which diet is characterized. Collections made during the egg laying period pertain to diet during courtship and pre-incubation. To describe diet during the brood rearing period, the pre-hatching collection must be kept and analyzed separately from subsequent collections made during and immediately after brood rearing (Booms and Fuller 2003b, Robinson 2016). Minimizing collections during the nesting period limits disturbance to breeding raptors. For instance, appropriate collection intervals when quantifying Gyrfalcon diet during brood rearing are once at nestling age 20–30 days, and once after all nestlings have fledged and deliveries to the nest site have ceased.

Diet can be quantified from pellets by identifying all items that represent prey types comprised by a single pellet (Poole and Boag 1988), or by a percent contribution of prey type for each pellet (Nielsen and Cade 1990). For example, if ptarmigan and ground squirrel are equally represented in a single pellet, the pellet would receive a score of 0.5 ptarmigan and 0.5 ground squirrel. The proportional diet composition by prey type is calculated by dividing the cumulative score of each prey type by the number of pellets in the analysis (Booms and Fuller 2003b).

The minimum number of individual prey items found in the diet can be estimated through the identification of prey remains based on the most commonly found bone, body part, or feathers representing one individual (e.g., the keel or humerus of ptarmigan). Once items are identified, average biomass values assigned to the number of prey items for that category provide percent contribution by prey type to overall biomass in the diet (Cade 1960, Nyström et al. 2005, Pokrovsky et al. 2014, Resano-Mayor et al. 2014). However, for biomass conversion it is important to consider that some prey types, such as large items, cannot be consumed in one meal and

their contribution is not truly represented in a single pellet or by remains (Katzner et al. 2006). Considering this detail in relation to the suite of prey types catalogued in the diet will ensure that proper biomass conversions are applied.

Coupled together, pellet and prey remains analysis offers an informative view and useful quantification of diet for Gyrfalcons. A primary advantage of pellet and prey remains analysis is that it requires less effort and cost than other approaches, thus allowing larger sample sizes and greater flexibility to describe diet during periods when prey remains do not accumulate in nests, such as the courtship period. However, these indirect methods are biased in ways that limit their ability to fully represent the true contribution of particular prey types to the diet (Marti et al. 2007, Robinson 2016). Prey remains may underestimate the contribution of small prey items to the diet, and overestimate the contribution of large conspicuous prey types due to detection biases. Pellets may overestimate the contribution of large prey items because multiple pellets may represent only one large prey item. This is especially true for species such as Gyrfalcon that have a tendency to cache prey. Additionally, large prey items may be fed to multiple nestlings and consumed by the adult as well, causing one prey item to be represented in many pellets. Pellets may also misrepresent the contribution of prey types because some body parts may be more digestible than others, rendering them difficult or impossible to detect in pellets. Therefore, pellet and prey remains analysis has been shown to misrepresent the true contribution of some prey types, for example a failure to detect Arctic ground squirrel (*Urocitellus parryii*) as the most used prey type in one year of study (Robinson 2016).

5.3 Stable isotopes

Stable isotope analysis (hereafter referred to as SIA) is a useful tool to investigate general patterns of prey use in raptors (Marti et al. 2007, Resano-Mayor et al. 2014). Most avian diet studies that have used stable isotope analysis have focused on ratios of the elements Carbon ($^{13}\text{C}/^{12}\text{C}$) and Nitrogen ($^{15}\text{N}/^{14}\text{N}$; Inger and Bearhop 2008). Dietary items differ in the isotopic ratios of these elements and, once incorporated into the predator's tissues, provide a signature that indicates their general dietary habits (Pearson et al. 2003, Becker et al. 2007, Inger and Bearhop 2008). In most cases, SIA provides a general view of diet and is most useful when a diet consists of two isotopically distinct sources (Hobson and Clark 1992a, Hobson 2011). Thus, SIA is limited in its ability to describe prey use in fine detail, and cannot replace conventional techniques that provide more detailed information of diet, such as taxonomic distinctions between food types. In Gyrfalcon diet studies, SIA can be useful to compare general prey use over a temporal scale and between geographic regions, particu-

larly populations along coastlines that may have differing dietary composition from populations breeding inland, due to the relative contribution of prey types such as marine birds vs. terrestrial mammals (Nielsen and Cade 1990).

Isotopic measures can be obtained from tissue such as feathers, blood, or talon clippings. Because tissues differ in isotopic turnover rates, it may be necessary to collect and analyze isotopic content of numerous tissue types to gain information on both short-term and long-term diet information (Tieszen et al. 1983, Pearson et al. 2003). For instance, isotopic signatures in blood represent diet over short time periods, i.e., days prior to capture, whereas feathers and talons contain information on dietary components at the time of tissue synthesis (Pearson et al. 2003). Analysis of multiple tissues provides a view of broad predatory habits to assess general trends in prey use on both a spatial and temporal scale given proper sampling.

Isotopic mixing models quantify relative contributions of isotopic sources to the diet (Moreno et al. 2010). Further, techniques such as Bayesian isotopic mixing models address issues related to variation and uncertainty in models, thus strengthening the power of inference (Moreno et al. 2010, Parnell et al. 2010). These techniques require information on the trophic ecology of the species to form dietary assumptions upon which the models depend, i.e., they require that a signature represent a known prey item in Gyrfalcon diet. Isotopic fractionation factors (hereafter referred to as IFF's), or the changes in isotopic ratios during assimilation into animal tissues, differ by species and the tissues used for analysis (Tieszen et al. 1983, Hobson and Clark 1992b). It is essential to have a basal understanding of fractionation factors specific to the Gyrfalcon before using this method for diet estimation. IFF's have not been investigated for the Gyrfalcon and represent yet another area of needed study for the species. However, IFF's have been investigated on the Peregrine Falcon and may provide a framework for developing studies on fractionation factors specific to Gyrfalcons (Hobson and Clark 1992b).

To my knowledge, there are at present no published Gyrfalcon diet studies that have used SIA to assess dietary habits. Future diet studies should consider this method to assess temporal or spatial patterns in prey use, and further our understanding of the Gyrfalcon as a predator in tundra ecology.

5.4 Nest cameras

Until recently, logistical challenges have limited the application of cameras as a method to study diet at raptor nests. Due to the challenges associated with the remote breeding locations of Gyrfalcons, only two studies have used cameras to quantify diet during nesting (Booms and

Fuller 2003b, Robinson 2016), although others have used this method to gather different information pertaining to Gyrfalcon diet and behavior (Jenkins 1978, Poole 1988, Poole and Bromley 1988, Tømmeraaas 1989). Use of nest cameras has been limited because of high cost per unit, increased human disturbance caused by time and effort required for camera maintenance, battery maintenance, and installation procedures that have involved long periods at nest sites (Booms and Fuller 2003c, Rogers et al. 2005, Smithers et al. 2005). New technology (e.g., greater memory capacity, improved battery life) reduces camera installation times and the number of visits post installation thus reducing effort while limiting disturbance (B. W. Robinson, unpubl. data).

Video systems require increased maintenance and a great deal of battery power, which limits sample size and increases disturbance (Lewis et al. 2004). These issues limit the use of video systems for study species such as the Gyrfalcon, which nest on widely dispersed cliffs in remote locations. For example, studies that employed video systems in Gyrfalcon nests gathered diet information from few nests in a single season (Poole 1988, Poole and Boag 1988, Poole and Bromley 1988, Tømmeraaas 1989, Booms and Fuller 2003a).

Motion-activated cameras that capture still images have been used for many years to monitor wildlife, however their utility for monitoring diet in raptor nests has been limited due to cost per unit, image quality, installation schemes, programming schemes, memory/battery life, technical failures, and altered subject behavior (Tornberg and Reif 2007, García-Salgado et al. 2015, Cutler and Swann 2016). Here I describe the advantages and uses of modern camera technology to describe Gyrfalcon diet during the brood rearing period (Robinson 2016).

With proper camera units, motion-activated photography can now provide fine scale views of prey use over long periods of time because of low data storage requirements, low power (battery) requirement, and menu driven programming that is adaptable to various project needs (Robinson 2016). If programmed and installed correctly, motion-activated cameras provide the most accurate measure of Gyrfalcon diet at nests. The use of cameras for quantifying diet at nests provides information regarding prey use at a scale that has not been achieved previously for Gyrfalcons, thus overcoming the past financial and logistical constraints of this technology.

The success of camera studies to quantify Gyrfalcon diet depends on multiple factors including camera selection, timing of camera installation, and decisions on installation and programming. Here I present considerations for conducting a camera study. A detailed description of guidelines and appropriate considerations for conducting a camera study are given in Appendix 2.

5.4.1 Formatting data from camera images

Here, I describe the process of quantifying data from camera images, and provide sample data to conduct analyses of Gyrfalcon prey use as obtained by cameras installed at nest sites. From this quantification comes the ability to empirically assess dietary trends, dietary habits, and to connect prey use to the broader ecosystem.

Many types of data can be recorded from nest camera photos. The following are suggested data categories: nest ID, date, nestling age, prey identification (species, age), time of day, treatment of item (fully consumed or not), comments, and photo organization information (e.g., camera period, photo group, photo number). Table 5.1 provides data organization as adapted from Robinson (2016) for quantifying diet during the brood rearing period. Each row represents a single prey item delivered to the nest. Nest (column 1) is defined as the unique nest label assigned by the researcher. For date (column 2) I recommend recording the calendar date in one column, and calculating Julian date in a separate column (column 3). Nestling age (column 4) is the age of the oldest nestling, calculated by either the hatch date of the first egg as captured by the nest camera, or backdated from data obtained from nestlings midway through the brood rearing period (see Appendix 1 for methods on aging Gyrfalcon nestlings). Camera period, photo group, and photo number (column 5) all refer to the file organization path to help find the exact photo from which the data in the spreadsheet were derived. This information differs among camera models and is needed to find a specific image that contains information regarding the prey item. Prey ID (column 6) is the lowest taxonomic level assigned to a prey item (Booms and Fuller 2003b, Robinson et al. 2015, Robinson 2016), and varies with the observer's confidence in identifying items (e.g., some items are identifiable to species, sex, age, and others only to "bird").

Assigning items to broad taxonomic distinction such as family or order remain helpful for biomass assignments and for understanding prey selection over time. For the sake of simplicity, all items in Table 5.1 are identified as PTAR (a 4-letter code for ptarmigan species). Prey age (column 7) refers to the relative age of the prey item (e.g., young or adult), which allows us to assign a more accurate biomass to individual prey items. In the case of a partially grown item, a percentage of adult size can be assigned by visually estimating its size as a percentage of adult size. Once items are identified, assign average mass values for the corresponding species or prey type to identified items for biomass calculations (column 8). In the case of a partially consumed item, an estimated percentage of the whole prey type can be determined visually and applied the average biomass value of the species (e.g., 70% applied to a 485 g PTAR equates to 339.5 g).

Table 5.1. Example data for quantifying Gyrfalcon prey deliveries. Each row represents one prey delivery.

Nest	Date	Date	Nesting Age	Photo Info. (Period, Group, #)	Prey Id	Prey Age	Mass	Time	Duration	Item Fully Consumed?	Comments
101	24-May	14144	5	1,100,26	PTAR	Adult	485	1601	7	N	Male brought item to nest. Female fed nestlings.
101	24-May	14144	5	1,100,62	PTAR	Adult	485	1745	9	N	Male brought item to nest. Female fed nestlings.
101	24-May	14144	5	1,100,126	PTAR	Adult	485	2145	10	N	Item appeared in nest with female feeding nestlings.
101	24-May	14144	5	1,100,148	PTAR	Adult	485	2325	1	N	Female left briefly and returned with item, then fed nestlings.
101	25-May	14145	6	1,100,325	PTAR	Adult	485	634	19	Y	Male brought item to nest. Female fed nestlings.

Additionally, a familiarity with the literature may also help place proper biomass assignments to prey types. For instance, due to the regional variation in Arctic ground squirrel mass in western Alaska, Robinson (2016) assigned an average mass from literature detailing squirrel biomass for Alaska (Sheriff et al. 2013). Biomass values for unknown items may be visually estimated by comparing them to a known item's size (e.g., an item approximately the size of a Lapland Longspur [*Calcarius lapponicus*] should receive a mass assignment of 27 g; [Booms and Fuller 2003a]), or statistical techniques may be applied to assign all unknown items to categories based on the probability an unknown item is a given prey type (Robinson et al. 2015). Time (column 9) corresponds to the time the item was delivered. Duration (column 10) tells us the length of the feeding bout, which can indicate if a prey item was fully consumed or likely to reappear in a subsequent prey delivery. Item fully consumed (column 11) refers to the condition of prey removed by adults following feeding, which is useful to note because it minimizes double counting of prey that are cached and delivered to the nest more than once (Booms and Fuller 2003a). Additionally, noting whole or headless prey as one item and noting individual parts delivered during a 24-hour period helps avoid double counting, because an individual prey item may comprise multiple parts brought to the nest over time (Booms and Fuller 2003a, Robinson 2016). Comments (column 12) are useful because some notes regarding a prey item or adult behaviors can be useful later in error checking the data.

5.5 Analysis of diet

5.5.1 Introduction to diet analysis

After diet has been quantified, there are a number of ways to process the data to investigate aspects of prey use. Simple descriptive measures include richness (the number of species comprised by the diet), evenness (representation by number of a given prey type relative to others), or the combination of the two, which is termed diversity (Pielou 1966). Diversity measures used in raptor diet studies illustrate the structure of prey use by characterizing the number of different prey groups relative to the number of prey items in each group (Magurran 2004). Assessing diet diversity is often of interest to illustrate where a predator, such as the Gyrfalcon, lies on the spectrum from generalist to specialist to better illustrate its role in its ecosystem (Glasser 1982, Malo et al. 2004). The potential broader utility of diversity measures in raptor studies are, for instance, to provide a method for diet comparison among populations or species (Steenhof and Kochert 1985, Bellocq 2000, Miller et al. 2014), or to relate dietary trends to other aspects of raptor life history (Korpimäki 1987).

The following section provides an overview of typical measures of dietary diversity used in raptor studies. In addition, this section provides a stepwise explanation for processing dietary data in preparation for analysis, and an example with generalized linear mixed models to investigate trends in prey use over time.

5.5.2 Assessing the completeness of a dataset

Rarefaction curves provide a method to quantify the completeness of a sampling effort (Gotelli and Colwell 2001) and lend greater confidence to the inferences drawn from analyses. Rarefaction curves represent the cumulative means of re-sampling the pooled individuals to produce the statistical expectation of adding additional categories to a dataset (Gotelli and Colwell 2001), such as prey categories in diet studies. Thus, its utility in Gyrfalcon diet studies is illustrated by the point at which the curve approaches an asymptote, which represents the number of samples (individual prey items) required to capture all species constituting the diet in a study area. Rarefaction curves are easily produced in statistical programs or environments such as EstimateS (Colwell 2013) and R (R Core Team 2016). In our case we provide an example of how to format data for input into R.

Here, we use a simulated dataset representing hypothetical sites in Alaska, Iceland, and Greenland. The first row in the data table names the sites, represented by columns one, two, and three (Table 5.2) and subsequent rows represent individual prey categories. Each cell therefore contains the number of a given prey category recorded at a given site. Once the data are loaded into R, we will use the `rarecurve()` function in the package `vegan` (Oksanen et al. 2017) to plot the rarefaction curves for each site. Note that we add the `t()` function within the code for `rarecurve` to transpose the dataframe.

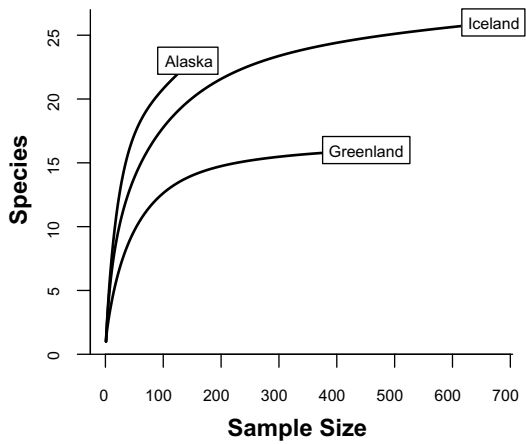
```
# plot rarefaction curve by site
rarecurve(t(preys))
```

Note that the rarefaction curves for Greenland and Iceland approach the asymptote whereas the curve for Alaska does not (Fig. 5.1). Examination of the curves therefore suggests that sampling is complete for Greenland and Iceland, but not for Alaska.

Table 5.2. Hypothetical data for use in constructing rarefaction curves for Gyrfalcon diet in three study areas. Rows correspond to prey species, and numbers are counts of prey items from each study area.

	Iceland	Greenland	Alaska
	202	300	38
	103	25	0
	68	39	5
	61	0	3
	28	3	2
	32	0	11
	35	19	10
	18	12	6
	39	0	7
	0	7	1

Figure 5.1. Rarefaction curves generated from data in Table 5.2. Where curves approach the asymptote (e.g., Greenland, Iceland), sampling is considered adequate for further statistical inference.



5.5.3 Characterizing diversity of diet

Diversity measures such as Simpson's index and Shannon index, or niche diversity measures such as Levin's index of diet breadth (Shannon and Weaver 1949, Simpson 1949, Hurlbert 1978, Krebs 1999) are frequently used to characterize raptor diet. Diversity measures represent the relative structure of groups in a sample set, such as prey in the diet of Gyrfalcons. Diversity generally incorporates two components: richness (the number of different categories), and evenness (the uniformity of individuals represented in each category; Pielou 1966). Below are diversity measures most commonly used in raptor studies:

Simpson's index:

$$D = \sum p_i^2$$

where p_i is the relative proportion of each category i in the diet. As D increases, diversity increases. For this reason Simpson's index is usually expressed as $1 - D$ or $1/D$

Shannon index:

$$H' = - \sum p_i \log p_i$$

where p_i is the relative proportion of category i in the diet. Larger values resulting from this equation indicate a greater diversity in the diet.

Levins' index:

$$B_i = \frac{1}{\sum p_i^2}$$

where p_i is the relative proportion of category i in the diet. Larger values resulting from this equation indicate a greater diversity in the diet.

Standardized version of Levins' index:

$$B_i = \frac{1}{n-1} \left[\frac{1}{\sum p_i^2} - 1 \right]$$

where n is the number of categories in the sample, and p_i is the relative proportion of category i . The standardized version of Levins' index provides values that range from 0 to 1, where values closer to 0 indicate dominance of one prey type over others and values closer to 1 indicate a more even representation of categories included in the calculation.

Traditional diversity measures have been criticized because they fail to account for the availability of prey species, i.e., rare and abundant prey species are weighted equally (Smith 1982). Newer diversity measures (Saikia 2012) incorporate prey use and availability, thus providing a measure for prey preference in raptors. Comparisons of prey use and availability elucidate the relative importance of prey types to reproduction, and can detect shifts in the use of particular prey species in raptor diet (Robinson 2016).

5.5.4 Assessing dietary trends with generalized linear mixed models in R

Modeling can be used to assess trends in Gyrfalcon prey use over time. Here we describe an example from Robinson (2016) in which we test the hypothesis that temporal factors of year and nestling age influence the importance of ptarmigan during the brood rearing period. We use two steps in this analysis. First, we construct generalized linear mixed models (GLMMs; binomial response variable) that represent our competing hypotheses of date and nestling age. We then use an information theoretic approach, e.g., Akaike's Information Criterion (Akaike 1974, Burnham et al. 2011) to test the support of multiple parameters against the intercept-only model.

The data we use were simulated to resemble a typical dataset that would be extracted from nest cameras. In the example data set the variable `nest` identifies a nest site; `year` is the year of study; `week` expresses the age of the nestling period for the entire study population, i.e., week 1 is the first week that Gyrfalcon nestlings were observed; `age` is the age in weeks of the brood in question; and `ptar` is a binomial variable indicating whether a prey item is a ptarmigan (1) or not (0). In the data set (Table 5.3), the first row of data represents nest site 108 in year 2014, week 9 of the nestling period for the population, age of 8 weeks for nest 108, and 0 ptarmigan delivered during that time period.

For this analysis we are using the function `glmer()` to run a generalized linear mixed model (GLMM), which is included in the `lme4` package (Bates et al. 2015). See Chapter 7 for a thorough description of GLMMs. We use a GLMM because our data represent whether a prey item is a ptarmigan as a function of time in weeks. The response variable is binomial (0 or 1), where prey items have been coded as a ptarmigan (1) or not ptarmigan (0). For mixed effects models where we expect certain variables to have an influence, we can include random intercepts such as the variable `nest` in the format `(1|nest)`, and include `year` as a fixed effect. Here, we give the model the name `model1`, `glmer` is the function, `ptar` is the response variable predicted by `week`, `year`, and the random intercept `(1|nest)`. We set `family` to `binomial` as indicated by the binomial response variable (`ptarmigan = 1`, no ptarmigan = 0). We also set `data` to `ptarmigan`, the name of our dataset. Note that I rounded some of the output for simplicity.

```

# build GLMM
modell=glmer(ptar ~ week + year + (1|nest),
family = binomial, data = ptarmigan)

# examine output
summary(modell)

# output

Generalized linear mixed model fit by maximum likelihood
(Laplace
Approximation) [glmerMod]
Family: binomial ( logit )
Formula: ptar ~ week + year + (1 | nest)
Data: dataname

      AIC      BIC  logLik deviance df.resid
 76.6     85.5   -34.3    68.6      65

Scaled residuals:
   Min       1Q   Median       3Q      Max
-3.1777  -0.50   -0.0980   0.5478  1.6603

Random effects:
 Groups Name          Variance Std.Dev.
 nest  (Intercept)    2.469     1.571
Number of obs: 69, groups: nest, 8

Fixed effects:
              Estimate  Std. Error  z value  Pr(>|z|)
(Intercept)  4.22        1.50      2.82    0.01 **
week         -1.12        0.34     -3.31    0.00 ***
year2015     -2.26        1.49     -1.52    0.13
--
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr)      week
week          -0.78
year2015     -0.58      0.20

```

Table 5.3. Example of coding a data set for assessing dietary trends in Gyrfalcons with linear models. Data coding is described in the text.

nest	year	week	age	ptar
108	2014	9	8	0
104	2014	6	4	0
101	2015	1	1	0
101	2015	2	2	1

Note the effect of **week**, indicated as significant by *P*-value and asterisks. We next code other possible combinations and run GLMMs to create all models with variables included that might influence whether an item is a ptarmigan.

```
model2<-glmer(ptar ~ year + (1|nest), family = binomial,
  data = ptarmigan)
model3<-glmer(ptar ~ (1|nest), family = binomial,
  data = ptarmigan)
```

Once all models investigating the predictors of an output variable are coded and entered into R, we create the AIC table using the function **aictab** where **cand.set** refers to the candidate set of the models, listed as **model11**, **model12**, **model13**. The **modnames** statement codes models to names that will appear in the AIC table. Note that we are here using AICc which is corrected for sample size, and we round some of the output for simplicity.

```
# create AIC table
```

```
aictab(cand.set= list(model11, model12, model13),
  modnames = c('model11', 'model12', 'model13'))
```

```
# output
```

```
Model selection based on AICc:
```

	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
model11	4	77.18	0.00	1	1	-34.28
model13	2	88.97	11.79	0	1	-42.40
model12	3	89.63	12.45	0	1	-41.63

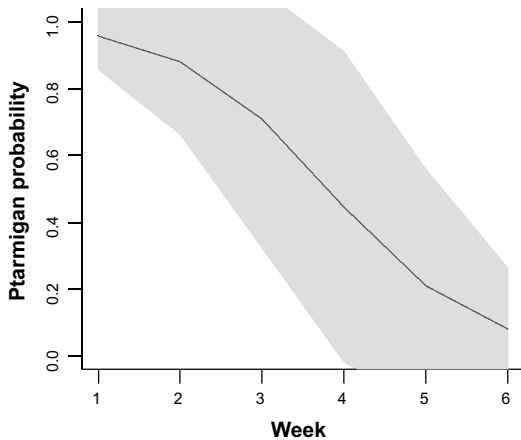


Figure 5.2. Probability that a prey delivery to Gyr Falcon nestlings is ptarmigan as a function of “week.” Gray shading indicates the 95% confidence interval. As “week” increases, the probability of ptarmigan as a prey item decreases.

Looking at the output, column 1 comprises the list of the candidate models. K is the number of parameters included in each model. AIC_c is a number provided by the information theory approach for a given model to then be compared to the AIC_c value of competing models. ΔAIC_c is the difference between the AIC_c of the model and AIC_c of the lowest model in the candidate set ($AIC_i - AIC_{\min}$). AIC_{Wt} is the probability that the respective candidate model is the best among the set of the models. $Cum.Wt$ indicates the cumulative weight of the addition of each model to the candidate set. In the example, Model1 is by far the most parsimonious model and thus we can base our inference on this single model. We conclude that time in weeks best explains changes in Gyr Falcon prey use. Next, we build a figure (Fig. 5.2) to visualize the change in Gyr Falcon diet over the study period.

```
# make figure

# build dataframe to use in prediction
p=data.frame(week=unique(ptarmigan$week),year='2014')

# use model to predict probability during each week
pred=data.frame(predictSE(model1,p),week=p$week)

# plot predictions and 95% confidence interval
plot(p$week,pred$fit,type="n",xlab='Week',
      ylab='Ptarmigan Probability', ylim=c(0,1))
lines(p$week,pred$fit)
polygon(c(p$week,rev(p$week)),c(pred$fit - 1.96 *
  pred$se.fit,rev(pred$fit + 1.96 *
  pred$se.fit)),col=rgb(0, 0, 0,0.5),border=NA)
```

5.6 Conclusion

Although many previous studies have provided a solid characterization of Gyrfalcon diet, quantitative analysis and hypothesis testing remain a frontier for research, and much remains to be learned about the role of the Gyrfalcon as an apex predator in the tundra ecosystem. Advances in camera technology provide tools for in-depth diet quantification across the breeding season. Robinson (2016) reported dietary shifts by Gyrfalcons breeding in Alaska from ptarmigan to ground squirrel between and within years that were missed by the indirect method of prey remains analysis. This finding highlights the benefits of improved camera technology for dietary studies in raptors.

The differences in dietary description provided by camera analysis (Robinson 2016) represent the need for continued implementation of these techniques for quantifying diet and assessing trends in prey use. With the proper considerations of camera placement and programming, researchers can quantify diet at a scale not seen in previous Gyrfalcon studies. These fine scale data across time provide the ability to empirically analyze data to assess dietary trends and connect Gyrfalcon prey use to ecological trends such as those precipitated by global climate change.

Stable isotope analysis represents an untouched area of study for understanding patterns in Gyrfalcon prey use. Its utility could provide further insight into Gyrfalcon dietary habits across both spatial and temporal scales. Additionally, in light of the potential impacts of climate change on tundra ecology it is increasingly important to monitor prey use on a constant basis. Trends in prey use may serve to track and assess changes in interactions among community members and underscore the impacts of climate change to Gyrfalcon life history, an understanding of which will be the foundation for the formation and implementation of conservation protocols when necessary.

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