CHAPTER 8

Monitoring prey populations with distance sampling surveys

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8.1 Introduction

Prey abundance has been shown to influence the productivity of Gyrfalcons and other raptors (Potapov 1997, Salamolard et al. 2000, Barichello and Mossop 2012, Mossop 2012). Prey abundance during the breeding season can influence the ability of raptors to lay full clutches at the optimal time, and their ability to provide adequate food to nestlings during the brooding period (Lack 1950, Perrins 1965, Daan et al. 1988). Nestlings that do not receive adequate food during development grow more slowly, increasing their chances of mortality in the nest or during the post-fledging period (Perrins 1966, Bortolotti 1989, Dewey and Kennedy 2001, Gonzalez et al. 2006, Markham and Watts 2008). One of the primary drivers of breeding success in birds is the degree of synchrony between predator and prey breeding cycles, which determines the amount of food available for nestlings (Visser et al. 1998, Visser et al. 2004, Hipfner 2008, McKinnon et al. 2012)

Prey and raptor populations can both be affected by seasonal temperature and precipitation (Poole and Bromley 1988, Steenhof et al. 1997, Visser et al. 1998, Krüger 2004, Keane et al. 2006, Hipfner 2008, Anctil et al. 2014, Robinson et al. 2014). Given that climate change is projected to affect temperature and precipitation particularly strongly in polar regions (Räisänen 2001), monitoring prey populations in conjunction with raptor species such as Gyrfalcons is essential for a complete understanding of their breeding ecology, and one that is critical for forecasting population trends in a changing Arctic. Although Gyrfalcons take alternative prey, they are often tied to populations of ptarmigan during the early portion of the breeding season when other prey sources are not available (Nielsen and Cade 1990, Barichello 2011, Barichello and Mossop 2011, Mossop 2011, Nielsen 2011, Potapov 2011). The predicted ranges of Gyrfalcons and both Rock and Willow Ptarmigan (*Lagopus muta* and *L. lagopus*, respectively) are expected to decrease over the next century as a result of climate change (Huntley and Green 2011, Booms et al. 2011). The effects of climate change are likely to be complex, and negative effects could be buffered by prey switching and the proliferation or shifts in distribution of alternative prey sources.

Here we present a sampling and analysis protocol for the quantification of prey populations based on a well-known data collection and modeling technique. We address typical issues involved in surveying avian populations, demonstrate correct data formatting using Rock Ptarmigan data, and describe analysis in the R programming environment (R Core Team 2016) using distance sampling. Our goal is to provide an introduction to the quantification of avian prey populations for Gyrfalcon and other raptor researchers hoping to address issues related to prey supply.

8.2 Distance sampling to estimate abundance

Over the past two decades, distance sampling has been one of the most prominent and effective animal survey methods (Buckland et al. 2001, Buckland 2004, Buckland et al. 2005, Buckland et al. 2015). This analytical method is superior to traditional, non-distance-based strip transects or point counts because it allows the surveyor to account for imperfect detection. Distance sampling has been used to quantify abundance in a wide range of study organisms, from north Pacific killer whales (Orcinus orca; Zerbini et al. 2007) to lentic clams (Katsanevakis 2007). Distance sampling has frequently been applied to the sampling of avian populations, including game species such as ptarmigan and grouse (Pelletier and Krebs 1997, Franceschi et al. 2014). By recording distance, geographic bearing, and observer location for each observation, distance sampling facilitates the construction of detection function curves, which allow the user to account for unobserved objects in their final abundance estimate. This is particularly useful for species that are difficult to detect or for multispecies surveys, because objects of different size, coloration, and behavior can produce large differences in detectability. Distance sampling surveys are relatively easy to design and simple to implement, making them ideal for general research or monitoring projects.

A freely available software, known as Distance, provides an easy to use interface for analyses involving distance sampling data (Thomas et al. 2010). A package for the open source R programming environment (R Core Team 2016) is also an excellent option for distance sampling (Miller 2016), and its use is described in the following sections. The following methodological framework leans heavily on previous publications regarding distance sampling, particularly the seminal works of Buckland et al. (2001, 2004, 2005, and 2015). Readers are encouraged to refer to these extensive resources during the process of designing and analyzing their own surveys.

8.3 Designing and implementing a distance sampling survey

The most basic distance sampling survey design would involve a series of transects randomly or uniformly distributed through the study area of interest. Transects can be of any length for distance sampling surveys, but for terrestrial avian surveys it is recommended that transects be 0.5–2 km in length to balance limitations in time, human resources, and coverage of the study area. If the study area is naturally divided into distinct habitat types, or if target species are thought to be fairly clustered, it is likely worthwhile to create a stratified study design using relevant environmental variables to define habitat types (see Robinson et al. (2014) for example). Another potential design that can make surveys more time efficient is to construct a zigzag pattern of transects, which eliminates time spent traveling between transects.

Timing of surveys is also important. If the research question involves the growth or survival of raptor nestlings, then it is best to survey prey during the brood rearing period. This can depend on the study population in question, but for Gyrfalcons brood rearing generally occurs from late May through early August (Poole and Bromley 1988, Burnham and Burnham 2011, Milligan and Powell 2014). Conversely, one may wish to determine the effects of prey abundance on the occupancy of nest sites, or the prelaying body condition and phenology of breeding adults, or nest abandonment during incubation. Male Gyrfalcons begin arriving on breeding territories as early as late January, with females arriving in mid-March. Pairs begin laying clutches in late March to mid-May (Cade 2011). These aspects of phenology also apply to the prey species in question, and can also affect survey design and effort. As in many biological surveys, a general working knowledge of the target species is critical for success.

Equipment needed for the surveys includes a handheld GPS, a laser rangefinder, a compass, and a field notebook or other method for recording data. It is essential that surveyors record their GPS track as they navigate each transect and that the distance, bearing, and observer location for each observation are as accurate as possible. If the observed objects occur in groups, the number of individuals should be noted as cluster size. Observed objects must be recorded at their initial location, prior to any movement that might be caused by the presence of the observer. Detection error increases with distance, such that distant observations may be unreliable for analysis. A limit of approximately 500 m from the observer is suggested as a reasonable distance beyond which avian observations can be ignored in tundra habitat. It is likely that observations farther than this distance will be truncated as part of methods undertaken in later analysis.

Distance sampling analysis makes several assumptions about the design and detection of objects in the survey (Thomas et al. 2010). The method assumes: 1) transects are arranged randomly with respect to the locations of the objects of interest, 2) objects on the transect line are observed 100% of the time, 3) objects are recorded at their initial position, and 4) observed location data are accurate. Elements of design and data collection should strive to meet these assumptions as best possible. To fit a relatively robust detection function and achieve an accurate population estimate, a minimum of 60 to 80 observations and 10 to 20 replicate transect lines are recommended (Buckland et al. 2001).

The following instructions describe additional data that can be collected to improve survey quality. They are not necessary to fit a basic detection function, but they can produce significant improvements in the robustness of the detection function and accuracy of abundance estimates. If the additional protocol does not compromise the accuracy of the basic survey data (distances, bearings, observer locations, GPS tracks, cluster sizes), which could violate the assumptions of the method, it is recommended that the user incorporate some of the following suggestions into their survey protocol.

Surveyors should take note of potential variables that may influence detection in a given transect. Surveyors should attempt to walk transects only on days with relatively low wind and no precipitation. In the case of unavoidable poor weather it is prudent to record a qualitative (for example 0-3 scale) or quantitative measurement of these conditions at the end of each transect. Insect activity can also pose difficulties for detection during the Arctic summer and should also be recorded in the same fashion.

Although long daylight hours during the Arctic summer make the daily timing of each survey less important (Reierth and Stokkan 1998), the start and end time of each transect should be recorded to account for potential bias in avian activity, and also to ensure that transects are given similar levels of time effort. The date of the survey can also be a critical detection covariate due to changes in behavior or plumage of the target species. In ptarmigan, molting, territorial courtship displays, and dust bathing behavior modify their detectability significantly during the breeding season (Montgomerie et al. 2001). For small passerines, singing behavior declines over the course of the breeding season, which can limit the number of birds detected by sound. Elements of behavior, plumage, and phenology can also vary by age and sex. Finally, if the goal is to determine habitat preferences for a given species, it is useful to record whether the bird or group of birds in question are observed in the air or on the ground. Migrating birds in the air will likely produce erroneous habitat associations and may confound estimates of a resident population. Observations that might potentially produce erroneous results can be omitted from later analysis.

8.3.1 Our dataset and further suggestions for ptarmigan surveys

To demonstrate proper protocol for distance sampling analysis, we will use survey data for male Rock Ptarmigan, critical prey for breeding Gyrfalcons in many areas. Ptarmigan surveys took place during May from 2003-2016 on Slétta, northeast Iceland. The timing of our surveys corresponds to territorial activity in male ptarmigan (Nielsen 1993) when they are relatively easy to detect against the bare ground, sit on prominent lookout posts, and display actively. Prior to this period the birds are in groups, are more mobile, and their white plumage makes detection difficult on the snow-covered ground. After mating, the males will stay on their territories and display well into June but become more difficult to detect as they soil their white plumage by dust-bathing, their display intensity diminishes, and they continue their molt into summer plumage (Montgomerie et al. 2001). Once molting occurs, ptarmigan are nearly impossible to detect via distance sampling transects, and collecting enough data to build a detection function may become a major issue. This concern also applies generally given the cyclical nature of ptarmigan populations. In certain years, survey effort may have to be increased to accumulate enough observations to fit a detection function. Once multiple years of data are collected, this becomes less of a concern because observations from different years can be pooled into a global detection function, as they have been in our analysis. Our data were mainly collected in the morning and evening, with a general avoidance of midday, which corresponds to patterns of male ptarmigan display behavior. Because we estimated only male ptarmigan abundance, extrapolation to the abundance of both sexes requires some knowledge of the sex ratio of the population. The sex ratio in the Icelandic Rock Ptarmigan population is equal (Gardarsson 1988), but other populations may be male-biased (Martin et al. 1990, Hannon and Martin 1992, Pedersen et al. 2012). Additional non-breeding adults that do not take part in territorial behavior may also exist in the population, and this again varies by study area (Gardarsson 1971, Moss 1972, Gardarsson 1988, Pedersen et al. 2014).

Although our data include only male ptarmigan observations in spring, other study protocols and timing of surveys are possible and can be important depending on the intent of the study. For example, if ptarmigan and Gyrfalcons were being studied in concert with each other, it may be useful

to distinguish between ptarmigan abundance in the late winter when they play a part in determining Gyrfalcon nesting site occupancy, and later in the spring and summer, when they may play a role in the growth and survival of Gyrfalcon nestlings (Nielsen and Cade 1990, Barichello 2011, Barichello and Mossop 2011, Mossop 2011, Nielsen 2011, Potapov 2011). Although spring ptarmigan abundance will generally correlate with late season abundance from year to year, estimates from both periods will help take into account seasonal events that may cause poor reproductive output, such as severe weather events. Because of the difficulty in detecting ptarmigan both late and early in the season, and the difficulty of detecting females and juveniles relative to breeding males, surveys targeted at those demographics and time periods are often accomplished with pointer dogs (http://honsefugl.nina.no/Innsyn/), or via different methods entirely, for example trapping and nest searching (http://ripforskning.se.preview. binero.se/). We argue that our protocol provides a simple yet effective option for achieving a general index of ptarmigan abundance in a season given limited time and resources.

8.3.2 Formatting data

To fit a detection function, the perpendicular distance from each observation to its corresponding transect is required in the input table. The GPS track for each transect and the location data for all observations must be uploaded into a Geographic Information Systems program such as ArcMap (ESRI), where the minimum perpendicular distance between an observation and its corresponding transect can be calculated. This process is not detailed in this chapter.

Table 8.1 shows example data and the column headings required for using the Distance package in R (Miller 2016). In our analysis we have used the year of study as the Region.Label, which will allow us to estimate abundance in each year. Each row represents a single observation, but it is essential to also include rows for transects in which no prey were observed, because these are also a factor in calculating abundance and uncertainty. Covariates that could potentially influence ptarmigan detection such as date, time of day, and the observer who conducted the survey are also included in the table.

Table 8.1. Colur (Lagopus muta) belongs; "objec "Region.Label" "Effort" is the le "size" is the nur the package Dis and "obs" are n	mn labels an on Slétta, nc on Slétta, nc is the identif angth of the mber of indiv stance in R, b ot necessary	d data for brtheast lc e identifie fier for the transect, ' iduals, or vut can be ' to run a o	mat for conducting a teland, spring 2003–20 r for each observation s region to which each distance " is the perp cluster size, in each o altered (requiring us distance sampling ana	distance samp 016. "Sample. 7; "Area" is th 1 observation l endicular dist bservation. Th bservation. Th to specify the to specify the	oling analysis in Label" is the id- e size of the stu belongs (in this ance in meters f ance in meters f ese heading na names separat shown as examp	R. Data are fron entifier for the t dy area in whicl case we define case we define case are coogr irom each obser irom each ob	n surveys of male Rc ransect to which ead in we wish to estimat I regions as differen vation to its corresp vation to its corresp ized automatically b e help files). Colum s that can be includ	ock Ptarmigan ch observation e abundance; t years of study); onding transect; y the ds function in ns "date," "start," ed in detection
Sample.Label	object	Area	Region.Label	Effort	distance	size	date	start ob

nnle I ahel	ohiect	Area	Region Label	Effort	distance	size	date	start	sqo
1	-	09	2003	2	161		2003-05-23	0.29	OKN
-	2	90	2003	2	80	-	2003-05-23	0.29	OKN
2	С	09	2003	2.2	169	-	2003-05-23	0.32	OKN
2	4	09	2003	2.2	275	-	2003-05-23	0.32	OKN
2	Ŋ	09	2003	2.2	275	-	2003-05-23	0.32	OKN
2	9	09	2003	2.2	376	-	2003-05-23	0.32	OKN
2	7	09	2003	2.2	81	-	2003-05-23	0.32	OKN
2	8	09	2003	2.2	248	-	2003-05-23	0.32	OKN
2	6	09	2003	2.2	55	-	2003-05-23	0.32	OKN
2	10	09	2003	2.2	61	-	2003-05-23	0.32	OKN
2	11	09	2003	2.2	224	-	2003-05-23	0.32	OKN
2	12	09	2003	2.2	170	-	2003-05-23	0.32	OKN
2	13	09	2003	2.2	37	-	2003-05-23	0.32	OKN
с	14	09	2003	2.1	10	-	2003-05-23	0.35	OKN
с	15	09	2003	2.1	341	-	2003-05-23	0.35	OKN
с	16	09	2003	2.1	27	-	2003-05-23	0.35	OKN
ო	17	09	2003	2.1	95	-	2003-05-23	0.35	OKN

8.4 Analysis of data collected during distance sampling surveys

8.4.1 The detection function

A detection function describes the relationship between the distance of observed objects from a point of reference (e.g., the line transect) and its probability of detection. The function itself is made up of a key function, which can take several forms, and optional additional parameters that can govern its shape more subtly. Covariates can also be included in the model to account for various sources of detection bias, e.g., multiple observers, weather conditions, or terrain. The key function determines the general shape of the detection function, starting at 100% detection at 0 m from the transect (assumption #2 for distance sampling), decreasing slowly at first (the "shoulder"), and then falling off smoothly to a minimum value. Adjustment terms add to the detection function, changing its shape more subtly to accommodate unusual distributions. Adding covariates to the detection function alters the rate at which detection decreases with increasing observation distance, seen visually as the width or spread of the distribution. Our choices of key functions and adjustments followed recommendations from Thomas et al. (2010), but more choices are possible and can be explored (see Buckland et al. 2001). Truncation distance selection is also an important part of distance sampling analysis. There are no absolute rules for selecting truncation distance but one common suggestion for line transects is to truncate where detection falls below 15% (Buckland et al. 2001). We provide sample R code from the package Distance that could be used to fit several detection functions and determine the best model using Akaike's Information Criterion (AIC; Akaike 1974) and the rule of parsimony. We will walk through this code in depth in a subsequent section.

8.4.2 Estimating abundance

Note: we distinguish here between survey area and study area. Survey area indicates only the area covered by line transects. Study area encompasses the full area, including areas surveyed and those not surveyed, in which we wish to estimate prey abundance.

The package Distance will calculate abundance automatically if we supply a study area in our data table (column name "Area"), but we will outline the calculation conceptually here. We know that detection decreases with increasing distance from the observer, so that at large distances we have almost certainly failed to detect objects that are nonetheless within our survey area. The assumption made in the calculation is that object distances (both detected and undetected) are distributed uniformly with respect to the transect (Buckland et al. 2015). The abundance calculation relies on the estimation of average probability of detection within the survey area, a calculation we will not delve into here, but refer to Buckland et al. (2001) and Buckland et al. (2015) for the mathematical details. This probability is then used to adjust the number of detected objects to achieve a population estimate within the survey area, which can then be scaled up to the entire study area. If there are covariates included in the detection function, the Distance package makes use of a Horvitz-Thompson-like estimator (modified from Horvitz and Thompson [1952]) where the probability of detection is allowed to vary by observation according to the detection covariate. Again, for details of these calculations and the calculation of variance, see Buckland et al. (2015).

8.4.3 Fitting detection functions and estimating abundance in R

Once our data are loaded into R and given the name dist, we explore the data by plotting a histogram of the detection distances with the function hist().

plot distribution of perpendicular detection distances hist(dist\$distance)

This can alert us to problems with our data, including violation of the assumption of 100% detection at zero m. The histogram can also be used to identify logical truncation distances, for example, to eliminate outliers or unusual distributions (such as detection increasing at large distances). In our example we selected a truncation distance of 400 m through visual inspection of the histogram of detection distances, keeping in mind the 15% detection rule (Buckland et al. 2001). Not presented here for the sake of brevity, it is recommended that the user fit detection functions for different truncation distances and compare goodness of fit using the Cramer von Miser, Kolmogorov-Smirnov tests, and quantile-quantile plot (henceforth, q-q plot). Note: we cannot use AIC to select truncation distances, because it is not useful to compare AIC for models using different data.

Next, we ensure the distance and area units in our table are the same. In our data the distance column was in meters, whereas the Effort and Area columns were in kilometers and km² respectively, so we convert Effort and Area to meters.

```
# convert Effort and Area columns to m so they match the
# distance columns
dist$Effort = dist$Effort * 1000
dist$Area = dist$Area * 1000000
```

Our Date column was given in yyyy-mm-dd format. To include date as a detection covariate, we need to convert these to Julian dates. For this we use the **as.POSIX1t()** command, specifying the format of the date with **format**, and converting the column to day of year by specifying the **yday**. Finally, we ensure that the column is recognized in R as numeric, by specifying **as.numeric()**, and rescale it between 0 and 1 by dividing the column by 365.

```
# convert dates to julian day
```

```
dist$date = as.POSIXlt(dist$date, format="%Y-%m-%d")
dist$date = dist$date$yday
dist$date = as.numeric(dist$date)
dist$date = dist$date/365
```

Note: similar issues can occur for time of day covariates (i.e., data in the HH:MM format are not usable) and so conversion is necessary here as well to scale the times between 0 and 1 on the 24-hour clock. We found this to be most easily accomplished in Microsoft Excel (2010), simply by changing the cell type of the column from Time to Number.

We can explore our data further by plotting detection distances against potential detection covariates, such as time of day and Julian date—plot() to create the scatterplot, abline(lm()) to create the line of best fit. Because time of day is not expected to have a linear effect (ptarmigan are predicted to be more active in the morning and evening, but less in the middle of the day), we will plot a smooth of best fit instead with lines(smooth.spline()). This function cannot take missing values, so we create a new dataset dist1 from dist by getting rid of the missing values with na.omit().

```
# create new dataframe without NAs
dist1 = na.omit(dist)
# set up window for plot
graphics.off()
windows(width = 10,height = 7)
par(mfrow = c(1,2))
# plot distance against start time of survey (start)
plot(dist1$start, dist1$distance, main = "",
    xlab = "Timeof Day/24", ylab = "Distance (m)", pch =
    19, cex = 0.5, col = rgb(0.74, 0.74, 0.74, 0.7))
    lines(smooth.spline(dist1$start,dist1$distance, spar =
    0.75))
```

```
# plot distance against julian date
plot(dist$date, dist$distance, main = "",
    xlab = "Julian Date/365", ylab = "Distance (m)", pch =
    19, cex = 0.5, col = rgb(0.74, 0.74, 0.74, 0.7))
    abline(lm(dist$distance~dist$date))
```

We can further plot separate histograms for different observers to see if there are obvious differences in detection skill. For this task we will use the **facet_wrap()** command from the ggplot2 package (Wickham 2009).

```
# histograms for different observers
ggplot(dist, aes(x = distance, group = obs)) +
geom histogram() + facet wrap(~obs, scales = "free y")
```

Having identified covariates to include in our candidate detection function models, we begin fitting different combinations of key functions, adjustment terms and covariates using the ds() command from the package Distance. Key functions are specified with key, adjustment terms with adjustment, truncation distance with truncation, and covariates in formula.

```
# fit detection functions (combinations of key functions and
# adjustment terms as described by Thomas et al. 2010)
# also include time of day (start) as a covariate for half
# normal and hazard rate functions
  hncos <- ds(dist, truncation = 400, key = "hn",</pre>
            adjustment = "cos")
  hnhp <- ds(dist, truncation = 400, key = "hn",
            adjustment = "herm")
  hrsp <- ds(dist, truncation = 400, key = "hr",</pre>
            adjustment = "poly")
  unicos <- ds(dist, truncation = 400, key = "unif",
            adjustment = "cos")
  hntod <- ds(dist, truncation = 400, key = "hn",</pre>
            formula = ~start)
  hrtod <- ds(dist, truncation = 400, key = "hr",</pre>
             formula = ~start)
  hnobs <- ds(dist, truncation = 400, key = "hn",</pre>
             formula = ~obs)
  hrobs <- ds(dist, truncation = 400, key = "hr",</pre>
            formula = ~obs)
  hnjul <- ds(dist, truncation = 400, key = "hn",
            formula = ~date)
  hrjul <- ds(dist, truncation = 400, key = "hr",</pre>
            formula = ~date)
```

The package Distance has a useful command for summarizing multiple models at once called **summarize_ds_models()**. The command automatically ranks the models by AIC and gives information on the Cramer von Miser goodness of fit test, average probability of detection and standard error.

```
# create summary table containing basic parameters for each
# model
```

```
summarize_ds_models(hncos,hnhp,hrsp,unicos,hntod,
hrtod,hnobs,hrobs,hnjul,hrjul)
```

We can then plot our models to inspect them visually (Fig. 8.1) with **plot()**, obtain further goodness of fit information including the quantile quantile (q-q) plot (Fig. 8.2) with **ds.gof()**, and get a full model summary, including abundance and density estimates with **summary()**.



```
Figure 8.1 Visualization of the top detection function, which included a hazard rate key function with Julian date as an additional covariate, over the distribution of observed detection distances and their probability of detection for our example study involving male Rock Ptarmigan (Lagopus muta) on Slétta, northeast Iceland, spring 2003–2016. The black line represents the average detection function, while the open circles represent the probability of detection of individual data points based on their covariate value (Julian date). We can see that there is noticeable variation in the response of detection to distance based on variation in the covariate.
```

```
# plot the top model
    plot(hrjul)
```

- # view Q-Q plot and goodness of fit test results
 ds.gof(hrjul)
- # view additional summary information for hncos.model
 summary(hrjul)



Figure 8.2 Quantile-quantile plot and goodness of fit test results for the top detection function, which included a hazard rate key function with Julian date as an additional covariate, for our example study involving male Rock Ptarmigan (*Lagopus muta*) from Slétta, northeast Iceland, spring 2003–2016. Y-axis represents the proportion of observations that are predicted to fall within a given distance from the transect line based on the detection function, whereas the X-axis represents the proportion of observations of observations that actually do fall within a given distance. The open circles represent the distances of real observations, such that points deviating from the shown y=x line indicate where model predictions diverge from the data. Our q-q plot indicates this model has a strong fit and this is confirmed by the Kolmogorov-Smirnov and Cramer von Miser goodness of fit tests indicated. We can see that the *P*-values calculated are well above the 0.05 significance level, indicating that the model is not significantly different compared to the data.

Because we specified the year of study as the Region.Label, our abundance and density estimates are calculated for each year. In the final step of our code, we create a new table based on the summary output for abundance and associated standard errors, and then plot those abundances using ggplot to see how abundance has changed over time.

```
# make a new table with abundance estimates and associated
# uncertainty
 ptarm_table <- summary(hrjul)$dht$individuals$N</pre>
 ptarm table = ptarm table[!(ptarm table$Label=="Total"),]
# plot abdundance by year with standard error
 ggplot(ptarm table, aes(y = ptarm table$Estimate,
      x = ptarm table$Label)) + geom point(size = 2) +
      geom errorbar(aes(ymin = ptarm table$Estimate -
      ptarm table$se,ymax = ptarm table$Estimate +
      ptarm table$se)) + xlab("Year") +
      ylab("Male Ptarmigan Abdundance") +
# change theme to improve look of plot
 theme(panel.grid.major = element blank(),
      panel.grid.minor = element blank(),
      panel.background = element blank(),
      panel.border = element rect(color="black", fill = NA),
       text = element text(size = 16))
```

8.4.4 Interpreting the output

In our analysis, the detection function selected as the top model by AIC and the rule of parsimony was a hazard rate key function with Julian date included as a detection covariate (Table 8.2). Visual inspection of the detection function in Fig. 8.1 shows a model that fits the data relatively well. The goodness of fit graphics output (Fig. 8.2) is a q-q plot, which plots the number of observations up to a certain detection distance against the number expected based on the detection function. A straight line of points following the illustrated y=x line represents good fit, and this is the case for our top model (Fig. 8.2). The Kolmogorov-Smirnov and Cramer von Miser goodness of fit tests, which test elements of the q-q plot for statistical significance (Miller et al. 2016), confirm the visual inspection: both *P*-values are easily > 0.05 significance level for the top model indicating that the model is not significantly different from the data. Our top model was AIC-best by a large margin, such that the rule of parsimony (selecting the model with the fewest terms) never came into effect in selecting from models with $\Delta AIC < 3$ (Table 8.2). Table 8.2 also indicates that the probability of detection within the survey area was around 50%, with relatively small error bars.

Table 8.2. Summary table for 10 candidate detection function models for our male Rock Ptarmigan (Lagopus muta). Key
function, covariate added, Cramer von Miser goodness of fit P-value, average probability of detection and standard error, and
ΔAIC are shown, and the models are ranked by AIC. Top model by AIC is a hazard rate key function with Julian date included as
a detection covariate.

Model	Key function	Covariate	C-vM P-value	{P_a}	se{P_a}	AIC
hrjul.model	Hazard-rate	~date	0.79	0.50	0.02	0.00
hncos.model	Half-normal + cosine adjust order 2	ΝA	0.91	0.49	0.01	16.95
hrsp.model	Hazard-rate	ΝA	0.90	0.52	0.02	16.97
unicos.model	Uniform + cosine adjust order 1,2,3	ΝA	0.91	0.49	0.01	17.00
hrtod.model	Hazard-rate	~start	0.90	0.52	0.02	18.68
hrobs.model	Hazard-rate	~obs	0.96	0.50	0.02	19.41
hnjul.model	Half-normal	~date	0.00	0.56	0.01	27.41
hnobs.model	Half-normal	~obs	0.00	0.56	0.01	28.18
hntod.model	Half-normal	~start	0.00	0.57	0.01	36.85
hnhp.model	Half-normal + Hermite polynomial adjust order 4	ΝA	0.00	0.56	0.01	36.88

Inspection of Fig. 8.3, which shows the relationship between detection distance and Julian date, indicates a negative relationship, i.e., as Julian date increases, detection distance decreases, indicating that male ptarmigan become more difficult to detect at later survey dates. Taking into account molting and dust-bathing behavior (Montgomerie et al. 2001) this makes a good deal of sense. The result of the inclusion of this variable into the detection function is that observations recorded at later dates will be additionally inflated during the abundance calculation to compensate for the decrease in detection.

Fig. 8.4 shows the plotted abundance for male ptarmigan through time in our study area with error bars. We can see that abundance was far higher from 2004–2006, declined steadily through 2012, and has remained relatively steady since, with a small peak in 2015. Buckland (2004) provides details for the analysis of temporally-based surveys. Because we pooled all of the detection distances into a single detection function, it is possible that our yearly estimates are biased due to variation in detection between years that we have not accounted for. In the ideal scenario, a separate detection function would be fit to each year of data, but this would have



Figure 8.3 Side-by-side plots of detection distance versus time of day and Julian date (expressed as a proportion of a 365-day year) respectively, for our male Rock Ptarmigan (*Lagopus muta*) study from Slétta, northeast Iceland, spring 2003–2016. The time of day plot is shown with a smooth line of best fit, because detection was expected to be highest early and late in the day, but lower in the middle. Julian date proved to be more significant in improving the fit of the detection function. The negative relationship indicates that detection became more difficult at later survey dates.

required 60–80 observations in each year to fit robust functions. This may not be realistic for cyclical species such as ptarmigan, but could theoretically be resolved by increasing survey effort during years of low abundance (i.e., walk more transects, or repeat transects). We could have included year as a detection covariate in a pooled model, just as we did for Julian date and time of day, but the year covariate would be a factor with 14 levels and would greatly inflate the number of parameters estimated in the model, making it less likely to improve AIC unless the gains in goodness of fit were substantial. Although the same transects were walked in all sampling periods, they were separated by a full year, which greatly reduces the risk of encounter rate bias, and may even be beneficial for comparing across years (Buckland et al. 2015).

In the context of a larger ecological study it would then be useful to explore potential reasons behind this temporal variation, which may include seasonal weather, predation pressure, or habitat disturbance, and it would also be useful to look for patterns of occupancy or reproductive output in predator populations that might indicate synchrony.



Figure 8.4 Plot of male Rock Ptarmigan (*Lagopus muta*) abundance (± standard error) by year from Slétta, northeast Iceland, spring 2003–2016.

8.5 Extensions for advanced users

Distance sampling has further applications in the realm of spatial analysis. Two methods in particular, known as the analysis of designed experiments, and density surface modeling, provide excellent options for advanced users interested in further exploring the spatial relationships between their study species and the landscape in which they reside. We will briefly describe each method and refer the user towards additional resources that provide comprehensive theory and instruction for users desiring to attempt such analyses.

Distance sampling projects with a stratified study design may be analyzed using a two-stage modeling approach to determine the statistical significance of treatment or stratum effects (Buckland et al. 2009, Buckland et al. 2015). Stage one of the method is estimation of the detection function as we explored earlier in this chapter. Stage two involves modeling counts as functions of treatment groups, habitat types, or time periods, for example. A good example of this kind of analysis is seen in Robinson et al. (2014) for a multispecies, Arctic study. Count data are modeled in generalized linear or additive models (GLM or GAM) that include an offset term to account for variation in detectability and survey effort in each treatment.

Density surface modeling (DSM) is another two-stage method of distance sampling analysis typically used for projects with a spatial component (Hedley and Buckland 2004, Miller et al. 2013, Buckland et al. 2015). In line transects, relevant spatial or environmental variables may vary not only between transects, but also within them, such that a DSM typically involves dividing transects into segments of relatively square shape and then modeling adjusted segment counts using environmental or spatial variables in a GAM (Hedley and Buckland 2004). The method is similar to the design-based approach mentioned earlier, but DSM studies need not be designed with prior stratification or an experimental approach, rather they make use of covariates extracted during or post-survey. In a GAM, spatial or environmental relationships are evaluated and visualized using smooths, and thus are flexible enough to handle non-linear relationships. After term selection, the resulting model can be used to predict distribution and abundance over a grid of the study area in question. Like the method used for analyzing designed experiments, DSM incorporates variation in survey effort into the modeled counts using an offset term.

Either method provides an option for the avid user that can provide further insight into the arrangement of organisms on the landscape, and can improve abundance estimates. Users are encouraged to explore further resources before attempting these methods (Wood 2003, Hedley and Buckland 2004, Wood 2006, Miller et al. 2013, Buckland et al. 2015).

8.6 Conclusions

Through this chapter we have attempted to illustrate the importance of monitoring prey populations in conjunction with raptors such as Gyrfalcons, and have provided some basic methodology that can be used to collect and analyze prey abundance data. Distance sampling provides an attractive option for researchers and conservation managers interested in exploring the link between Gyrfalcons and prey communities, particularly ptarmigan populations. Such relationships will become increasingly important in a changing Arctic and will be necessary for the effective management of Gyrfalcon populations. Readers are encouraged to make use of the vast resources available describing distance sampling design and analysis.

Literature cited

- Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC-19:716–723.
- Anctil, A., A. Franke, and J. Bêty. 2014. Heavy rainfall increases nestling mortality of an arctic top predator: experimental evidence and longterm trend in peregrine falcons. Oecologia 74:1033–1043.
- Barichello, N. 2011. Gyrfalcon courtship a mechanism to adjust reproductive effort to the availability of ptarmigan. Pages 339–354 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.
- Barichello, N. and D. Mossop. 2011. The overwhelming influence of ptarmigan abundance on Gyrfalcon reproductive success in the Central Yukon, Canada. Pages 307–322 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.
- Booms, T., M. Lindgren, and F. Huettmann. 2011. Linking Alaska's predicted climate, Gyrfalcon, and ptarmigan distributions in space and time: a unique 200-year perspective. Pages 177–190 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.
- Bortolotti, G. R. 1989. Factors influencing the growth of Bald Eagles in north central Saskatchewan. Canadian Journal of Zoology 67:606–611.
- Buckland, S. T. 2004. Advanced distance sampling. Oxford University Press. Oxford, UK.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 2005. Distance sampling. Encyclopedia of Biostatistics 2nd Edition. John Wiley and Sons, Ltd.

- Buckland S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.
- Buckland, S. T., E. A. Rexstad, T. A. Marques, and C. S. Oedekoven. 2015. Distance sampling: methods and applications. Springer, New York, New York, USA.
- Buckland, S. T., R. E. Russell, B. G. Dickson, V. A. Saab, D. N. Gorman, and W. M. Block. 2009. Analyzing designed experiments in distance sampling. Journal of Agricultural, Biological, and Environmental Statistics 14:432–442.
- Burnham, K. K. and W. A. Burnham. 2011. Ecology and biology of Gyrfalcons in Greenland. Pages 1–20 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume II. The Peregrine Fund, Boise, Idaho, USA.
- Cade, T. J. 2011. Biological traits of the Gyrfalcon (*Falco rusticolus*) in relation to climate change. Pages 33–43 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors, volume I. Gyrfalcons and ptarmigan in a changing world. The Peregrine Fund, Boise, Idaho, USA.
- Daan, S., C. Dijkstra, R. Drent, and T. Meijer. 1988. Food supply and the annual timing of avian reproduction. Pages 392–407 *in* Proceedings of the International Ornithological Congress. University of Ottawa Press, Ottawa, Canada.
- Dewey, S. R., and P. L. Kennedy. 2001. Effects of supplemental food on parental-care strategies and juvenile survival of Northern Goshawks. Auk 118:352–365.
- Franceschi, S., L. Nelli, C. Pisani, A. Franzoi, L. Fattorini, and A. Meriggi. 2014. A Monte Carlo appraisal of plot and distance sampling for surveys of black grouse and rock ptarmigan populations in Alpine protected areas. The Journal of Wildlife Management 78:359–368.
- Gardarsson, A. 1971. Food ecology and spacing behavior of rock ptarmigan (*Lagopus mutus*) in Iceland. Dissertation. University of California, Berkeley, California, USA.
- Gardarsson, A. 1988. Cyclic population changes and some related events in Rock Ptarmigan in Iceland. Adaptive strategies and population ecology of northern grouse. Pages 300–329 *in* A. T. Bergerud and M. W. Gratson, editors. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Gonzalez, L. M., A. Margalida, R. Sanchez, and J. Oria. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). Biological Conservation 129:477–486.

- Hannon, S. J., and K. Martin. 1992. Monogamy in willow ptarmigan: is male vigilance important for reproductive success and survival of females? Animal Behaviour 43:747–757.
- Hedley, S. L., and S. T. Buckland. 2004. Spatial models for line transect sampling. Journal of Agricultural, Biological, and Environmental Statistics 9:181–199.
- Hipfner, J. M. 2008. Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. Marine Ecology Progress Series 368:295–304.
- Horvitz, D. G., and D. J. Thompson. 1952. A generalization of sampling without replacement from a finite universe. Journal of the American Statistical Association 47:663–685.
- Huntley, B. and R. E. Green. 2011. The utility of bioclimatic models for projecting future changes in the distribution of birds in response to climate change. Pages 117–123 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.
- Katsanevakis, S. 2007. Density surface modelling with line transect sampling as a tool for abundance estimation of marine benthic species: the *Pinna nobilis* example in a marine lake. Marine Biology 152:77–85.
- Keane, J. J., M. L. Morrison, D. M. Fry, and M. Morrison. 2006. Prey and weather factors associated with temporal variation in Northern Goshawk reproduction in the Sierra Nevada, California. Studies in Avian Biology 31:87.
- Krüger, O. 2004. The importance of competition, food, habitat, weather and phenotype for the reproduction of Buzzard *Buteo buteo*. Bird Study 51:125–132.
- Lack, D. 1950. The breeding seasons of European birds. Ibis 92:288-316.
- Markham, A. C., and B. D. Watts. 2008. The influence of salinity on provisioning rates and nestling growth in Bald Eagles in the lower Chesapeake Bay. Condor 110:183–187.
- Martin, K., S. J. Hannon, and S. Lord. 1990. Female-female aggression in white-tailed ptarmigan and willow ptarmigan during the pre-incubation period. Wilson Bulletin:532–536.
- McKinnon, L., M. Picotin, E. Bolduc, C. Juillet, and J. Bêty. 2012. Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. Canadian Journal of Zoology-Revue Canadienne De Zoologie 90:961–971.
- Miller, D. L. 2016. Distance: Distance Sampling Detection Function and Abundance Estimation. R package version 0.9.6. https://CRAN.R-project.org/package=Distance.
- Miller, D. L., M. L. Burt, E. A. Rexstad, and L. Thomas. 2013. Spatial models for distance sampling data: recent developments and future directions. Methods in Ecology and Evolution 4:1001–1010.

- Miller, D. L., E. Rexstad, L. Thomas, L. Marshall, and J. Laake. 2016. Distance Sampling in R. bioRxiv. doi: http://dx.doi.org/10.1101/063891.
- Milligan, H., and T. Powell. 2014. Gyrfalcon Survey. Yukon Department of Environment. Whitehorse, Yukon, Canada.
- Montgomerie, R., B. Lyon, and K. Holder. 2001. Dirty ptarmigan: behavioral modification of conspicuous male plumage. Behavioral Ecology 12:429–438.
- Moss, R. 1972. Social organization of willow ptarmigan on their breeding grounds in interior Alaska. Condor 74:144–151.
- Mossop, D. H. 2011. Long-term studies of willow ptarmigan and gyrfalcon in the Yukon Territory: A collapsing 10-year cycle and its apparent effect on the top predator. Pages 323–335 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.
- Nielsen, Ó. 1993. Initiation of territoriality among Icelandic rock ptarmigan in spring. Náttúrufræðingurinn 63:29–37.
- Nielsen, Ó. K. 2011. Gyrfalcon population and reproduction in relation to Rock Ptarmigan numbers in Iceland. pp. 21–47 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume II. The Peregrine Fund, Boise, Idaho, USA.
- Nielsen, Ó. K., and T. J. Cade. 1990. Seasonal changes in food habits of Gyrfalcons in NE-Iceland. Ornis Scandinavica 1990:202–211.
- Pedersen, Å. Ø., B. J. Bårdsen, N. G. Yoccoz, N. Lecomte, and E. Fuglei. 2012. Monitoring Svalbard rock ptarmigan: distance sampling and occupancy modeling. Journal of Wildlife Management 76:308–316.
- Pedersen, Å. Ø., M.-A. Blanchet, M. Hörnell-Willebrand, J. U. Jepsen, M. Biuw, and E. Fuglei. 2014. Rock Ptarmigan (*Lagopus muta*) breeding habitat use in northern Sweden. Journal of Ornithology 155:195–209.
- Pelletier, L., and C. J. Krebs. 1997. Line-transect sampling for estimating ptarmigan (*Lagopus* spp.) density. Canadian Journal of Zoology-Revue Canadienne De Zoologie 75:1185–1192.
- Perrins, C. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. Journal of Animal Ecology:601–647.
- Perrins, C. 1966. Survival of young Manx Shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. Ibis 108:132–135.
- Poole, K., and R. Bromley. 1988. Natural history of the Gyrfalcon in the central Canadian Arctic. Arctic:31–38.
- Potapov, E. R. 1997. What determines the population density and reproductive success of rough-legged buzzards, *Buteo lagopus*, in the Siberian tundra? Oikos 78:362.
- Potapov, E. 2011. Gyrfalcon diet: spatial and temporal variation. Pages 55– 64 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov,

editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.

- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
- Räisänen, J. 2001. CO₂-induced climate change in CMIP2 experiments: Quantification of agreement and role of internal variability. Journal of Climate 14:2088–2104.
- Reierth, E., and K.-A. Stokkan. 1998. Activity rhythm in High Arctic Svalbard ptarmigan (*Lagopus mutus hyperboreus*). Canadian Journal of Zoology 76:2031–2039.
- Robinson, B. G., A. Franke, and A. E. Derocher. 2014. The influence of weather and lemmings on spatiotemporal variation in the abundance of multiple avian guilds in the Arctic. PLoS ONE 9:e101495.
- Salamolard, M., A. Butet, A. Leroux, and V. Bretagnolle. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. Ecology 81:2428–2441.
- Steenhof, K., M. N. Kochert, and T. L. Mcdonald. 1997. Interactive effects of prey and weather on golden eagle reproduction. Journal of Animal Ecology 1997:350–362.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.
- Visser, M. E., C. Both, and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. Pages 89–110 in A. P. Møller, W. Fielder, and P. Berthold, editors. Birds and Climate Change. Elsevier, Amsterdam, The Netherlands.
- Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society of London Series B-Biological Sciences 265:1867–1870.
- Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, New York, USA.
- Wood, S. 2006. Generalized additive models: an introduction with R. CRC press. Boca Raton, Florida, USA.
- Wood, S. N. 2003. Thin plate regression splines. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 65:95–114.
- Zerbini, A. N., J. M. Waite, J. W. Durban, R. LeDuc, M. E. Dahlheim, and P. R. Wade. 2007. Estimating abundance of killer whales in the nearshore waters of the Gulf of Alaska and Aleutian Islands using linetransect sampling. Marine Biology 150:1033–1045.

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