Annual Dispersal of Endangered Burrowing Owls (*Athene cunicularia*): Implications for Estimating Survival

by

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Abstract

The migratory population of Burrowing Owl (*Athene cunicularia*) in Canada has undergone significant declines over the past five decades. Monitoring of Burrowing Owl includes estimation of annual survival which is predominantly obtained using mark-recapture data. Survival is calculated based on individuals resighted each year. These survival estimates are very low and a fundamental question is why? Two methodological explanations exist to explain low survival estimates: 1) emigration outside the study area is not accounted for; and/or 2) individuals within study areas are not always detected. Both of these issues are likely to result in survival being underestimated. To accurately estimate survival, a better understanding of dispersal is required. I corrected survival estimates using three different methods that account for dispersal and detection error within finite study areas. I also evaluated whether mark-recapture estimates that integrated dispersal provides similar answers relative to using dispersal patterns from satellite-tracked individuals (tracked via platform transmitter terminals). First, I used dispersal simulations to determine what proportion of individuals was likely to move outside a fixed study area each year due to chance. This approach ignores detection error within a study area. Second, I used a standard Cormack-Jolly-Seber model (CJS) that adjusts for missed detections which could be caused by individuals moving in and out of study areas between years or being present within a study area but not detected. Finally, I used a spatial CJS model that accounts for missed detections in a spatial context by explicitly including dispersal patterns in survival estimates and actual nest locations within study areas. For juveniles, survival was estimated to be 0.060 with 95% CI [0.046, 0.077] from the dispersal simulations, 0.41 [0.33, 0.49] using CJS, and 0.036 [0.00, 0.17] from spatial CJS. For adult males, survival was estimated from the dispersal simulations to be 0.37 [0.28, 0.45], 0.32 [0.22, 0.45] using CJS, and 0.36

[0.30, 0.43] from spatial CJS. For adult females, survival was 0.17 [0.12, 0.21] using dispersal simulations based on banding, and increased to 0.29 [0.21, 0.37] using dispersal simulations based on tracking data. The standard CJS model estimated survival to be 0.26 [0.19, 0.34] which increased to 0.28 [0.19, 0.36] in the spatial CJS model. The detection probability parameters estimated from both the adult female CJS model (0.40 [0.25, 0.56] and spatial CJS model (0.42 [0.25, 0.59]) were used to correct the dispersal simulations for the platform transmitter terminal (PTT) tracked birds. The resulting survival estimates were much higher than the previous methods: CJS detection informed = 0.74 [0.44, 1.3], and spatial CJS detection informed = 0.69 [0.43, 1.2]. While each method increased the observed survival estimate compared to uncorrected methods, they all are limited by one or more factors that make it difficult to estimate true survival. Future studies must develop approaches that better incorporate detection and long-distance dispersal to correctly estimate survival for migratory species such as Burrowing Owls, especially when these numbers inform management strategies. In particular, more tracking of individual dispersal patterns using satellite tags is needed to better estimate survival rates for Burrowing Owl in Canada.

Keywords: Survival, Dispersal, Burrowing Owls, Migratory

Preface

This thesis is an original work by Morganne Wall. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name “Radio-Telemetry Study of the Nocturnal Foraging Behaviours of Wild Burrowing Owls”, AUP00000020.

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Contents

List of Tables:

List of Figures

Chapter 1: Introduction

Ecology often involves studying individuals of a species and their interactions within their environment (Slobodkin 1961). These interactions include any factor or process that impacts their persistence. Survival is an important demographic parameter in ecology and estimating it is a necessary step to determining how well a species is responding to a changing environment. Certain actions, such as dispersal, can influence how survival and other demographic parameters are estimated by biasing return rates and expected distribution across a study area. The consequences of dispersal behaviours extend beyond the individual, and can affect both the population and species by regulating metapopulation dynamics, gene flow, and directly affecting population size and density (Greenwood 1980). For example, individuals that disperse may have a better chance of surviving disruptive events in the environment (Fahrig and Merriam 1994; Hoover 2003). In this way, dispersal can affect the survival of a species, but it can also influence the estimation of survival for a study population. Therefore, the interplay of these two factors is of key interest to wildlife managers as these metrics can inform us of how likely a population is to persist in time and space.

1.1 Methods to Estimate Survival

Survival is often estimated using capture-mark-recapture (CMR) data, as this is the most practical method for estimating survival over time and space for many species (Lebreton et al. 1992). While CMR methods are commonplace and useful, problems can arise in detectability and recapture following initial capture events where individuals may be missed (Kéry and Schmidt 2008). Reasons for missing individuals could include individuals returning outside of the study area boundary or poor detection rates within the study area. When a population is considered to be closed, individuals are assumed to remain within the study site permanently (Pollock et al.

1990). However, this assumption is not feasible when individuals are capable of moving distances greater than the dimensions of the study area; thus, open population modelling is necessary in many long-term wildlife studies. Poor precision or bias in survival estimates can result when returning individuals are overlooked, especially if they are more likely to be missed within particular groupings, such as age, sex, or survey period (Lebreton et al. 1992). Researchers must be cognizant of these issues when conducting and analyzing CMR studies and different methods have arisen to attempt to better model species survival across the landscape.

In many population studies, researchers delineate discrete study areas within the species range to measure two key population influences: recruitment, or the addition of new individuals, and loss of existing individuals (Baker et al. 1995). Recruitment can be seen through birth or immigration, while loss can include death or emigration. CMR relies on capturing and marking individuals, typically at breeding sites such as nests or dens, and then waiting to see if that individual will be resighted or recaptured within the study area again. Individuals returning to that breeding site again are exhibiting site fidelity, while individuals alive, but not returning, are exhibiting dispersal. While dispersal is a natural behavior exhibited by many species, delineated study areas to determine survival estimates are typically arbitrary. Depending on the size of the study area, return rates and the survival estimates they inform could be biased, with larger study areas showing higher return rates and sex specific biases conditional on equal effort in resampling taking place (Reed and Oring 1993).

There have been different approaches to handling the effects of discrete study areas when estimating survival and accounting for dispersal. A common approach is to use a distribution to fit the observed dispersal data to allow for the distribution to fill-in data resulting from missed detections inside the study area (Van Noordwijk 1984) and those returning outside the study area

(Barrowclough 1978; Baker et al. 1995). These methods can provide better survival estimates for populations where some individual's dispersal events are missed, for example, long-distance dispersals typically undertaken by young individuals or sex-biased dispersers. Baker et al. (1995) accomplished this by applying Bayes' Theorem to the observed dispersal distances, stating that these distances were the result of actual dispersal occurring as well as the probability of an individual being observed while recruiting or returning. They were able to produce a corrected distribution of dispersal distances and determine the probability of observing dispersal events from various distances and ultimately corrected survival estimates to include the effect of recruitment in and outside their study area. This technique makes various assumptions including that no dispersal distances can be longer than the longest dimension of the study area, equal dispersal directions were taken by individuals, no effect of habitat or edge effects on recruitment, and equal productivity across the study area to produce a weighting function for that specific site. This method accounts for study area shape where previous methods could not. Accounting for study area shape is important because study areas are often shaped around suitable habitat.

Another common technique for estimating survival is the use of open population CMR models. While closed population models are typically selected to estimate population abundance or size (Otis et al. 1978), they are difficult to use in long-term studies due to the assumption of no individuals entering or leaving. Open populations are systems where individuals may leave and enter the study area and/or population over time from other populations through emigration, immigration, birth and death; open populations best reflect most wildlife populations, especially those where individuals are capable of long-distance movements. Open-population models, such as the Jolly-Seber model are commonly used to estimate survival, population size, recruitment, and capture probability. The Cormack-Jolly-Seber model (CJS) also allows for the estimation of both individual survival and capture probabilities as well as the ability to use grouping and other covariates (Cormack 1964; Jolly 1965; Seber 1965). These models rely on the use of capture histories in a population where an individual *i*, is scored a 1 if they were alive and captured at certain sampling periods *t*, otherwise they are scored a 0. These models require that: capture and survival probability is the same for all individuals at period t (unless using covariates), no errors occur in mark detection, no effects of marking, marks are not lost, instantaneous sampling periods where release occurs immediately after an individual is marked, permanent emigration, individual independence from each other, and recaptures on separate sampling periods are independent (Williams et al. 2002; Mu 2019). While CJS models allow for the researcher to determine recapture probability it may not be able to correct for biases related to study area size and shape.

Survival estimates produced from most traditional CMR models, including CJS, do not allow for the separation of mortality and emigration. This results in an apparent survival estimate produced from the probability of both actual survival and returning to the study area. In these instances, the survival estimates are typically lower than actual survival unless all individuals are returning to that study area. Although CJS models attempt to better represent population and study dynamics, emigration can affect the ability for these models to accurately depict these parameters.

Recent work has estimated survival using CMR data and CJS models while adjusting these estimates to include a spatial component that accounts for dispersal and detection probability (Schaub and Royle 2014). Recapture probability can be biased when individuals undergo temporary random emigration from a population; this occurs when some individuals are not recaptured during at least one sampling occasion (temporary) and all of those individuals have the same probability of being missed during that sampling occasion (random) (Kendall et al. 1997; Schaub et al. 2004). Temporary-random emigration will not affect survival estimates however, temporary non-random emigration, where an individual's likelihood of being absent for a sampling occasion depends on that individual being absent in the previous sample (i.e. Markovian) will (Kendall et al. 1997). Temporary emigration can appear in many populations where individuals are missed during sampling - this could be due to them not present in the area, such as the breeding grounds, or because they are unavailable for recapture due to dormancy/torpor/hibernation (Schaub et al. 2004).

Instead of using robust survey design, methods such as those explored by Gilroy et al. (2012) and Schaub and Royle (2014) have attempted to produce models that can estimate survival and temporary emigration with CMR data. This method requires both the capture history used in CJS models as well as the spatial data pertaining to those histories. This spatial CJS method uses a state-space simulation where two states occur, survival is modelled in the first state and then dispersal location in the second state process. Survival is modelled first in a typical CJS model where the capture history is summarized in a matrix Y, along with a latent state variable, z, which describes the individual, z_i, as alive = 1 or dead = 0 at a specific sampling time, t. First capture of that individual is indicated by f_i so that $z_{i,f_i} = 1$ and then $z_{i,t+1}|z_{i,t} \sim$ Bernoulli ($z_{i,t}s_{i,t}$) as shown as equation 1 in Schaub and Royle (2014). Survival probability is then set as $s_{i,t}$ of that individual between the time of capture, t , and recapture at $t+1$. Dispersal is then modelled using a separate state and location is stored in the variable G so that both the x-coordinate, $G_{i,t,1}$, and the y-coordinate, $G_{i,t,2}$, are used. Each individual's location at time t_{+1} is then determined by equation 2 in Schaub and Royle (2014) assuming a normal distribution of dispersal, $G_{i,t+1} \sim$ *Normal* ($G_{i,t}, \sigma^2_G I$) using the dispersal variance in both directions, x and y, which are stored as a vector with two values so that dispersal distance is not used but is described by the dispersal variances where distance, D, = $\sqrt{(2(\sigma^2_x + \sigma^2_y) / \pi)}$. Lastly, the observation process is modelled where A represents the state-space for the study area and the model determines an individual's location within or outside a study area at time t using $r_{i,t}$. If $G_{i,t}$ falls within A, then $r_{i,t} = 1$ and if it falls outside then $r_{i,t} = 0$. The final equation in Schaub and Royle (2014) describes the observation model where $p_{i,t}$ is the recapture probability at time t for each individual i as $y_{i,t}|z_{i,t},r_{i,t} \sim \text{Bernoulli } (z_{i,t}r_{i,t}p_{i,t})$. This model requires assumptions where measurement errors are non-existent, re-encounters can occur anywhere within the study area which is spatially defined as the area where capture first occurs and recaptures can occur later, survival and recapture probability are constant, and dispersal is normally distributed.

By developing spatially explicit CMR models using open-population assumptions, true survival might be better estimated with spatial generalization and allow for data with poor recapture and observed dispersal rates in fixed study areas, which is common in species-at-risk monitoring data. The spatial CJS technique improves upon generalized CJS models and allows biologists to infer more realistic survival estimates since the effect of study area can be addressed. Study areas are often arbitrary or logistically-defined areas rather than being biologically informed so such models may be crucial (Thomas and Kunin 1999; Schaub et al. 2013). The spatial CJS should produce the most realistic survival estimate, but it relies on strong mark-recapture data. Thus, incorporating unbiased dispersal data is needed to produce the most realistic estimate. By combining ways of measuring dispersal, both issues with the previous models could be addressed. The combination approach involves using the recapture probability estimated from the CJS models, standard and spatial, to inform the Baker methods while using the tracking informed distributions. The Baker methods uses observed dispersal patterns to simulate distances but also assumes perfect detection within the study area. Exploring methods where unbiased dispersal and detection corrected probabilities are used should help us understand how to best estimate survival. For generalist species this is especially important when making conservation decisions as their dispersal and return habitat might extend past historical study areas across their expected range where perfect detection cannot be attained.

1.2 Study Species

Burrowing Owls (*Athene cunicularia*) (hereafter BUOW) are small grassland favoring owls that are found across North America. Within Canada they are migratory (AESRD 2012) and this northernmost population has undergone significant declines compared to populations across their range. In 1995, BUOW were listed as Endangered in Canada (COSEWIC 2017) in 1999 they were listed as Endangered in Saskatchewan, and in 2006 they were listed as Endangered in Alberta (AESRD 2012). Internationally, BUOW are protected by the United States Fish and Wildlife Services (USFW) (Clayton and Schmutz 1999); in Mexico they are subject to special protection (Klute et al. 2003; Wellicome et al. 2014).

The western BUOW (*Athene cunicularia hypugaea)* is unable to dig its own burrow, unlike the Florida subspecies (*Athene cunicularia floridana)* (Millsap and Bear 2000), and relies heavily on other fossorial mammals such as American badgers (*Taxidea taxus*), black-tailed prairie dogs (*Cynomys ludovicianus*), and Richardson's ground squirrel (*Urocitellus richardsonii*) (Green and Anthony 1989). Within the provinces of Alberta and Saskatchewan, BUOW nest within previously excavated burrows; these typically occur on dryland crop or rangeland grazing operations (Poulin et al. 2005). BUOW select for burrows located within short grass or areas with sparse vegetation across the landscape. However, they have also been found to use areas located along edges, such as roads or irrigation ditches, especially for foraging

(Marsh et al. 2014). Klute et al. (2003) have also documented a population nesting within irrigated cropland within southern California. These findings suggest BUOW are habitat generalists within prairie ecosystems, with the main requirement for nesting being access to burrows (Klute et al. 2003; Poulin et al. 2005; Marsh et al. 2014). Use of these burrows allows the owls to conceal their nests from threats including various predators and inclement weather events. Their reliance on these burrows has aided biologists in their management, as trapping for marking is easily accomplished by leaving traps at the entrance to their burrow. BUOW also use artificial burrows for nesting and prey caching when available aiding detection, monitoring, and reproduction in various studies and recovery actions within Canada (Wellicome 2000).

Monitoring for BUOW populations within their Canadian range occurs during their time on their breeding grounds. These populations winter in the southern United States and central Mexico (Wellicome et al. 2014) and return to breed in Canada in April. BUOW males return to select a nesting site during the early spring and actively defend their resources such as nesting or foraging habitat which then attracts a female to both the male and the resources he defends (Greenwood 1980; Forsman et al. 2002; Fisher et al. 2004). The males role shifts to vigilance and provisioning behaviors during the remainder of the breeding season and he typically spends most of his time on a perch or nearby roost (Scobie et al. 2014). Vigilance requires the male to play an active defensive role focusing on chasing, vocalizing, or crouching behaviors. The male BUOW is primarily responsible for delivering prey items to the nest usually during dawn/dusk (Marsh 2012; Scobie et al. 2014). These items include vertebrates such as mice, voles, and amphibians, and invertebrates such as beetles and grasshoppers (Poulin et al. 2001; Ayma et al. 2019). Female owls will spend most of the breeding season in the burrow whether incubating or brooding if successfully paired. The female will have an average clutch size of nine eggs, typically in May, which will hatch approximately 30 days following the first egg laid (Wellicome 2000). Typically, only half of the hatchlings will survive to fledging at 35 days old (Wellicome et al. 2013). Fisher et al. (2015) found that inclement weather contributed significantly to this mortality rate due to nest flooding and related owlet starvation. The period following fledgling is believed to be the limiting stage of survival in BUOWs (Todd et al. 2003). Low survival during this post-fledgling stage is likely due to the increased threats due to predation, starvation, and anthropogenic features such as collision with vehicles. Predators of BUOW are primarily fossorial mammals (such as American badgers) and large raptors such as Swainson's hawk (*Buteo swainsoni*) and great-horned owl (*Bubo virginianus*). These threats differ across their range which is believed to be due to the differences in land use (Clayton and Schmutz 1999). In Saskatchewan, the grassland region is highly fragmented with a mosaic of cropland and rangeland resulting in high mortality due to road collisions, canid predation due to increased edge, and avian predation due to increased anthropogenic structures (Clayton and Schmutz 1997). In Alberta, the grassland region is less fragmented but has higher reported hawk predation (Clayton and Schmutz 1999).

BUOW dispersal patterns have been studied across their North American range (Lutz and Plumpton 1999; Hoyt 2001; Millsap 2002; Todd et al. 2007; Catlin and Rosenberg 2014; Riding and Belthoff 2018), however population distribution and size remain difficult to model especially in areas with low observed returns. Duxbury (2004 as described in AESRD 2006) using isotope analysis suggested that long distance dispersal across their entire range is occurring, resulting in a high degree of gene flow between populations. For metapopulations to be maintained, individuals would have to disperse distances not detected by localized studies (Greenwood 1980). Stepinsky (1998) reported in the Canadian range that female BUOW typically disperse further than males (median values were 13.3 km versus 6.9 km in natal dispersers; 0.5 km versus 0.3 km in breeding dispersers) and juveniles further than adults (median values were 10 km in juveniles versus 0.4 km in adults). However, it remains unclear whether these observed dispersal distances are representative of actual dispersal patterns or whether these represent minimums caused by the area searched.

This thesis compares three methods to estimate and correct survival estimates for BUOW within delineated study areas while taking into account dispersal and detection error. I use observed annual dispersal patterns from BUOWs captured using historical CMR studies within discrete historical study areas in Alberta and Saskatchewan. These patterns were used to characterize frequency distribution curves to simulate dispersal events and determine the effects they may have on apparent survival estimates based on their probability of observing a return within the study areas. The observed data were then compared to tracking data made available by satellite transmitters on a subset of the population. The observed data is also analyzed using traditional CJS models to determine the survival and recapture probability within groups. Finally, a spatial CJS model is constructed to determine how temporary emigration may affect these CJS models. How accurately each of these methods estimates survival is then discussed.

Understanding dispersal is crucial to understanding a species life history and quantifying survival within a population (G.L. Holroyd and Trefry 2011); this is true for BUOW conservation when considering strategies to aid in their survival (Catlin et al. 2005). Specifically, in Alberta, there is a significant knowledge gap pertaining to the owls' emigration and annual survival, as highlighted in the *Alberta Burrowing Owl Recovery Plan* (AESRD 2012). The topic of this study is also emphasized as a research need in the *Recovery Strategy for the Burrowing Owl in Canada* (ECCC 2012). My thesis provides insight on modelling annual dispersal and survival and will be helpful in guiding management actions to assist in BUOW population recovery in Alberta and Canada.

Chapter 2: Using Novel Survival Estimates to Account for Annual Dispersal in Burrowing Owls

1.0 Introduction

Survival rate is a key parameter for informing the management of wildlife populations (Oli and Dobson 2003; Karczmarski et al. 2017). Annual survival of individuals in a study population is often estimated using capture-mark-recapture (CMR) methods by assuming that surviving individuals show sufficient site fidelity to allow their recapture (Hupman et al. 2018). However, this approach can be misleading, particularly for migratory species, as not all individuals may return to the same natal or breeding location in subsequent years (Marshall et al. 2004). Lack of site fidelity makes it difficult to determine how many non-returning individuals have died versus how many have moved to a different location, thus confounding the separation of dispersal and mortality. Consequently, most studies report apparent rather than true survival, with apparent survival often being far lower than true survival, which has significant implications for managing migratory populations (Schaub and Royle 2014).

Dispersal can be measured using recovery, resighting, or recapture at a site different from the original capture location (Barrowclough 1978) or, more recently, using multi-year satellite telemetry to determine exactly where individual birds disperse (Cadahía et al. 2010; DeSorbo et al. 2015). Knowing dispersal distances and rates makes the adjustment of apparent survival rates possible to more accurately estimate true survival (Lebreton et al. 1992; Baker et al. 1995; Winkler et al. 2005). However, the accuracy of such adjustments depends on numerous assumptions about dispersal patterns and the spatial extent over which dispersal events are tracked (Greenwood and Harvey 1982). Using CMR there is a risk that dispersal distances are biased to shorter distances because of the constraints of surveying a finite study area (Barrowclough 1978; Gilroy et al. 2012). This bias is due to the inverse probability of recapturing or observing dispersal events as the distance *x* increases, particularly in situations where long distance dispersal can occur. When *x* is greater than the longest dimension of the study area, there is a probability of zero that the dispersal event is observed by the investigators. Furthermore, if an individual study organism is initially located near the edge of the study area, that individual may be less likely to be resighted than an individual in the center of the study area because both the distance and direction of movement could result in a higher chance of return outside of the study area. Thus, properly characterizing dispersal distances and directions is essential for accurately correcting apparent survival estimates. In contrast, satellite-based telemetry provides accurate estimates of both short- and long-distance movements, assuming the device itself does not influence annual dispersal patterns but is typically limited by a much smaller sample size that may or may not be representative of the target population.

1.1 Study Species

The northern extent of the Western BUOW range reaches into southern Canada, with migratory populations currently found within Alberta and Saskatchewan (COSEWIC 2017). A noticeable decline in their population has been recorded in the Canadian Prairies. During the 1990s population declines were estimated to be 90% across Canada and the species was considered extirpated from British Columbia and Manitoba; population declines were then believed to have slowed but remained at 57% from 1994 - 2004 (Environment and Climate Change Canada 2012). Sheffield (2021) used national Breeding Bird Survey data to determine BUOW population declines over the last 50 years noting a decline of 1.1% per year across North America and 6.4% per year across Canada. The decline has been recorded along with a range contraction in both Canada and the United States where it appears the population is contracting southward unlike many other avian species that appear to be expanding northward. Possible reasons for decline include the extirpation of burrow building mammals, heavy pesticide use, human-caused mortality, and extreme weather events (Clayton and Schmutz 1999; Klute et al. 2003; Smallwood et al. 2007; Wellicome et al. 2014). However, Wellicome et al. (2014) hypothesized that low adult survival could also be due to high emigration of individuals into the southern parts of their range. This behavior could have an important effect on population models in Canada, as managers may be incorrectly assigning mortality rather than emigration as the cause of local population decline. Apparent survival rates of BUOW in this region as currently estimated are sufficiently low that the population would have been extirpated many years ago if immigration and/or emigration were not occurring, but at what scale and to what degree remains unclear (McDonald et al. 2004; COSEWIC 2017).

My objective was to estimate survival of BUOW in the northern most portion of the species' range using methods that make differing assumptions with respect to how to account for dispersal when estimating survival. I compare apparent survival estimates across age and sex classes within a migratory population of BUOWs and correct for dispersal using resighting data gathered across their Alberta/Saskatchewan range from 1986-2019 and satellite-telemetry (PTT) data collected between 2014-19. Specifically, I modify the Baker et al. (1995) method to test how dispersal might influence survival estimates by populating a spatially explicit computer simulation based on measured dispersal patterns. I mapped the original capture locations (nest sites) in each study area and then I simulated, for each individual, the probability that, if they survived to the following year, they would remain in the same study area. This probability of study area fidelity was calculated by simulating 10,000 dispersal events (probability of dispersal, distance dispersed, and angle of dispersal), and calculating the proportion of these inter-annual dispersals that would result in the individual returning inside the study area, and thus available to be resighted the following year. I then compare the dispersal distributions created from observed CMR returns to patterns using PTT tracking methods to assess bias in the frequency distribution for dispersals when they are based on band returns rather than tracking via satellite.

While the Baker method may be an effective approach to account for dispersal, it assumes the detection rate is 100% within the study area, which is unrealistic given the large size of many study areas. The simulation approach uses data that requires visiting a site and measuring presence/absence, so failing to detect in at least some cases can cause an underestimation, which ultimately impacts survival estimates (Hutchinson et al. 2011). Models that account for possible detection issues are ultimately more flexible and useful for endangered species management. An alternative approach that can account for imperfect detection is Cormack-Jolly-Seber (CJS) methods. Use of a CJS model is common in survival studies as the output survival parameter provides both the number of individuals surviving and remaining on the study area while incorporating detection probability (Marshall et al. 2004). I use CJS models to compare dispersal probabilities to the Baker method and produce both survival and recapture probabilities. Finally, I produce spatial CJS models to account for temporary emigration as described by Schaub and Royle (2014). The spatial CJS attempts to account for both dispersal and imperfect detection, theoretically producing the most realistic survival estimate. I then compare the survival estimates produced from all three methods for each dispersal category, as well as comparing survival estimates for females produced from PTT dispersal distributions and from banding dispersal distributions. I also attempt to incorporate the detection probability produced from both the standard CJS and the spatial CJS into the Baker method for PTT owls. This method allows for the incorporation of the PTT data, a significantly different dispersal distribution from the banding data, while not assuming perfect detection within a study area.

Since banding data appears to be biased to short-distance dispersals and perfect detection is unlikely, this could provide the most realistic survival estimate. Studies of BUOW survival have referenced emigration and dispersal (James et al. 1997; Millsap 2002) but have not used dispersal distance or dispersal direction explicitly when correcting apparent survival estimates.

2.0 Methods

2.1 Study Areas

The selected sites and methods for this study are based on historical data and current studies involving Canadian BUOW populations (Wellicome et al. 2014). These include two study areas in Alberta and three study areas in Saskatchewan near the northern edge of the historical BUOW range (Figure 1).

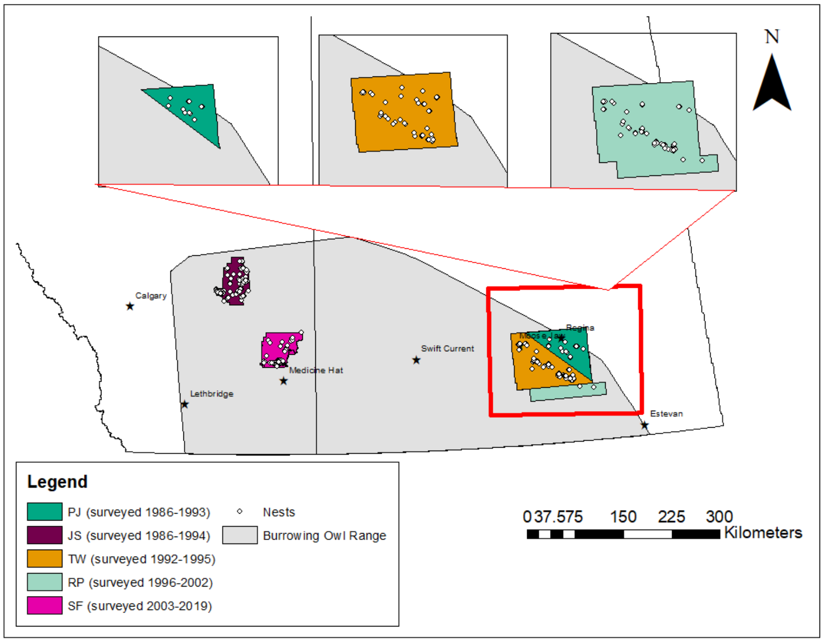

Figure 1: Map of study areas used in analysis. BUOW range in Canada is shown in grey and nests where banding occurred are shown as white dots. Suffield (SF) and Schmutz (JS) occur in Alberta whereas James (PJ), Wellicome (TW) and Regina Plain (RP) occur in Saskatchewan.

The two study areas in Alberta (AB) are geographically and temporally isolated from each other. The first study is located near Hanna, AB. The land use in this area is approx. 85% grazed native grassland used for ranching within the dry-mixed grass prairie. Due to the limited annual precipitation (Schmutz et al. 1980), < 20% of the study area is farmed for annual crops and forage crops (i.e., non-native annual or perennial grasses, herbs, or forbs), and most of the land is managed to protect the landscape and soil from erosion. The limited agricultural conversion has resulted in a stable agroecosystem coinciding with wildlife (Clayton 1997). The historical study took place from 1986 – 1994, and the study area is coded as "Schmutz".

The other Alberta study area takes place within a secured military base CFB (could define as Canadian Forces Base – many won't know this) Suffield near the town of Ralston, AB with 2700 km^2 of mostly native grassland that provides protected, unfragmented habitat for many species-at-risk. Frequent, patchy fires and varied amounts of grazing by livestock and wild ungulates occur, providing a similar disturbance regime to that with which grassland species evolved in North America's Great Plains (Fuhlendorf et al. 2006). While military training and oil developments occur on large portions of the property, a National Wildlife Area (designated in 2003) makes up 458km^2 of CFB Suffield's native grassland with the purpose of protecting wildlife and habitat, so human disturbances are heavily regulated and limited. There are various wildlife populations found and monitored by biologists, and any BUOW observations by military personnel are reported and investigated. Data used in this analysis were collected between 2003 – 2019 and is coded as "Suffield".

The study areas in Saskatchewan (SK) are nested within a region called the Regina Plain. Unlike the Alberta study areas, the landscape within this region has been significantly modified and altered for agricultural use due to its productive soils and higher annual rainfall. The Regina

Plain landscape is approximately 90% cropland which is cultivated each year for the production of non-irrigated cereal crops (Poulin et al. 2005). Few native grassland patches exist as many grassland pastures have been converted to introduced forage species for grazing livestock. From 1986 – 1993, BUOW location data were collected within the northeast triangle of the Regina Plain (Figure 1 – green triangle), coded as "James" for the analysis. From 1992–1995, this study area was expanded to include the area southwest of the James area but north of the bottom portion (Figure 1– orange polygon), coded as "Wellicome" for the analysis. From 1996–2002, the study area was further expanded (Figure 1 – blue polygon) data; this area is coded as "Regina Plain" for the analysis.

2.2 Survey Protocol

BUOW arrive in Canada from mid-April to late-May, with earliest nesting beginning in late-April (Wellicome 2000), and individuals start their southward migration during September and October (Todd et al. 2003). Data collection took place from April-September to ensure adult and juveniles could be found and banded. The 6758 encounter record dataset covers 33 years of nest monitoring from BUOW nesting and capture events. Nest visits and survey sites were selected based on previously active nests and landowner/citizen science sightings in each study area.

Sampling occurred annually beginning in April when BUOW would return to the breeding grounds, the sample areas were visited using a combination of call playback (where recorded sounds of male BUOW were played repetitively) and visual surveys to find any active nests. Nests known to have been occupied in previous years were further investigated by approaching and looking for signs of recent activity at the entrance to the burrow (ie. whitewash, pellets, prey items, BUOW feathers). This method ensures any individuals that may have been missed during call playback surveys would be included. Once determined, nest locations were mapped using GPS coordinates, and repeatedly visited to gather information on adults of both sexes and on their clutches/broods. Pre-fledging, trapping was conducted at all nests in an attempt to capture and mark each individual BUOW adult or young-of-the-year.

Individual owls were trapped at nest and roost burrows using walk-in traps, bal-chatris and/or noose carpets placed directly at the burrow entrance or by opening artificial nest burrow cavities; this ensured the owls captured were actively nesting at capture locations (Clayton and Schmutz 1997; Wellicome et al. 1997). Once captured, all individuals were banded with one aluminum leg band plus one auxiliary marker on the opposite leg to determine if dispersal patterns differed by age and sex class. Use of binoculars, scopes, or remote ‘trail’ cameras (Reconyx), allowed for individual recognition by observing alphanumeric codes without necessarily recapturing owls. From 2014–2019, 53 adult owls were fitted with a 5g solar Platform Terminal Transmitter (PTT) (Microwave Telemetry, Inc.) to track their migration and dispersal patterns using satellite data (Wellicome unpublished data). Of these 53, 6 lasted from one breeding season to a subsequent breeding season, so that return location was determined.

2.3 Measuring dispersal dynamics

Dispersal was determined by combining all banding and recapture records from across the studies and then measuring the Euclidean distance between the burrow location in the first year of capture to the burrow location in the subsequent year of re-encounter. Individuals were grouped first into their respective study area and then into the following dispersal categories for analysis based on their initial year of capture: Adult-Female or Adult-Male and Juvenile. Data were filtered to remove original capture events that were outside the study area, first captured in the final year of the study, or found dead before the next nesting attempt for breeding dispersers or before the first nesting attempt for natal dispersers. Banded individuals that were observed >1 year apart were included in dispersal estimates. Individuals banded as juveniles but not recaptured in their second year were put in the natal dispersal category on the observation that breeding dispersal is less than natal dispersal (Stepinsky 1998). For those individuals not recaptured in their original study area, (i.e., first captured in the James study area and recaptured in Regina Plain), the individual was not considered recaptured but was 'reset' and counted as a new capture in the subsequent study area as the Regina Plain study area grew over time. Individuals were classed as either returning to the same nesting territory (0) if their subsequent burrow was ≤ 250m of their previous nesting attempt or dispersing (1) if > 250m.

2.4 Modified Baker Simulation Method

The modified Baker method (Baker et al. 1995), requires the observed dispersal distance and fits the data to a known statistical distribution. The different sex and age categories were tested using the 'fitdistrplus' package (Delignette-Muller and Dutang 2015) in program R to compare fit to lognormal, exponential, and gamma distributions and comparing Akaike Information Criterion (AIC) values and quantile-quantile (Q-Q) plots and the distribution that best matched the observed (lowest AIC and closest Q-Q plot) was selected. 0s were then removed from the data to see if this would improve fit. The selected distribution was then used to inform distances in simulated dispersal events across the study area. In simulations, BUOW disperse from known breeding locations to determine the probability that individual returns to or disperses outside of the study area. Simulating dispersal events informs how many individuals are likely missing due to the constraints of the study area size and shape. Simulations also can allow for directional dispersal if evidence for such behaviors exists however, dispersal bias was checked for first using a Rayleigh z test (Landler et al. 2018).

The most basic survival estimates mark-recapture/resight studies are typically calculated as (Eq. 1).

$$P(Survive) = \frac{number\ resighted\ in\ year\ t{+}1}{number\ marked\ in\ year\ t} \qquad \text{Eq.1}$$

The problem with relying solely on this approach is it assumes all individuals marked will be available to be resighted in the following year. However, this assumption is not always valid because dispersal can confound dispersal with mortality.

One way to account for dispersal, is calculating the probability of observing an individual within a study area to correct survival estimates for individuals surviving but returning outside the study area (Baker et al. 1995). This correction allows us to determine the number of individuals available for resighting in the following year. The conditional probability of resighting an individual depends on the probability it survived multiplied by the probability it returned to the study area (Eq. 2).

$$P(Resight) = P(Survive) * \ P(In\ study\ area\ |Survived) \qquad \text{Eq. 2}$$

This equation can be rearranged to solve for the probability of survival for that individual (Eq. 3).

$$P(Survive) = \frac{P(Resight)}{P(In\ study\ area\ |Survived)} \qquad \text{Eq. 3}$$

With observational data, one calculates the number of individuals alive in year *t* and observed within year *t+1*. Baker et al (1995) then substituted in the following equations into Eq. 3 by calculating the numerator as Eq. 4 and the denominator as Eq. 5.

$$N(Observed) = \frac{1}{N}\sum_{j=1}^{N} I_j \qquad \text{Eq. 4}$$

$$N(Expected) = \frac{1}{N}\sum_{j=1}^{N}\left(\frac{Simulated\ Owls\ In\ Study\ Area}{Number\ of\ Simulations}\right) = \frac{1}{N}\sum_{j=1}^{N} p_j \qquad \text{Eq. 5}$$

This equation allows calculation of *P(Resight)* by calculating the apparent survival of the population, or simply the proportion of individuals that are resighted in Year $t + 1$ or *N(Observed).* Individuals were assigned either a 0 for not seen again, or a 1 for resighted in following years (represented by the I_j term in Eq. 4 above).

To solve for the denominator in Eq. 3, *P(In study area|Survived),* simulations were used to calculate the number of individuals expected to be resighted in the following years based on dispersal behavior. *N(Expected)* is solved using simulations where the p_j variable represents the probability of an individual being resighted. Resighting depends on the nest location within a study area, age class, and sex of the individual (Eq. 5). Sample size is often limited in long-distance dispersal studies, so to estimate this probability, simulations were used to calculate the proportion of individuals returning outside of the study area versus those returning inside using dispersal distribution curves from observed dispersal data.

Dividing *N(Observed)* by *N(Expected)* simplifies Eq. 3 by cancelling out the 1/N in both terms so *P(Resight)* becomes $\sum_{j=1}^{N} I_j$, which equates to the number of individuals resighted. *P(In study area | Survived)* becomes $\sum_{j=1}^{N} p_j$, which is the sum of Bernoulli trials where the probability of success (the probability of an individual being resighted) will vary between individuals. When multiple Bernoulli trials occur the sum of the probabilities is the expected number of individuals to be resighted (or successes in the Bernoulli trials) if all individuals survived to be resighted which tends to follow a Poisson binomial distribution and resulted in the final equation to calculate survival (Eq. 6).

$$P(Survive) = \frac{N(Observed)}{N(Expected)} = \frac{\sum_{j=1}^{N} I_j}{\sum_{j=1}^{N} p_j} \qquad \text{Eq. 6}$$

To avoid the simulated dispersal distances being restricted to the study area's dimensions, this method was modified to correct survival using dispersal curves generated from data collected across multiple study areas (see the Appendix for R code). The curves were produced using observed dispersal distances and fitted to one of three possible distributions (log-normal, gamma, and exponential). Both AIC values and QQ plots were used to assess distribution fit.

The probability of dispersal, $p_{disperse}$ was first calculated to account for the high degree of site fidelity in BUOW. The probability was calculated by summing the total number of individuals that dispersed (distance $\leq$ 250m) by the total number of individuals that were re-encountered. This probability was calculated separately for each dispersal age class by determining the number of returns across all individuals in that class. Juveniles were grouped together, as sex was very rarely known unless that individual was captured again as an adult. The simulation first applied this probability to those individuals in their corresponding group to determine what an individual would do, disperse or not, before selecting a distance from the curve and simulating a dispersal event.

Angles (θ) were simulated from an arc of 0-359 degrees. This was done 10000 times to create a circle around each location – similar to Baker et al. (1995). Simulated coordinates were then calculated from these random distance and angles using trigonometry based off the original capture location (X_i,Y_i) where endpoints (X Loc, Y Loc) were simulated by pulling a distance and a bearing and applying it to the original banding (nest) location (Figure 2).

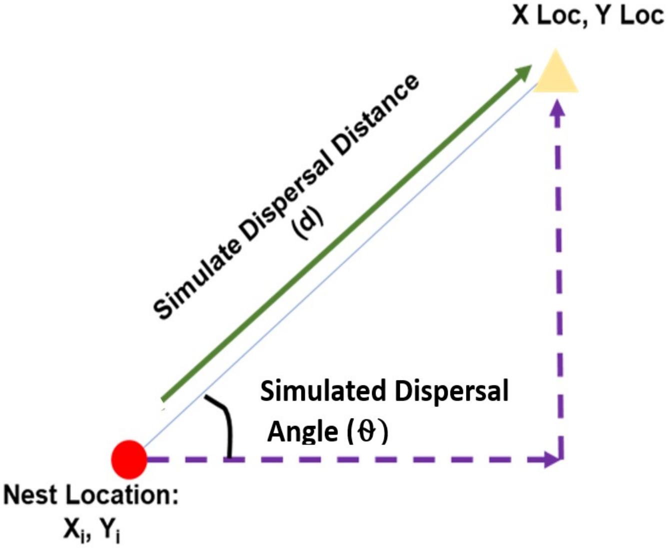

Figure 2: Simulation process using randomly generated dispersal distance pulled from the dispersal distribution and the original location the individual was resighted ('Nest Location') to determine where each simulation ends up ('X Loc, Y Loc'). NOTE – should be "Simulated" – add "d" to label.

These simulated dispersal locations were then assessed as to whether or not they fell within the study area. For each individual, all successes (falling inside) were averaged across the total number of simulations and this probability was averaged across all individuals to calculate *N(Expected)*. For instances where a gap year occurred (an individual was banded in year n, unseen in year $_{n+1}$ but resighted in year $_{n+x}$), a variable, *gapYear*, was assigned to account for this in survival estimates (assigned NA for original capture, 0 if resighted consecutively or 1 if one gap year occurred). The total years an individual survived was then taken by summing the *gapYear* variable plus 1 so that recaptures counted for 1 and recaptures counted for 1 + as many gap years that occurred. The *gapYear* variable assumes that individuals missing in one year were alive and were just missed in detection as birds typically disperse greater distances in their first dispersal compared to subsequent years. Older individuals are more likely to return to their previous nesting location (Greenwood 1980), which suggest they were more likely to be missed in a given survey year if they were found in later years. Birds banded in the final year of the study were removed. This step gave the total number of birds expected (*N(Expected))*. The total years survived (observed returns) divided by the number of birds expected to be observed provided a corrected survival estimate for each study area. These were averaged across all study areas to provide a survival estimate per category (Adult-Female, Adult-Male and Juvenile). the acronyms are a not overly informative.

Following these simulations, the banding-recapture data were then compared to tracking data acquired from individuals tracked via satellite telemetry. The PTT data were acquired from Holroyd and Trefry (2011); it was used to compare the potential for biases in dispersal distance caused by sampling within a fixed study area. Few data points were available and as such only adult female dispersal data were used in this simulation to estimate adult female survival. The distributions were first compared to determine the probability of dispersal based on those exhibiting site-fidelity or dispersal events on their return to their breeding range. The distributions were then used in the simulation to compare how these different methods, CMR versus PTT, affected the probability of resighting. These probability values were then used to calculate P(Survive) values for both methods to determine the effect they have on estimated survival based on a delineated study area.

The assumptions for this simulation approach include: 100% detection probability across the study area, no effect of study area on observed distances, no heterogeneity in productivity on the study site, and no directional bias.

2.5 Cormack-Jolly-Seber Method

The second method used to estimate survival is the more common CJS model. These models are commonly used with CMR data as they produce two essential parameters while allowing for an open population with non-perfect detection: detection/recapture probability (rho (ρ), or the probability that an individual will be observed during a certain time, t); and apparent survival probability (phi (φ), or the probability that an individual survived and is in the study area between t and t+1) (Williams et al. 2002). CJS models allow for grouping variables and individual covariates such as age and sex. Because the capture histories were created per subset, only study was used as a grouping factor.

The CJS models were created using the package *marked* (Laake et al. 2013) in Program R (R Core Team 2020). Capture histories for each study area were combined to account for the low overall re-capture frequencies across each study area. Multiple models were generated and then compared using AIC values and comparing CI intervals. The top 3 models were reviewed to compare the survival estimate (p). The best model was selected based on low AIC score and reasonable CI intervals. The best fitting model was used to generate the survival estimate that was compared to the other methods.

The assumptions for the CJS model are every individual in the study has the same probability of being captured or resighted and surviving until the next sample period, no errors in observing marked individuals, sampling and release periods are instantaneous, emigration is permanent, and individual fate is independent from other individuals (Williams et al. 2002).

Goodness-of-fit was tested for the CJS data using the package *R2ucare* (Gimenez et al. 2017). This package includes three tests, and each were run using the output from the ADULT-FEMALE CJS model. The first test, or the omnibus test, was used to see if there is equal capture probability and survival across individuals. If the data passed this test indicating good fit, then the other tests were not run. The second test determines if recapture was affected by the initial capture event. The third test determines if marking affected survival. The variance inflation factor was also calculated to check for overdispersion as well as goodness-of-fit.

2.6 Spatial Cormack-Jolly-Seber Method

While the previous two methods are useful to produce survival estimates, they are challenged with real world data by some of their assumptions related to detection error (Baker et al 1995) and the effects of emigration (CJS) that ultimately bias these survival estimates. The third method to handle these challenges is modified from Schaub and Royle (2014) to introduce a spatial component to the CJS model. This method attempts to combine the previous two methods by producing a CJS model informed by the dispersal distributions captured from the banding data in each study area. The spatial CJS models were created using the code from Schaub and Royle (2014) in Program R (R Core Team 2020). Input parameters to run this model were specified by Schaub and Royle (2014) and are summarized in Table 1; full code found in the Appendix.

Table 1. The input parameters required for the spatial CJS model and the values used in this analysis.

Variable	Description	Source
Y.in	Capture history for each individual	Banding data
G.in	Spatial coordinates, 1 matrix for X coordinates, 1 matrix for Y coordinates, NA for non-encountered	Banding data
F	Year of first captured	Capture history
D	Year searches were terminated	Capture history
sa	Study area an individual was captured in	Banding data
grid.x.study.area	x-coordinate of the grid cells, scaled by minimum value to start at 0	Study area grid

grid.y.study.area	y-coordinate of the grid cells, scaled by minimum value to start at 0	Study area grid
ngrids	Number of grid cells per study area	Study area grid

The capture history data is first stored in a matrix and each record details the capture event, shown as $Y_{i,t}$ where the individual $_{i}$ is scored 1 if it was recaptured during time $_{t}$ and if not it is scored a 0. The capture coordinates are stored in an array G where each x and y coordinate is stored, $G_{i,t,1}$ and $G_{i,t,2}$ each time a recapture occurs. If the individual is not recaptured at time $_{t}$ then these values are presented as missing values. This model assumes no measurement errors, recaptures can occur across the entire study area, the study area is defined by the capture and recapture locations, and survival does not vary across the study area as well as outside the study area. Schaub and Royle (2014) describe this method as using a state-space formulation; the first state process models survival and the second models the dispersal locations. A latent state variable z indicates the individuals state of being alive $z_{i,t} = 1$ or dead $z_{i,t} = 0$; z is assumed to be independent among individuals but conditional upon the survival probability. An observation process is also described because individuals must be alive and in the study area to be recaptured so this process is conditional on the individual surviving and staying in the study area.

The spatial CJS model requires the input parameters and functions to simulate the data using the code for irregularly shaped study areas as described in Schaub and Royle (2014). A function to simulate both the survival process and the dispersal process were then run and then another function checks if a location is within the study area. The first step was to create the study area and produce a grid overlay to assign which cells are inside the study area and those that are outside. The next step was to create the data using the input parameters, and then bundle and analyze it using the package *R2jags* (Su and Yajima 2012). The initial values for the known state CJS model are created using a function (Kéry and Schaub 2012) and the model was specified with the MCMC settings which were set so that two Markov chains were run with 10000 iterations, discarding the first 5000 samples (ni = 10000, nt = 1, nb = 5000, nc =2).

2.7 Comparing Survival Estimates Across Methods

Each survival estimate and their confidence intervals were then compared to see how each method estimated survival per class. For adult females, the banding and tracking data were used and compared in the Baker Simulations, while adult male and juveniles could only be compared using the banding data across the Baker Simulations, the CJS and the Spatial CJS models. Additionally, I attempted to include the detection probability parameter as estimated by the two CJS methods into the survival estimate of the Baker Simulation for the PTT birds. While my sample size for PTT birds (n = 7) is small, I believe it is an informative estimate in that it helps us understand how important the 100% detection assumption made by the Baker method is. To do this, Monte Carlo samples were drawn from the CJS model estimates of p and transformed to a probability scale. Monte Carlo samples were also drawn from the spatial CJS model and thinned to 1000 to match the bootstrapping method used in the Baker method so that every 10th sample was kept. The Baker method was then run with 10000 more simulations per bird and the mean, standard deviation, and probability of dispersal were incorporated from the tracking data distribution for dispersal. Using this method, the number of expected birds was then corrected for the detection probability produced from the CJS and spatial CJS models. Uncertainty was assessed using a bootstrapping method and a correction for detection probability was included.

3.0 Results

3.1 Data Exploration

A total of 6758 encounters were recorded. From this capture history, 64 were removed as the birds were used in captive breeding and capture-hold-release programs, resulting in 6694 encounters. These events were then categorized by the sex (if adult at first capture) and age class of the individual. Table 2 shows the breakdown of encounters per category. Categories were combined to create 3 final categories: Adult-Female, Adult-Male and Juvenile.

Table 2. Records of encounter history from BUOW data collected between 1986-2019 in Alberta and Saskatchewan. Encounter histories were combined into 3 categories to inform simulations: Adult-Female, Adult-male and Juvenile.

Adult_F	Adult_M	Adult_Unk	Juvenile_F	Juvenile_M	Juvenile_Unk	NA_F	NA_M
1051	866	8	86	117	4560	5	1

The original capture count once filtered was: Adult-Female (n = 564), Adult-Male (n = 449) and Juvenile (n = 2910).

Total recapture events for each category were as follows for Adult-Female (n = 64), Adult-Male (n = 104) and Juvenile (n = 85). The tracking data available from PTT birds (n = 7) were used to compare to the banding dispersal distribution for adult females only.

All four banding dispersal categories exhibited a right-skewed (or positive skewed) distribution (Figure 3). The distributions from the banding data exhibited an increased density of short dispersal events, whereas the distribution from tracking data showed a higher spread of dispersal distances greater than 25km.

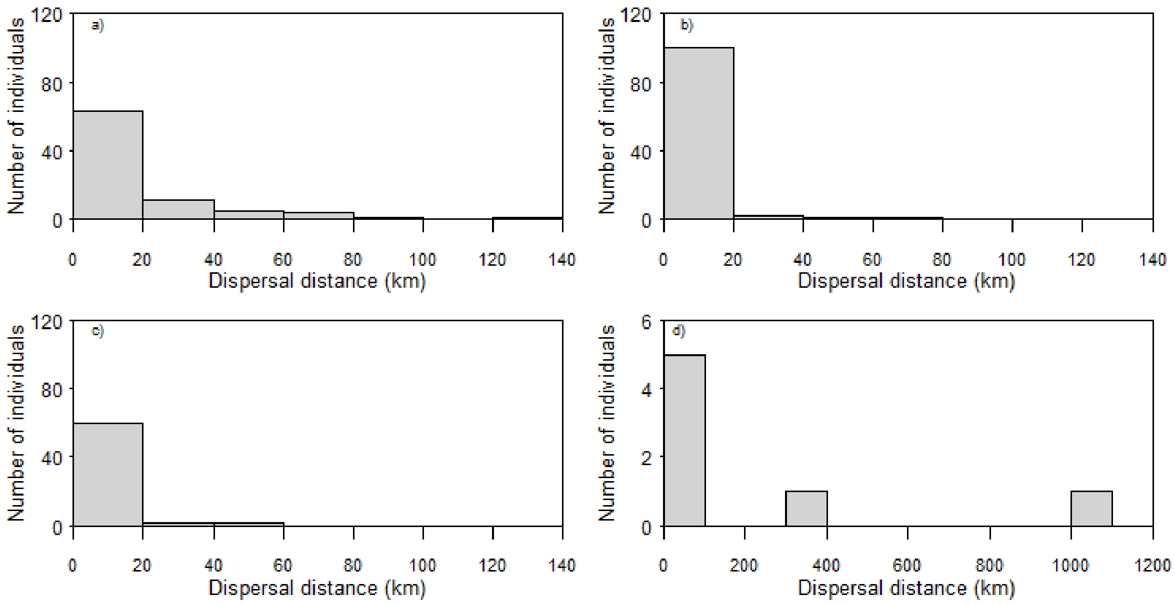

Figure 3. BUOW dispersal distances across AB/SK. Observed dispersal distances for a) juveniles, b) adult male, c) adult female and d) PTT tracked adult female. Data were gathered using mark-recapture of banded individuals for panels a, b and c, and from tracking data acquired by satellite transmitters on adult females for d. Observed distances calculated by taking the Euclidean distance between banding and re-encounter locations.

Each category was tested for a suitable distribution to use for the Baker methods. Data were first log-transformed and then a Shapiro-Wilks test was used to check for normality. Each of the banding categories was not normally distributed when log-transformed ($P < 0.05$).

Table 3. AIC values for distribution fit for 3 banding data distributions compared to 3 distributions. Chosen distribution based on lowest AIC value; visual analysis relied on Q-Q plots and showed slightly better fit when removing 0s first.

Juvenile	***Lognormal***	*Exponential*	*Gamma*
	510.45	625.18	526.23
Adult-Male	***Lognormal***	*Exponential*	*Gamma*
	104.54	365.50	222.00
Adult-Female	***Lognormal***	*Exponential*	*Gamma*
	170.19	305.84	215.64

None of the categories fit the exponential or gamma distribution well compared to lognormal. For all categories, the AIC value and the Q-Q plot best fit a lognormal distribution. Due to the high frequency of nest-site fidelity (distances of 0-250m), a nested approach was taken. First, the probability of dispersing was calculated for each category: for natal dispersers (Juvenile) the probability of dispersing > 250m was 0.74, for female dispersers (Adult-Female) the probability of dispersing > 250 m was 0.39, and for male dispersers (Adult-Male) it was 0.30. All nest-site fidelity events were then removed, and the distribution was tested again for fit against lognormal and gamma distributions. Once these 0s were removed, the AIC and visual analysis proved lognormal to be the best fit for all categories. This truncated log-normal distribution was used to simulate the dispersal events when adjusting survival.

The five study areas were compared to determine if dispersal distributions varied across them (Figure 4). The study area distributions differed significantly (Kruskal-Wallis $X^2 = 42.325$, $df = 4$, $P < 0.05$).

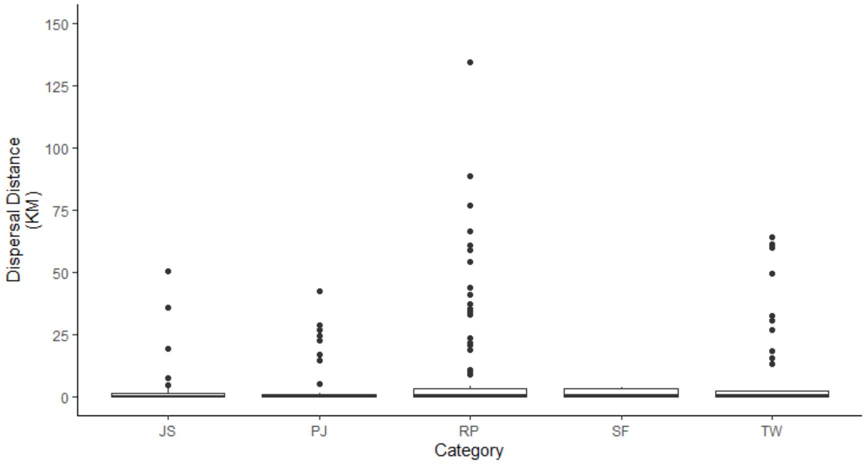

Figure 4. Boxplot of BUOW dispersal distances across the 5 study areas. FIGURES should stand alone – acronyms explained.

Removing the site-fidelity events (distance ≤ 250m) there was still a significant difference in dispersal distributions between the five study areas ($X^2 = 15.266$, df = 4, $P < 0.05$) (Figure 5).

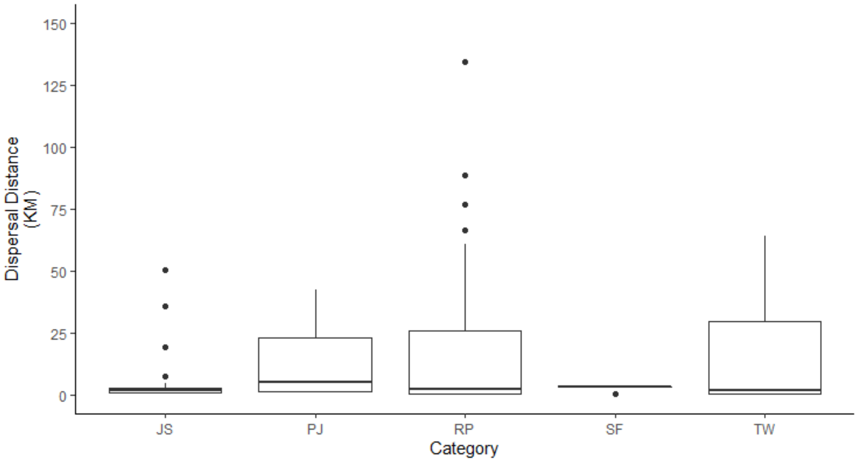

Figure 5. Boxplot of BUOW dispersal distances across the 5 study areas with site-fidelity events removed.

Due to limited sample size for each dispersal category in each study area, each was tested for directionality separately (Figure 6). Dispersal did not show a significant direction across the study areas: Schmutz (R = 0.168, P = 0.513), James (R = 0.147, P = 0.503), Regina Plain (R = 0.035, P = 0.924), Suffield (R = 0.231, P = 0.631), and Wellicome (R = 0.172, P = 0.201).

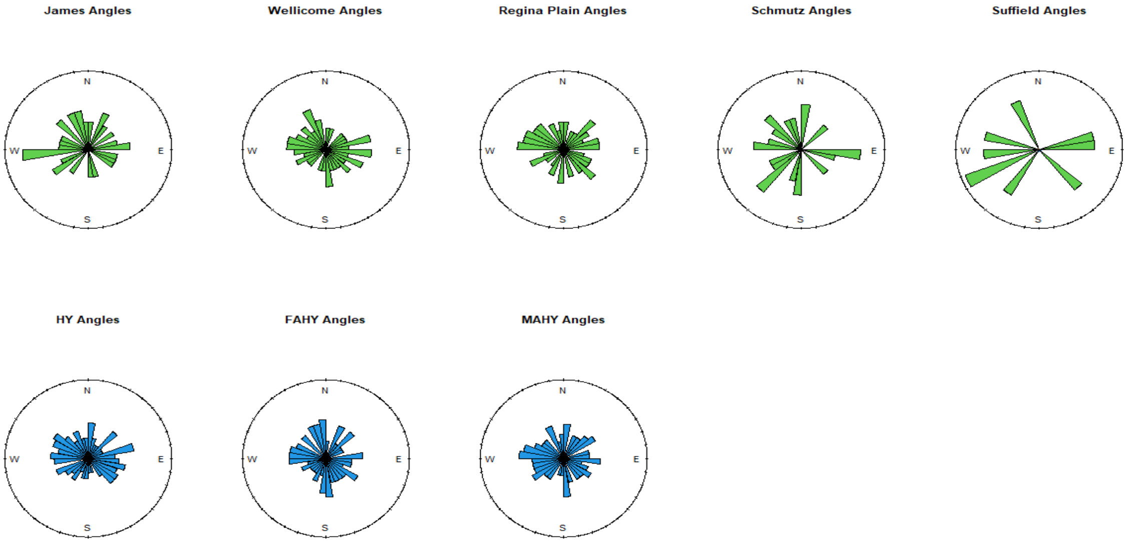

Figure 6. Rose diagrams depicting directions of dispersal across each study area (green) and dispersal category (blue). Each were tested for directionality bias using a Rayleigh z test.

Similarly, direction of dispersal did not show a significant trend across the 3 dispersal categories: Juvenile (R = 0.138, P = 0.107), Adult-Male (R = 0.116, P = 0.323), and Adult-Female (R = 0.049, P = 0.824).

3.2 Baker Method

The Baker method first required input parameters from each subset's dispersal distribution, these values differed across each subset based on the distribution shape (Table 4).

Table 4. Input parameters for each data subset used in the Baker methods. Dispersal data were log-transformed prior to calculating the mean and sd. The probability of dispersing, $p_{disperse}$ *was calculated from the number of observed dispersal events compared to the number of observed returns.*

Parameter	*Adult-Female banding*	*Adult-Female PTT*	*Adult-Male*	*Juvenile*
mu	1.112	3.563	0.383	1.650
sd	1.641	2.523	1.611	1.867
$p_{disperse}$	0.391	0.857	0.298	0.741

Based on the results above, each individual owl captured and banded in the study area had 10000 dispersal simulations produced using the input parameters from each dispersal distribution. The simulations were used to calculate the probability of observing a dispersal event within the study area boundaries in the following year. These probabilities remained high across each study area and banding informed data subset while halved for the tracking informed data subset (Table 5). An example of the simulation output can be seen in Figure 7.

Table 5. Simulated probability of observing a dispersal event in year n + 1 within the study area boundaries. Probability was determined by the SimLN function found in the Appendix based on the location of the nest, mean and standard deviation of the distribution and the $p_{disperse}$ *found in Table 5.*

Study Area	*Adult-Female banding*	*Adult-Female tracking*	*Adult-Male*	*Juvenile*
James	0.960	0.539	0.987	0.855
Wellicome	0.973	0.593	0.992	0.894
Regina Plain	0.976	0.610	0.993	0.907
Schmutz	0915	0.461	0.963	0.761
Suffield	0.933	0.484	0.977	0.797

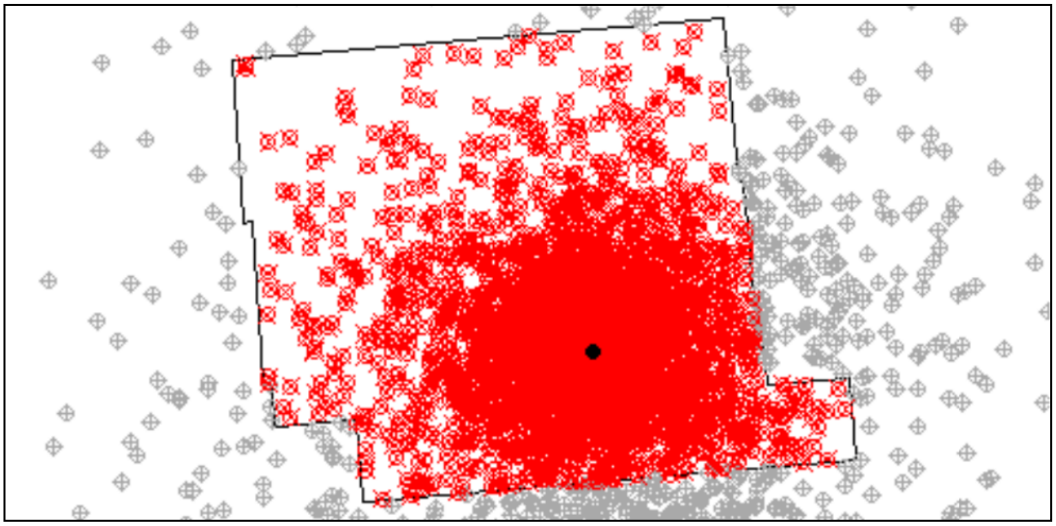

Figure 7. Example of the output from one round of simulations (n=10000). Original nest location indicated by black circle, red points represent dispersals inside study area, and grey point represent those falling outside study area. Example simulation run pulled from Adult-Male distribution within Regina Plain study area.

Each of the probability of observing a dispersal values were averaged across each study area per category; the values were nearing 1.00 for all 3 banding informed data subsets while appearing halved for the tracking informed data (Figure 8).

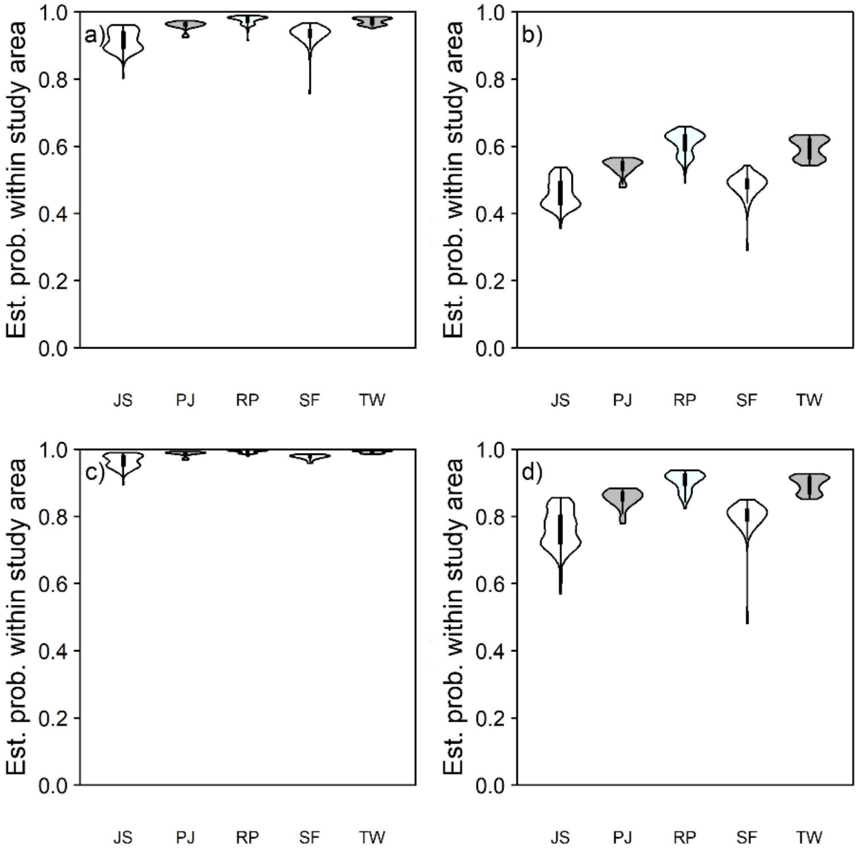

Figure 8. Violin plots showing the distribution of the estimated probabilities of birds remaining within the study areas, based on spatially explicit simulations using the dispersal rates and distances. Female adult results shown in panel a) banding informed, and b) tracking informed; male adult results in panel c) and juveniles in panel d). The corrected survival estimates were calculated by dividing the observed returns by the total expected to observe, the probability of observing a dispersal values found in Table 5.

Hatch year birds had the lowest survival estimate at 0.060 [0.046, 0.077] (Table 6). Adult male birds had the highest survival estimate at 0.37 [0.28, 0.45] (Table 6). For adult female birds, the banding data provided a lower survival estimate, 0.17 [0.12, 0.21] compared to a survival estimate of 0.29 [0.21, 0.37] when using the tracking data to inform the dispersal distribution.

Table 6. Apparent survival estimates for BUOW of each dispersal category across each study area accounting for dispersal trends. Survival estimates were calculated by dividing the total number of years survived across individuals by the expected number of birds to remain in study area given they survived across each study. The number of expected birds follows a poisson binomial distribution so the sd values were calculated using the sums of the variance of the n Bernoulli trials. Uncertainty assessed using a bootstrapping method.

	mean	*sd*	*CI_Low*	*CI_High*
Adult-Female-banding	0.17	0.023	0.12	0.21
Adult-Female-tracking	0.29	0.041	0.21	0.37
Adult-Male	0.37	0.043	0.28	0.45
Juvenile	0.060	0.0080	0.046	0.077

3.3 Comparative Analysis of Tracking Data to Recapture Data

The observed mark-recapture data were compared to available tracking data from female adults fitted with PTT tags (Figure 9). Although the sample size was much smaller in the tracking data (n = 7) compared to that of the banding resight data (n = 64), probability of dispersal tended to be higher in tracked birds (Figure 9a). The probability of dispersal in the banding-recapture dataset was 0.39 and 0.86 in the PTT dataset. The two datasets showed different distributions when the distance (km) was plotted; tracking data had a mean dispersal distance of 211km compared to the mark-recapture data which had a mean only of 9.7km in adult female owls. Dispersal data were then lognormally transformed and plotted in Figure 9b to show the differences between the two distributions.

The distributions were then used to simulate dispersal 10000 times per nest where adult females were banded (n = 564) and the estimated probability of returning to the study area and being resighted were compared between the two methods, shown as a violin plot in panel c of Figure 9. The banding-recapture data showed high probability of returning to the study area, with a mean of 0.95 compared to that of the tracking data which was 0.54 These probabilities resulted in corrected survival estimates for adult females using mark-recapture and PTT data as 0.17 and 0.29, respectively (Figure 9d).

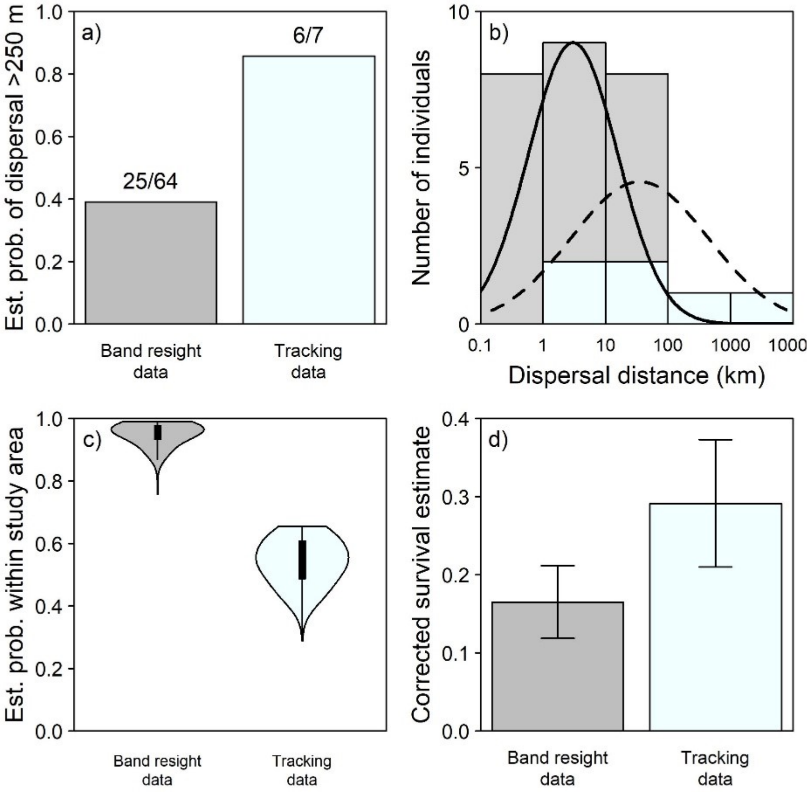

Figure 9. A comparison of the results obtained from banding data (gray) versus tracking data (blue) to correct for survival of female birds tagged as adults. a) Tracking data tended towards a higher probability of dispersal from the nest. Numbers above bars indicate the proportion of birds in each dataset that dispersed. b) observed dispersal distances from banding resights and tracking data, with the best fit log-normal distribution shown for each (solid line = banding data; dotted line = tracking data). c) Violin plot showing the distribution of the estimated probabilities of banded birds remaining within the study areas, based on spatially explicit simulations using the dispersal rates and distances shown in panels a and b. d) Corrected survival estimates using the estimated probabilities shown in panel c and 95% confidence intervals.

3.4 Cormack-Jolly-Seber Method

Cormack-Jolly-Seber models were ran for each of the banding data subsets. Models were run separately for each category and the candidate models were ranked based on AIC values. The estimates from the top 3 candidate models from each category are shown below.

3.4.1 Adult Females

For the Adult-Female category, the best candidate model (lowest AIC) kept survival constant and detection based on the study (Phi(~1)p(~study)), see Table 7. Based on this model, survival estimates for Adult-Female were estimated with 95% confidence where phi = 0.26 [0.19, 0.34], while estimates for recapture probability (p) were based on the study area the bird was banded in (Figure 10).

Table 7. Candidate models for Adult-Female CJS models. Models ranked based on lowest AIC value.

	model	*npar*	*AIC*	*DeltaAIC*	*weight*	*neg2lnl*
2	Phi(~1)p(~study)	6	460.664	0.000	0.645	448.664
4	Phi(~study)p(~1)	6	463.106	2.443	0.190	451.106
1	Phi(~1)p(~1)	2	464.220	3.556	0.109	460.220
5	Phi(~study)p(~study)	10	465.833	5.169	0.049	445.833
8	Phi(~time)p(~study)	38	470.444	9.781	0.005	394.444
7	Phi(~time)p(~1)	34	473.385	12.721	0.001	405.385
3	Phi(~1)p(~time)	34	473.876	13.213	0.001	405.876
6	Phi(~study)p(~time)	38	474.244	13.580	0.001	398.244
9	Phi(~time)p(~time)	66	523.170	62.506	0.000	391.170

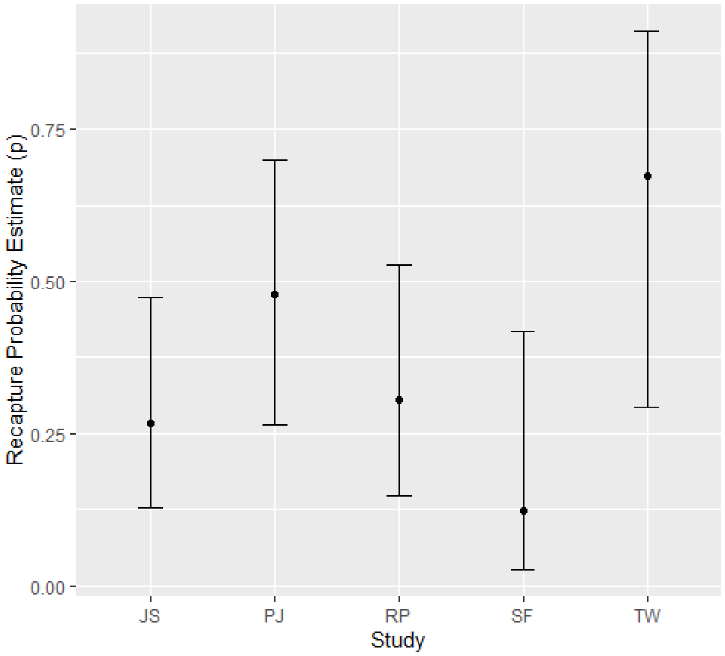

Figure 10. Recapture probability estimates and 95% confidence intervals (p) from top ranked Adult-Female CJS model Phi(~1)p(~study). Survival estimate from this model was kept constant (phi = 0.26 [0.19,0.34]).

The second and third candidate models for Adult-Female contained similar estimates. The second model had survival vary over study but kept recapture probability constant while the third kept both constant. Survival estimates for the second model (Phi(~study)p(~1)) were: Schmutz: phi = 0.18 [0.11, 0.29], James: phi = 0.32 [0.22, 0.45], Regina Plain: phi = 0.20 [0.12, 0.31], Suffield: phi = 0.13 [0.040, 0.33], Wellicome: phi = 0.31 [0.20, 0.45]; and for the third model (Phi(~1)p(~1)): phi = 0.25 [0.18, 0.33] for Adult-Female.

The capture history data were checked for goodness-of-fit and passed the omnibus test showing there was no strong evidence of lack-of-fit (p value > 0.05, $\chi^2 = 8.48$, n =19). The variance inflation factor ($\hat{c}$) was calculated to be 0.45, indicating some under-dispersion.

3.4.2 Adult Males

For the Adult-Male category, the best candidate model (lowest AIC) kept recapture probability constant and survival across each study area (Phi(~study)p(~1)), see Table 8. Based on this model, recapture estimates for Adult-Male were p = 0.65 with 95% confidence of [0.51, 0.76], while estimates for survival (phi) were based on the study the bird was banded in (Figure 11) and were as follows: Schmutz: phi = 0.26 [0.19, 0.35], James: phi = 0.43 [0.33, 0.53], Regina Plain: phi = 0.23 [0.15, 0.33], Suffield: phi = 0.20 [0.077, 0.43], and Wellicome: phi = 0.48 [0.35, 0.62].

Table 8. Candidate models for Adult-Male CJS models. Models ranked based on lowest AIC value.

	model	*npar*	*AIC*	*DeltaAIC*	*weight*	*neg2lnl*
4	Phi(~study)p(~1)	6	567.578	0.000	0.691	555.578
5	Phi(~study)p(~study)	10	569.274	1.696	0.296	549.274
2	Phi(~1)p(~study)	6	576.264	8.686	0.009	564.264
1	Phi(~1)p(~1)	2	578.122	10.544	0.004	574.122
7	Phi(~time)p(~1)	34	592.326	24.748	0.000	524.326
8	Phi(~time)p(~study)	38	592.872	25.293	0.000	516.872
6	Phi(~study)p(~time)	38	593.179	25.601	0.000	517.179
3	Phi(~1)p(~time)	34	594.841	27.263	0.000	526.841
9	Phi(~time)p(~time)	66	649.092	81.514	0.000	517.092

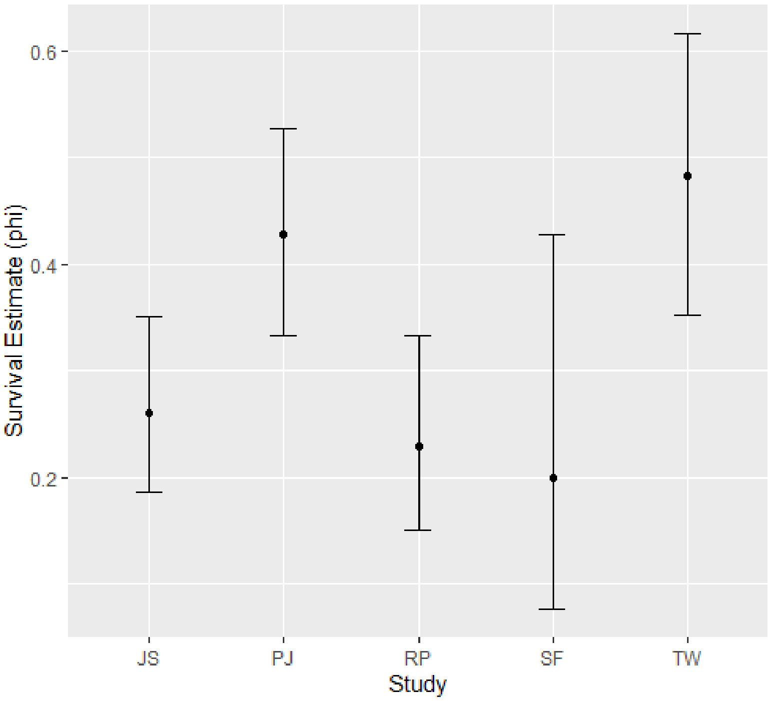

Figure 11. Survival estimates (phi) and 95% confidence intervals from top ranked Adult-Male CJS model Phi(~study)p(~1). The recapture probability estimate from this model was kept constant (p = 0.65 [0.51,0.76]).

The second and third candidate models for Adult-Male contained similar estimates. The second model had survival and recapture probability vary over study while the third kept the survival estimate constant and recapture probability vary over study. Survival estimates for the second model (Phi(~study)p(~study)) were: Schmutz: phi = 0.29 [0.19, 0.41], James: phi = 0.41 [0.32, 0.52], Regina Plain: phi = 0.17 [0.11, 0.26], Suffield: phi = 0.39 [0.087, 0.81], Wellicome: phi = 0.50 [0.36, 0.64]; and for the third model (Phi(~1)p(~study)): phi = 0.36 [0.30, 0.43] for Adult-Male.

The capture history data were checked for goodness-of-fit and passed the omnibus test showing there was no strong evidence of lack-of-fit (p value > 0.05, χ^2 = 11.533, n =28). The variance inflation factor ($\hat{c}$) was calculated to be 0.41, indicating some under-dispersion.

3.4.3 Juveniles

For the Juvenile category, the best candidate model (had the lowest AIC and the simplest model) kept both survival and recapture probability constant (Phi(~1)p(~1)), see Table 9. Based on this model, recapture estimates for Juvenile were estimated with 95% confidence where p = 0.044 [0.030, 0.065]. Survival estimates were estimated with 95% confidence to be phi = 0.41 [0.33, 0.49]. The highest scoring model based only on AIC had both recapture probability survival based on the study (Phi(~study)p(~study)) Schmutz: p = 0.024 [0.00, 0.066], James: p = 0.033 [0.016, 0.067], Regina Plain: p = 0.14 [0.054, 0.31], Suffield: p = 1.0 [0.00, 1.0], and Wellicome: p = 0.037 [0.018, 0.075] (Figure 12); estimates for survival (phi) were as follows: Schmutz: phi = 0.51 [0.31, 0.71], James: phi = 0.54 [0.40, 0.68], Regina Plain: phi = 0.18 [0.086, 0.33], Suffield: phi = 0.032 [0.012, 0.083], and Wellicome: phi = 0.44 [0.30, 0.59] (Figure 13).

Table 9. Candidate models for Juvenile CJS models. Models ranked based on lowest AIC value.

	model	*npar*	*AIC*	*DeltaAIC*	*weight*	*neg2lnl*
5	Phi(~study)p(~study)	10	952.571	0.000	0.670	932.571
1	Phi(~1)p(~1)	2	954.644	2.074	0.238	950.6441
4	Phi(~study)p(~1)	6	956.787	4.216	0.081	944.787
2	Phi(~1)p(~study)	6	961.057	8.486	0.010	949.057
6	Phi(~study)p(~time)	38	966.673	14.103	0.001	890.673
3	Phi(~1)p(~time)	34	969.993	17.423	0.000	901.993
8	Phi(~time)p(~study)	38	971.050	18.479	0.000	895.050
7	Phi(~time)p(~1)	34	983.756	31.186	0.000	915.756
9	Phi(~time)p(~time)	66	990.304	37.734	0.000	858.304
10	Phi(~1)p(~1)	2	954.644	2.074	0.238	950.644

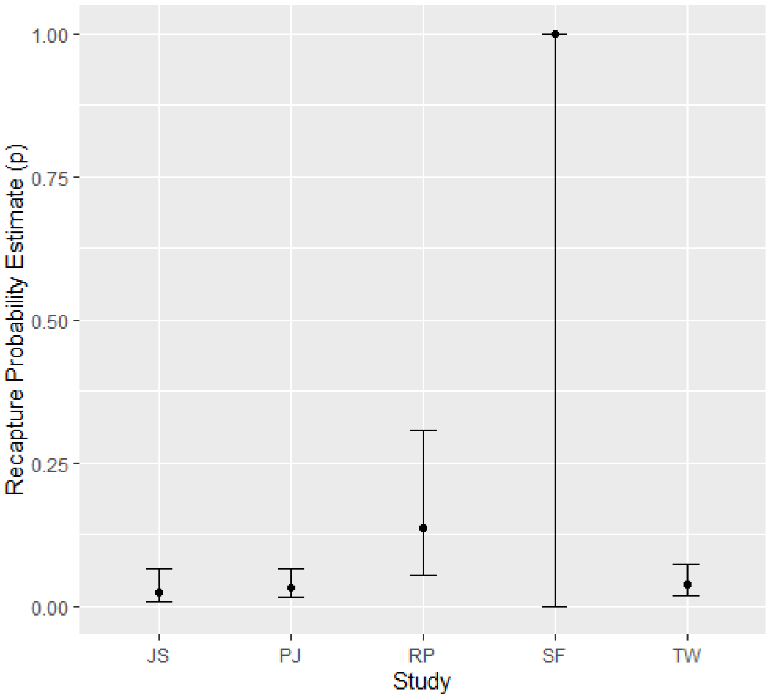

Figure 12. Recapture probability estimates (p) and 95% confidence intervals from the lowest AIC ranked Juvenile CJS model Phi(~study)p(~study). The survival estimate from this model varied across studies.

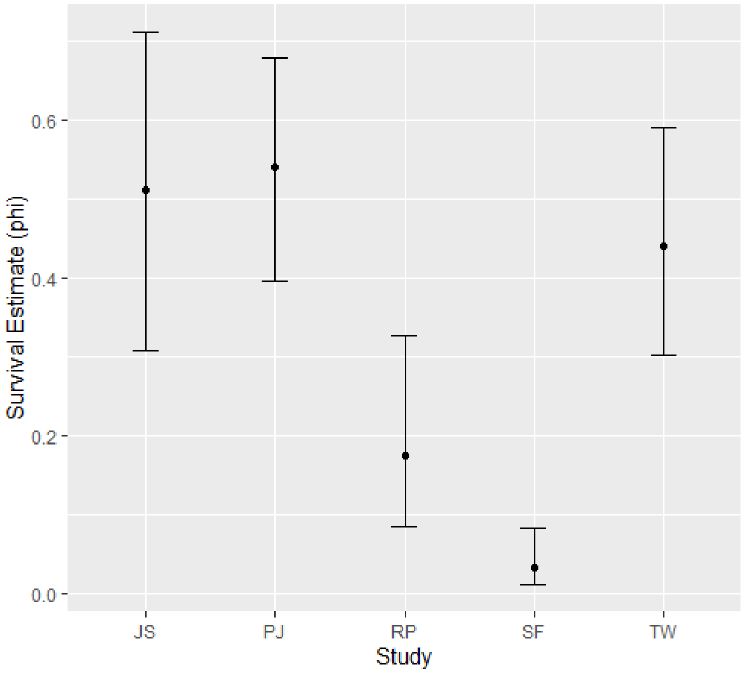

Figure 13. Survival estimates (phi) and 95% confidence intervals from the lowest AIC model ranked Juvenile CJS model Phi(~study)p(~study). The recapture probability estimate from this model varied across studies.

The third candidate model for Juvenile contained similar estimates. The third model kept the survival estimate constant and recapture probability vary over study. Survival estimates for the second model (Phi(~1)p(~1)) were phi = 0.41 [0.33, 0.49]: and for the third model (Phi(~study)p(~1)): Schmutz: phi = 0.34 [0.28, 0.54], James: phi = 0.49 [0.38, 0.59], Regina Plain: phi = 0.34 [0.241, 0.45], Suffield: phi = 0.36 [0.15, 0.65], Wellicome: phi = 0.40 [0.30, 0.51] for Juvenile.

The capture history data goodness-of-fit passed the omnibus test showing there was no significant lack-of-fit (p value > 0.05, $\chi^2 = 8.31$, n =30). The variance inflation factor ($\hat{c}$) was calculated to be 0.28, indicating some under-dispersion.

3.5 Spatial CJS Model

Spatial CJS models were ran for each of the banding data subsets. The output for each category is shown below when MCMC settings were ran at n_i =10000 and n_b = 5000. Grid size was set at 5km in each study area; an example of this can be seen in Figure 14 using the Adult-Female capture locations as an example.

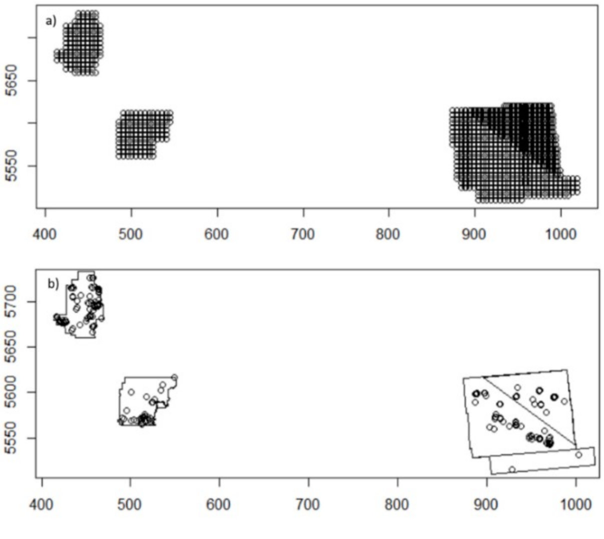

Figure 14. Gridded study areas when grid size = 5km (a); study areas and (b) Adult-Female original capture locations shown as an example.

3.5.1 Adult females

Survival estimates for Adult-Female was estimated from the spatial CJS model with 95% confidence to be 0.28 [0.19,0.36] and the recapture probability was estimated to be 0.42 [0.25,0.59] (Table 10). Sigma values were also produced indicating measures of dispersal estimated from the banding data. Dispersal in the x-direction (longitude) was estimated to be 8.1km [5.9, 10] and in the y-direction (latitude) was estimated to be 8.2km [6.7, 9.6].

Table 10. Output from Adult-Female spatial-CJS model. 2 chains of 10,000 iterations were run and the first 5000 were discarded. Mean. p is the detection probability and mean.phi is the survival estimate. For each parameter, n.eff is a crude measure of effective sample size, and Rhat is the potential scale reduction factor (at convergence, Rhat=1).

	mean	*sd*	*2.5%*	*25%.*	*50%*	*75%*	*97.5%*	*Rhat*	*n.eff*
deviance	1095	30.5	1035	1074	1096	1116	1154	1.00	10000
mean.p	0.42	0.085	0.27	0.36	0.42	0.48	0.60	1.00	2800
mean.phi	0.28	0.042	0.20	0.25	0.27	0.30	0.36	1.00	10000
sigma[1]	8.1	1.1	6.3	7.2	8.1	8.9	10	1.3	10
sigma[2]	8.2	0.71	7.0	7.6	8.1	8.6	9.6	1.0	350

3.5.2 Adult Males

Survival estimates for Adult-Male from the spatial CJS model was estimated with 95% confidence to be 0.36 [0.30,0.43] and recapture probability was estimated to be 0.61 [0.47,0.75] (Table 11). Sigma values were also produced indicating measures of dispersal estimated from the banding data. Dispersal in the x-direction (longitude) was estimated to be 6.4 km [5.3, 7.4] and in the y-direction (latitude) was estimated to be 2.3 km [1.9, 2.6].

Table 11. Output from Adult-Male spatial-CJS model. 2 chains of 10,000 iterations were run and the first 5000 were discarded. Mean. p is the detection probability and mean.phi is the survival estimate. For each parameter, n.eff is a crude measure of effective sample size, and Rhat is the potential scale reduction factor (at convergence, Rhat=1).

	mean	*sd*	*2.5%*	*25%.*	*50%*	*75%*	*97.5%*	*Rhat*	*n.eff*
deviance	1322	33.0	1259	1300	1321	1344	1388	1.00	10000
mean.p	0.61	0.069	0.48	0.57	0.61	0.66	0.74	1.00	2200
mean.phi	0.36	0.032	0.30	0.34	0.36	0.38	0.43	1.00	10000
sigma[1]	6.4	0.51	5.5	6.0	6.3	6.6	7.6	1.05	53
sigma[2]	2.3	0.17	2.0	2.1	2.3	2.4	2.6	1.01	10000

3.5.2 Juveniles

Survival estimates from the spatial CJS model for Juvenile was estimated with 95% confidence to be 0.036 [0.0, 0.17] and recapture probability was estimated to be 0.18 [0.00, 0.70] (Table 12). Sigma values were also produced indicating measures of dispersal estimated from the banding data. Dispersal in the x-direction (longitude) was estimated to be 0.33km [0.24, 0.42] and in the y-direction (latitude) was estimated to be 0.43km [0.27, 0.60].

Table 12. Output from Juvenile spatial-CJS model. 2 chains of 10,000 iterations were run and the first 5000 were discarded. Mean. p is the detection probability and mean.phi is the survival estimate. For each parameter, n.eff is a crude measure of effective sample size, and Rhat is the potential scale reduction factor (at convergence, Rhat=1).

	mean	*sd*	*2.5%*	*25%.*	*50%*	*75%*	*97.5%*	*Rhat*	*n.eff*
deviance	1.43	1.74	0.000	0.142	0.843	2.06	6.13	1.02	110
mean.p	0.18	0.26	0.000	0.007	0.051	0.26	0.86	1.4	9
mean.phi	0.036	0.067	0.000	0.001	0.0040	0.026	0.24	1.4	7
sigma[1]	0.33	0.044	0.27	0.29	0.33	0.37	0.40	8.4	2
sigma[2]	0.43	0.083	0.33	0.36	0.41	0.48	0.59	4.6	2

3.6 Comparing Survival Estimates

Uncorrected survival values for BUOW are low (Table 13). Comparing these uncorrected values to those produced by the 3 methods shows an increase in survival estimates after accounting for dispersal and detection error.

Table 13. Number of captured and recaptured owls and uncorrected survival estimates for each dispersal category. Survival calculated by taking number banded in year n / number recaptured in year n +1

	Adult-Female	*uncorrected survival*	*Adult-Male*	*uncorrected survival*	*Juvenile*	*uncorrected survival*
Banded	564	**0.113**	449	**0.232**	2910	**0.0292**
Recaptured	64		104		85	

For adult females, a comparison with the tracking data is also included. Survival estimates across all three correction methods resulted in improved similar survival estimates compared to the uncorrected, however the CJS methods did increase survival estimates more than the Baker method. Comparisons for each of the categories are shown in Figure 15.

For adult females, survival increased from the Baker method of 0.17 [0.12, 0.21] and 0.29 [0.21, 0.37] for the banding and tracking data respectively to 0.26 [0.19, 0.34] from the standard CJS model and finally to 0.28 [0.19, 0.36] from the spatial CJS model. For adult males, survival was estimated from the Baker method of 0.37 [0.28, 0.45], 0.32 [0.22, 0.45] averaged across study areas in the CJS model, and 0.36 [0.30, 0.43] from the spatial CJS model. For juveniles,

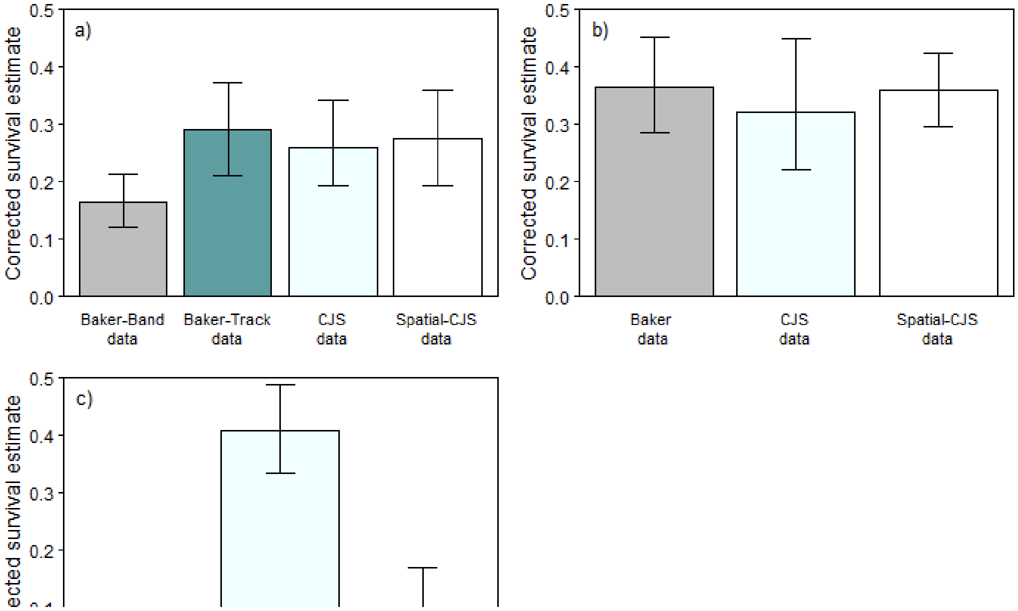

Figure 15. Boxplots of survival estimates across each category a) Adult-Female, b) Adult-Male, c) Juvenile; showing mean survival estimates from Baker methods, CJS models, and spatial CJS models. Error bars show low and high 95% confidence limits.

survival was estimated to be 0.060 [0.046, 0.077] from the Baker method, 0.41 [0.33, 0.49] averaged across study areas in the CJS model, and 0.036 [0.00, 0.17] from the spatial CJS model.

The detection probability parameters estimated from both the CJS model (0.40 [0.25, 0.56] and the spatial CJS model (0.42 [0.25, 0.59]) were used to correct the Baker methods for the PTT birds. The resulting survival estimates were much higher than the previous methods: CJS detection informed = 0.74 [0.44, 1.3], and spatial CJS detection informed = 0.69 [0.43, 1.2] (Figure 16).

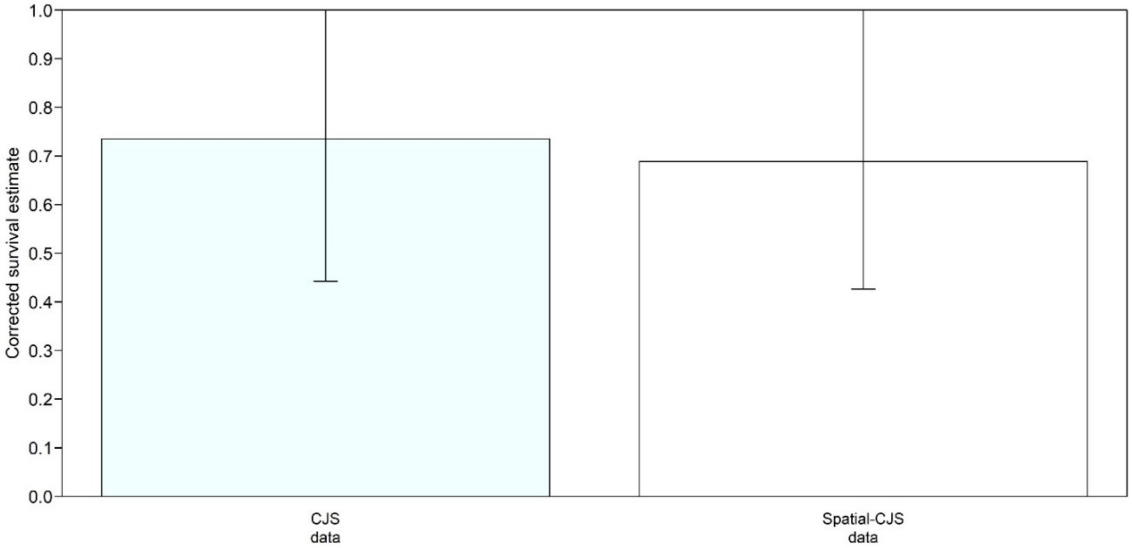

Figure 16. Boxplots of survival estimates produced from correcting the Baker methods of the PTT owls with detection probabilities produced from CJS method (azure) and the spatial CJS method (white). Error bars show low and high 95% confidence limits. Upper confidence intervals were truncated at 1.0.

4.0 Discussion

The Canadian population of BUOW has exhibited low survival estimates based on few returns to the breeding range observed each year following migration. Attempts to monitor these populations relied heavily on mark-recapture methods within finite study areas to track band returns and estimate survival rates (Wellicome et al. 1997; Stepinsky 1998; Hoyt 2001). However, this method continues to be problematic due to the varying degrees of dispersal and site fidelity observed by BUOW based on their age, sex, and proximity to the study area boundaries. Monitoring a population that exhibits these varying degrees of dispersal leaves the confidence in survival estimates unclear as they are likely underestimated because individuals are not returning to the study areas. This problem is further complicated when the species in question is a habitat generalist and is not limited to nesting within the boundaries of the study areas (Baladrón et al. 2015).

Each of the methods I used to estimate survival showed an increase in survival compared to their uncorrected value. The first method, based on Baker et al. (1995) produced low survival estimates for each category; however, incorporating tracking data using the PTT data from Adult-Female owls produced higher survival estimates as the probability for dispersing and dispersal kernel were higher. The third method allowed me to correct for missed detections but not dispersal, which produced higher estimates that are likely more realistic than the uncorrected values. The final method allowed correcting for missed detections and dispersal informed by the banding datasets which produced similar estimates across all dispersal categories to those produced by the Baker methods.

By incorporating observed dispersal patterns using the Baker methods, survival estimates could be corrected for observed dispersal. Through simulating these dispersal events, survival estimates increased across all study areas and dispersal categories of BUOW. Accounting for sex, age and study area affected the probability of resighting a return in that study area due to the different patterns each dispersal category showed when comparing distances between nest locations inter-annually. The probability of resighting or detection ultimately affected apparent survival estimates due to the reliance on mark-recapture surveys for banded individuals. This method of correcting survival estimates using dispersal could be widely useful for population monitoring if data on dispersal patterns exists. However, in studies where dispersal distances are limited to observations within a delineated study area, it likely remains an underestimate of true survival.

The simulations used in this method rely on an understanding of BUOW dispersal distribution across their northern range. Although long-distance dispersals (those determined outside of discrete study areas) were used to inform the distribution, these events were rarely observed and resulted in a thin right tail on the distribution. This distribution could be due to the high site-fidelity exhibited by BUOW (Martin 1973; Rich 1984; Stepnisky 1998; Rosenberg and Haley 2004; Catlin et al. 2005), low detection probability within the study area, or the difficulty in capturing these long-distance dispersal events based on current mark-recapture methods, or some combination thereof. Dispersal events are often captured in areas where BUOW studies are already occurring, in areas of high visibility, or in urban settings; if individuals disperse to novel areas their breeding attempt will likely not be known to researchers. This creates a bias based on study area dimension as noted by Baker et al. (1995) where dispersals will only be observable in distances no longer than the longest dimension of the study area. Not enough is known regarding these long-distance dispersals in BUOW so there is a strong need to characterize the dispersal distribution as best as possible through improved tracking and resighting methods..

Recent attempts to improve survival estimates have used other methods to track migratory BUOW within their Canadian range; these methods include VHF transmitters, stable-isotope analysis, and solar-powered satellite transmitters (Microwave Telemetry Inc.) applied to adult female BUOW using a backpack-style harness fitted over their back (Holroyd and Trefry

2011; Wellicome et al. 2014). This data has allowed some insight into dispersal patterns of the few females that have been successfully tracked. Holroyd et al. (2009) used stable isotope analysis to estimate the average annual BUOW dispersal at 400km, and maximum annual dispersal at 3500km (COSEWIC 2017). In one study, a female owl fitted with a satellite transmitter in southern Alberta was found breeding in Colorado the following year, exhibiting a breeding dispersal of roughly 1000km (Holroyd et al. 2011). A recent study fitted PTTs on adult BUOWs in Saskatchewan and Alberta (Wellicome Unpublished Data). Although sample size was limited (n = 6), one of these individuals was found breeding >300km away from the original banding location the year prior; however, the other individuals showed levels of fidelity to their previous nesting site that were within the range of a typical study area (0-29km). When the PTT tracking data were compared to the observed band resighting data, the distributions were different. Sample size is an issue however if 1/6 adult female breeding dispersal events includes a long-distance dispersal event (> 300km) then perhaps these truly are not accurately capturing the distribution exhibited by migratory BUOW within the finite study areas.

Comparing the two adult female datasets showed that there are major differences between the distributions: the mark-recapture data is likely overestimating the probability of site-fidelity events while underestimating the probability of a long-distance dispersal happening compared to the tracking data. The PTT data revealed that long-distance dispersal is occurring in adult females. Long-distance dispersals are possibly happening more frequently in young and/or male birds where dispersal is typically longer/more common (Greenwood and Harvey 1982). Therefore, current methods are likely missing many long-distance dispersers and assuming many individuals are dying based on low returns, which also biases the probability of an individual not dispersing. These assumptions affect the probability of resighting an individual based on the simulation approach used. If only mark-recapture data is used to inform the simulations, the results estimate a high probability of birds returning (> 60% in adult females). However, when using the tracking data, the probability dropped substantially (14% in PTT tracked adult females). The simulation approach then reveals how this affects current survival estimates – survival was roughly 17% given mark-recapture data and this nearly doubles to 29% when the PTT data is used. The PTT data and the banding data were not combined for the analysis. Combining the two datasets would increase the sample size and the mean p(disperse) would near 50%. However, the banding data is biased because it confounds dispersal events with mortality. In truth, the p(disperse) is likely larger than 50%, because so many dispersals are not being recorded. As a point of comparison, p(disperse) from the PTT data is 6/7, or 86%. The banding data is biased by underestimating the probability of dispersing and the resulting mean dispersal distance, whereas the PTT data, while limited in sample size, should not bias the survival estimate as mortality is not confounded with dispersal. This leads to the conclusion that using mark-recapture data within a finite study area is biased towards those individuals with site fidelity and has consequences on annual survival estimates for that population.

It is important to note the limitations imposed by the PTT data. The probability of dispersal and dispersal distance are affected by sample size and a need for a larger size is required for effective statistical analysis. Unfortunately, these PTT units are more costly than leg bands and planning to use these to track each individual would be impractical; however, use of tracking data for a subset of individuals each year could be used to characterize dispersal and these distributions could then be used to simulate from mark-recapture observations to calculate apparent survival. It would also be interesting to collect tracking data on the other subsets–given the time, resources and improved tracking technology were available to monitor adult male and natal dispersers. For studies using species-at-risk, an inherent risk of mortality and behavioral changes are also an issue when devices are attached to an individual and these effects have been studied in BUOW (Gervais et al. 2006). Barron et al. (2010) conducted a meta-analysis of the negative effects transmitters had on different bird species (n = 84 studies), with the most significant being increased energy expenditure and decreased likelihood to nest following attachment. Lamb et al. (2020) found sea ducks would change their dispersive behavior following radio-marking however this method included surgical implantation. These effects could influence an individual's ability or choice to sustain long-distance flights during and following migration regardless of attachment style. However, it is important to understand and study the effects on movement behavior these transmitters may have on an individual and more study is needed. Minimizing mortality risk as well as other behavioral effects to an individual is critical and the risk must outweigh the reward which needs to be considered when using invasive tracking methods. As technology improves, hopefully transmitters will continue to be improved upon (cheaper, smaller, etc.) and become more commonly available to improve available data while reducing risk of mortality to individuals.

The simulation approach assumed 100% detection of individuals within their respective study areas. Incorporating the CJS models allowed a comparison of the parameter estimates for both detection probability and survival estimates. Specifically looking at Adult-Female, I could see how different the survival estimates were when compared to the tracking dataset. For Adult-Female birds, the probability of recapture estimate varied over study area but averaged at value of 0.370 indicating that there was a low probability of recapture for female birds, and alternatively, the probability that they were not resighted/recaptured was quite high. The simulations provided $p_{disperse}$, which includes the probability of dispersal and the probability of missing a detection in the study area but is unable to disentangle dispersal from a missed detection. Therefore, the CJS method of calculating survival estimates appears to be more effective in a large-scale study as it is able to correct the survival estimates based on missed detections from any possible cause, whereas the Baker method approach can only correct survival estimates based on long-distance dispersals. In studies where detection probability is high and certainty around missing individuals is low this simulation approach would likely provide more accurate survival estimates. However, based on the probabilities and uncertainties presented here, dispersal and detectability appear to be an important and common factor in the low apparent survival of migratory BUOW.

The study areas could also introduce some bias in observed dispersal distributions due to their varying sizes. Smaller study areas with more returns will show shorter distribution curves that could influence the overall shape used to inform the simulations when pooling them together (Zimmerman et al. 2007). This likely occurred as the study areas varied quite greatly in size and ultimately the distribution curves were significantly different when compared across each of the 4 study areas. Larger study areas allow long-distance dispersal to be observed whereas these same distances may go unobserved in smaller study areas as well as include higher changes of missing nests when conducting surveys due to the vast range of land to cover (Barrowclough 1978; Marshall et al. 2004). Another aspect of bias introduced is the spatial variability of the nests I simulated from in each study area. Study areas where nests are more clustered in the center compared to those areas where nests are located around the edges will have more dispersals outside of the study area inherently (Barrowclough 1978). This effect introduces some bias towards short-distance dispersals and should be considered when deciding to pool together dispersal data across different studies. The CJS models showed that study area appeared to have some strong effects on the model outputs, likely since the variable encompasses both a spatial and temporal variability. Each of the dispersal categories had study area as a grouping factor in at least one of the top candidate models for p and phi estimates. Lahaye et al. (2001) found that incorporating recapture data from larger study areas increased their survival estimates for Spotted Owls (*Strix occidentalis*) up to 60%. In studies where survival estimates rely on re-encounters, the study area must be sufficiently large to capture long-distance events or be corrected for the biases that occur within finite study areas, as well as a method to quantify search within the study area each year to maximize re-encounters.

The CJS models provided the highest survival estimates for each dispersal category among the three methods, however had high uncertainty values especially for juveniles. When each capture history was tested for goodness-of-fit, the data appeared to be exhibiting under-dispersion ($\hat{c} < 1.0$). Looking at the capture histories, there are few recaptures thus the variance across the data is expected to be low. While overdispersion is generally corrected for, under-dispersion is typically not adjusted for in capture histories as its implications on uncertainty values likely make the confidence intervals wider than expected (Cooch and White 2019). The under-dispersion and large uncertainty values are likely brought on by the data itself, as the hatch-year data contained a significant number of capture events with few recaptures (85 out of 2910 captures). Adult females also had low recapture records (64 out of 564 captures) while males had the most recaptures (104 out of 449 captures). Limited recapture probability in juveniles is likely the cause of the large uncertainty around the parameter estimates especially when study areas were used as a grouping variable in the CJS models; for example, recapture probability for Juvenile in Suffield ranged from 0.0 -1.0 where no juveniles were recaptured in that study area as adults (Hoyt 2001). The CJS models appeared to provide slightly more realistic survival estimates, however they are unable to account for dispersal outside of these finite study areas, which was likely happening and thus reducing the ability to capture returns especially in second year birds (Cormack 1964; Schaub and Royle 2014).

While the spatial CJS model allows for incorporating both missed detections and dispersal, it also is affected by the biased distance estimates that the banding data produces. The spatial CJS model produces an estimate of dispersal distance (sigma.x and sigma.y parameters). Comparing these values with the PTT data shows that dispersal is underestimated by the banding data which informed the CJS model similarly as the Baker methods underestimated dispersal. For Adult-Female, the model estimated distances of about 8 km on average and was centered around 0. This is one shortcoming of the spatial CJS as it assumes that dispersal is normally distributed with a mean of 0. Distances such as those shown by the tracking data would be basically impossible as they extend far into the tail of the expected distribution. The spatial CJS model expects most birds to disperse short distances and only a few birds disperse longer distances. It utilizes the data from the band recoveries to estimate the dispersal kernel – or how far birds tend to disperse. Then, it uses that dispersal kernel to correct for missed detections of birds that dispersed outside the study area. For this reason, it is not able to incorporate the PTT data, although it can be compared using the estimated dispersal kernel to the one estimated from the tracked birds. In the Baker methods, the dispersal distributions from the PTT data showed dispersal of tens or hundreds or thousands of km. The next steps for this analysis would be to use the observed dispersal kernel from the tracking data to inform the spatial CJS model as it currently relies on estimating a kernel from the banding data (Schaub and Royle 2014).

An attempt to incorporate the detection probabilities estimated by both the regular CJS and the spatial CJS methods showed increased and similar annual survival estimates around 70%

for adult female BUOW however issues with uncertainty were obvious as this method estimated survival values with wide confidence intervals showing survival as >1.00 which is impossible. This issue likely resulted from how detection probability was used to correct survival *post-hoc* which results in the model assuming no correlation exists between survival and detection. Future analyses should attempt to reproduce this method in a self-contained model where a negative correlation occurs between these parameters so that survival cannot exceed 1.00. The problem is further complicated when considering how detection probability is addressed. In both CJS and spatial CJS methodologies the assumption remains that an individual has to be in the study area and was missed to estimate survival (Schaub and Royle 2014). However, by incorporating dispersal outside of the study area via the Baker method the reality is that some of the individuals were missed in the study area because they were either not detected or they had left the study area and then came back. Therefore, the CJS estimate is a bit problematic as a result because it has both reasons incorporated. To improve upon this method, developing a way to separate these effects might produce a more realistic estimate so that simulations determine if an individual leaves a study area it does not include any detection rate correction but if that individual stayed in the study area the detection correction is applied as the current method likely overestimates detection error. Another method would be to address the detection error when conducting the data collection phase using a robust design where multiple visits to a study area occur to determine the rate of missed detections by comparing the primary survey to the multiple secondary surveys (Pollock et al. 1990). Using a robust design would allow confidence in the researcher's detection assumption across a study area for a species that relies mostly on visual detection.

BUOW detections are largely visual as opposed to most other birds where auditory cues are heavily relied upon to determine presence; their behavior of standing on mounds or nearby vertical features aids in their visibility more than other birds in detection surveys (Conway and Simon 2003). Surveys were conducted during daylight hours throughout the breeding season and often historical nesting areas were visited more than once in the season to maximize detection probability (Conway et al. 2008). By visiting historical nests and surrounding pastures, and checking reported sightings, I suspect the likelihood of missing occupied nests within the study area was low (Wellicome et al. 1997). However, future studies using this technique need to account for detection probability within the study area to ensure this assumption is met and to ensure further bias is not introduced by potentially missing long-distance dispersals away from known nesting locations across the entire study area. Future studies should look to calculate a detectability rate for known active nests. Researchers could visit nests multiple times per breeding season and determine the number of times occupancy is correctly scored or use PTT birds to determine how often visual survey methods fail to detect when the individuals are known to be in the area. Combining a detectability rate with a simulation approach should provide a better correct for survival estimates.

One additional aspect that may have affected survival estimates could lie in the confirmation of band status of detected owls throughout the breeding season. Individuals were marked with leg bands to aid in resighting; however, confirming band status can be difficult due to the behaviors of this ground-dwelling raptor. Often females spend the beginning of the breeding season underground in the nest burrow and incubating eggs, it is not until the nestling stage that they will spend more time above ground (Plumpton and Lutz 1993; Conway et al. 2008).Although the use of the underground scope aids in viewing the nest cavity, nest debris, prey, feathers, nestlings, and the eggs can often obscure her legs. A combination of binoculars, scopes, trapping, and Reconyx Hyperfire cameras (Reconyx) were used to maximize observer's ability to view each nest (Gorman et al. 2003). Male owls undertake a vigilance role throughout the breeding season, improving their visibility compared to females (Plumpton and Lutz 1993; Scobie et al. 2014); however, confirming their band status can be difficult due to their defensive behaviors at their nest when approached (Martin 1973). This difficulty resulted in a high proportion of reported BUOW sightings to have "unknown" band status compared to "unbanded", "newly banded", and "previously banded". In Alberta, the average proportion of birds with unknown band was similar for both sexes (Males: Schmutz = 0.32 Suffield = 0.31; Females: Schmutz = 0.34; Suffield = 0.29); in Saskatchewan, these averages were higher (Males: Wellicome = 0.54, Regina Plain = 0.19; Females: Wellicome = 0.61, Regina Plain = 0.31); there was no data available for the James study area regarding band status of individuals recorded. The discrepancy between these proportions was likely due higher nest density in relatively smaller pastures in Saskatchewan, causing more owls to flush when surveys were conducted and increased difficulty in identifying individual owls (C. Scobie, pers. Comm). The landscape is also predominantly cropland in Saskatchewan, which increases the difficulty of confirming band status as the growing season progresses compared to the native short grassland in Alberta. Thus, the later studies had more methods available to confirm band status across the entire breeding season (i.e. Reconyx cameras, improved optical equipment). It is possible that some previously banded individuals were unconfirmed and recorded as "unknown" thus lowering apparent survival estimates based on observed returns. Future studies using mark-recapture data could attempt to calculate a detectability rate for banded individuals; this rate could be calculated by planning to visit nests with known banded individuals multiple times throughout the breeding season and determine how often that individual's band status can be confirmed. This approach would improve the ability to model BUOW survival if relying only on band resighting data.

Breeding dispersers often exhibit shorter dispersal distances than natal dispersers (Stepnisky 1998; Lutz and Plumpton 1999; Todd et al. 2007; Riding and Belthoff 2018), so it is possible that many of the younger birds are dispersing distances outside of their respective study area. Applying these values to uncorrected survival estimates did increase the survival across all dispersal categories in varying degrees. Although the differences between the uncorrected values and the dispersal-corrected values appear to be minor, dispersal should be considered in future estimates for migratory populations in finite study areas due to the effects it has on resighting. There is a need for a better understanding of the tail on each of the dispersal category distributions to ensure long-distance dispersals are not missed or under-represented in simulations, especially natal dispersers.

It is hypothesized that the tendency of BUOW to disperse annually, particularly for first-year owls, results in permanent emigration, so without permanent immigration to fully counteract this loss of individuals, the Canadian population is classified as declining based on resight data. Some have suggested that long distance dispersers from the Canadian range are short-stopping their return to the breeding grounds, and instead choosing to nest along their migration routes within the United States Great Plains (Holroyd and Trefry 2011). Southern populations may also be dispersing into the northern range (Holroyd et al. 2011), however, known events of this occurring are rare based on resighting data alone. To better understand these movements, international collaboration and improved tracking methods are necessary when studying this long-distance dispersal species.

Annual survival estimates for BUOW uncorrected for dispersal out of finite study areas were low and nearing 0 for juveniles when informed by CMR data. Estimates these low have not been seen across other owl species who are also suffering from population declines. Le Gouar et al. (2011) estimated annual survival for the little owl (*Athene noctua*) at 0.26 (juvenile) and 0.75 (adult) when using CMR data and dispersal was accounted for using a similar multi-state capture model. The low survival estimates of juveniles has been suggested for their population decline occurring across Europe. These estimates appear higher than what I estimated for BUOW but similar when detection estimated from the tracking data was used to inform the simulations. Annual survival rates for adult female snowy owls (*Bubo scandiacus*) were estimated between 0.85 and 0.92 when satellite transmitters were used to inform survival estimates (Therrien et al. 2012). Northern spotted owls (*Strix occidentalis caurina*) are facing annual population declines between 2-9% however their annual survival estimates were estimated between 0.84-0.90 (Franklin et al. 2021). Newton et al. (2016) summarized survival estimates for multiple raptor species including BUOW where annual survival ranged from (n=5 studies): 0.21-0.69 (adult female), 0.44-0.81 (adult males), however the higher estimates occur in studies where individuals are non-migratory (Millsap 2002; Barclay et al. 2011). Sheffield (2021) used national Breeding Bird Survey data to determine BUOW population declines over the last 50 years noting a decline of 1.1% per year across North America and 6.42% per year across Canada. While these declines are occurring, it is unlikely that the apparent survival for BUOW is realistically estimated by the uncorrected banding informed estimates. BUOW face many threats to their survival including habitat modification, severe weather, predation, and anthropogenic effects and their population decline is estimated between 50-100% over the next decade (COSEWIC 2017). Improving survival estimates can aid in determining the population outcomes over time and guide management decisions across temporal and spatial change (Maslo et al. 2015). Beyond improving our annual survival estimates, conservation goals need to focus on improving our understanding of species distribution and long-distance movements to aid large scale approaches in conserving species-at-risk (Saunders et al. 1991; Fahrig and Merriam 1994).

Future studies pertaining to monitoring populations of BUOW along their northern range should emphasize improving the accuracy of the dispersal distribution due to the effect it has on annual survival and population estimates. The population decline for these owls is one of the main reasons for their listing as Endangered in Canada (COSEWIC 2017) and is therefore crucial to model as accurately as possible. Improving accuracy could be facilitated by improved tracking methods such as PTTs or other satellite tracking methods as well as improving detection and confirmation of marked individuals within their entire range. This study shows that survival estimates can be improved using dispersal distribution and could be used in other populations however the challenge remains in properly characterizing their dispersal distribution to ensure site fidelity and long-distance dispersals are being accurately simulated. Future analyses should look to see if there is further modifications to these methods, such as incorporating detection probability into the Baker methods or having the spatial-CJS model use a defined dispersal kernel, possibly from the tracking data, rather than estimate it.

5.0 Conclusion

Dispersal and site-fidelity are both expressed in the migratory populations of BUOW along the northern edge of their range; the extent that each of these occur vary depending on the age and sex of the individual. These events affect estimations of inter-annual survival based on the current ability to observe these dispersal events and their proximity to study area boundaries. Although factoring in dispersal on apparent survival did increase estimates, these increases were slight due to the low returns and limited distances informing dispersal frequencies as captured within finite study areas. Therefore, there is a need to both improve confidence in band returns within these populations and to improve the ability to detect long-distance dispersal distances (outside of finite study areas) to better understand the distribution of these events in all four dispersal categories. Use of satellite tracking can aid in the understanding of what limitations or biases are occurring in current methods and could be used to best characterize dispersal distributions. With these improvements, applying simulation style dispersal events to breeding locations will improve understanding of inter-annual survival in these migratory populations. This technique could be modified and applied to other studies where dispersal distributions are properly captured to better estimate annual survival.

Chapter 3: Conclusion

Dispersal has a significant role beyond the individual as it has implications on population demography and a species' ecology (resources, co-existence, metapopulations) and evolution (gene flow, structure, and diversity). It also presents a challenge to researchers as it obfuscates our estimates of mortality in population dynamic models. This study used known dispersal patterns captured through capture-mark-recapture studies of BUOW across their northern range to correct annual apparent survival estimates using three methods. Using simulations or models to better understand expected dispersal frequencies across adults and returning first-year breeders increased apparent survival estimates.

These methods offered a unique procedure to deal with a species where both site fidelity and dispersal is common and could be used by many researchers dealing with similar species with low interannual returns when there is high confidence in dispersal frequencies. Using a method that accounts for detection and long-distance dispersal could help recalibrate our survival estimates of many species where long-distance dispersals were overestimating mortality in finite study areas. Using simulations to model and account for expected dispersal frequencies offers researchers an ability to better estimate apparent survival such as those where better marking systems such as PTTs or other satellite trackers are used. At this time, PTTs remain costly and difficult to obtain for a small avian species such as BUOW but could be reassessed in future studies where better tracking methods can be used. Realistic survival estimates are essential for biologists, managers, and policymakers as they guide our decisions made around land protection and habitat needs including dispersal pathways and connectivity among fragments. Studies like this can improve these survival estimates when the models are properly informed and ultimately shape our species-at-risk legislation and recovery plans/strategies for the better.

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Appendix

Code For Baker Simulation Functions

```
#Code needed for Baker methods. Some of the functions in the SpatialCJSFunctions script are #also used.

#Dispersal distance calculation. ####
dispersalDistance = function(bands, years, eastings, northings, proj) {

 require(rgeos)

 #Initiate vector with indicator -1
 OUT = rep(-1, length(bands))

 #First entry is NA, since it was first banded bird.
 OUT[1] = NA

 #For each capture, identify distance dispersed since previous capture.

 for(i in 2:length(bands)) {

  #Current band
  curb = bands[i]
  #Previous band
  prevb = bands[i-1]

  #If they are not same bird, NA.
  if(curb != prevb) {
   OUT[i] = NA
   next
  }

  #Check that years are different, and that order is correct.
  if(years[i] == years[i-1] | years[i] < years[i-1]) {stop("Multiple observations in one year")}

  #Spatial points 1.
  sp1 = SpatialPoints(coords=matrix(c(eastings[i-1], northings[i-1]), ncol=2), proj4string=crs(proj))

  #Spatial points 2
  sp2 = SpatialPoints(coords=matrix(c(eastings[i], northings[i]), ncol=2), proj4string=crs(proj))

  #calculate and store distance.
  OUT[i]=gDistance(sp1, sp2)

 }

 #Check that none of the vector are -1.

 if(sum(OUT == -1, na.rm=T)>0) {stop('Problem occurred')}
```

```
 #Return distances.
 return(OUT)
}

#Simulate birds dispersing according to log-normal####

SimLN = function(NestPoint, sps, NSim, meanlog, sdlog, pDisperse) {

 #Get polygon
 Polygon=sps[sps@data$project==NestPoint$study,]

 #Produce Dispersal Distribution based on category

 #Distance
 DistanceSim = rlnorm(NSim, meanlog = meanlog, sdlog = sdlog)
 #did the bird disperse?
 DisperseSim = rbinom(NSim,1, prob=pDisperse)
 #Multiply to get realized distance.
 DistanceSim = DistanceSim*DisperseSim

 #Simulate random angles
 Theta = runif(NSim, min=0, max = 2*pi)
 #Produce movements from nest using simulated dispersal distance and angle
 Ymove = DistanceSim* sin(Theta)
 Xmove = DistanceSim* cos(Theta)
 #Produce vector of original locations
 InitialUTMeastings=rep(coordinates(NestPoint)[,1],NSim)
 InitialUTMnorthings=rep(coordinates(NestPoint)[,2],NSim)

 #Produce new locations owl disperses to
 Xloc = as.numeric(InitialUTMeastings) + Xmove
 Yloc = as.numeric(InitialUTMnorthings) + Ymove

 #Convert locations to coordinates
 Coords = SpatialPoints(coords=cbind(Xloc, Yloc), proj4string=crs(Polygon))

 #Calculate number inside study area
 Numberinsidestudyarea <- !is.na(over(Coords, as(Polygon, 'SpatialPolygons')))
 #Probability Value
 Prob=sum(Numberinsidestudyarea)/NSim

 return(Prob)

}

#gapYear#####

#Identify number of gap years between banding and resight.
#df is a SpatialPoints object.
```

```
gapYear = function(df) {

 df = df@data

 df$index = 1:nrow(df) #Create order index.
 #check order is correct.

 df = df[base::order(df$year),]
 df = df[base::order(df$band),]

 #Checking to see if reordering the df altered it from the original. If not, can safely proceed.

 if(sum(df$index == 1:nrow(df)) != nrow(df)) {stop('df is incorrectly ordered')}

 df$gapYear = NA

 for(i in 1:nrow(df)) {
  status = df$type[i]
  if(status == 'original') {df$gapYear[i]=NA} else {
   diff = df$year[i] - df$year[i-1] - 1
   df$gapYear[i] = diff
  }
 }

 return(df$gapYear)

}
```

Code for CJS and Spatial CJS Functions

```
#All functions here.


#Read and combine shapes.####

#shapefiles is paths to shape files.
#shapenames is how those are named, and this function returns a SpatialPolygonsDataFrame object with
#Names stored in the data frame.

read_combine_shps = function(shapefiles, shapenames) {

 shapefiles = shapefiles[order(shapenames)]
 shapenames = shapenames[order(shapenames)]

 for(i in 1:length(shapefiles)) {
  shp = readOGR(dsn=shapefiles[i], verbose=F) #Read shape file
  shp@polygons[[1]]@ID = as.character(i) #Set UID

  if(i == 1) {
   C = crs(shp) #Get CRS
```

```
   spatial_polygons_list = list(SpatialPolygons(list(shp@polygons[[1]]), proj4string = C))
  } else {
   spatial_polygons_list = append(spatial_polygons_list,
                SpatialPolygons(list(shp@polygons[[1]]), proj4string = C))
  }
 }
 joined = SpatialPolygons(lapply(spatial_polygons_list, function(x){x@polygons[[1]]}), proj4string = C)
 joined = SpatialPolygonsDataFrame(joined, data=data.frame(names=shapenames))

 return(joined)
}

#Grid study area. ####

#sps is a SpatialPolygonsDataFrame with the study area polygons.
#prj is the projection string.

grid_study_area = function(sps, prj, grid.size) {
 require(raster)
 for(i in 1:length(sps)) {
  x = sps[i,] #polygons
  grid = raster(extent(x),resolution = c(1,1), crs = proj) #Grid.
  values(grid)=1 #Make all values 1

  #Overlay with study area.
  grid = raster::mask(grid, x, updatevalue=0)

  #upsample to desired grid.size
  grid = raster::aggregate(grid, fact=grid.size, fun=max)

  if(i == 1) {out = list(grid)} else {out = append(out, list(grid))}
 }
 names(out) = sps@data$names
 return(out)
}

#Known state cjs function####
#This function was provided in the original code, and is needed in order for the
#script to work.

known.state.cjs <- function(ch){
state <- ch
for (i in 1:dim(ch)[1]){
 n1 <- min(which(ch[i,]==1))
 n2 <- max(which(ch[i,]==1))
 state[i,n1:n2] <- 1
 state[i,n1] <- NA
}
state[state==0] <- NA
return(state)
}
```

```
#Grid coordinates.####
#Grid coordinates (grid.x and grid.y) for lower left corners of each cell in
#the study area. This will be provided as a list.

grid_coordinates = function(grids, xy=c('x','y')) {

 if(length(xy)==2) stop('specify one of x or y')

 Ns = sapply(grids, function(x) sum(values(x)))

 grid.study.area = matrix(NA, nrow=max(Ns), ncol=length(grids))

 for(i in 1:length(grids)) {
  if(xy == 'x') {ind=1}
  if(xy == 'y') {ind=2}

  g = coordinates(grids[[i]])[which(values(grids[[i]])==1),ind]-grid.size/2

  grid.study.area[,i] = c(g, rep(NA, max(Ns)-length(g)))
 }

 colnames(grid.study.area) = names(grids)

 return(grid.study.area)

}

#inferAge####
#Infer age from capture history. This amounts to replacing NAs with "Adult" for recaptures, since
#all recaptures were adults, but there are some other error checking steps involved to ensure the data
#makes sense.



inferAge = function(bands, captureAge, years) {

 allBands = unique(bands)


 for(i in 1:length(allBands)) {
  inds = which(bands == allBands[i])
  if(length(inds)==1) {next}

  #Get ages
  ages = captureAge[inds]

  #Get years
  y = years[inds]

  #Check if multiple captures per year (there are none, which is good)
```

```
  if(length(unique(y)) != length(y)) {stop(paste('Multiple captures per year for band', allBands[i]))}
  #Get years with unknown ages and check.
  unknownAges = which(is.na(ages))
  check = 2:length(ages)

  if(sum(unknownAges == check) != length(unknownAges)) {stop(paste0('unknown ages dont make
sense', i))} else {
   ages[is.na(ages)] = 'Adult'
   captureAge[inds] = ages
  }
 }

 return(captureAge)

}

#checkNA#####
#Check that first capture has an age, and recaptures have NA
checkNA = function(bands, years) {
 for(i in 1:length(unique(bands))) {
  #Get band
  b = unique(bands)[i]
  #Subset year data
  y = years[bands == b]
  #Check that the first entry is a year (nchar=4)
  if(nchar(y[1])!=4) {stop('First entry is not a year')}
  #Check that all entries after the first year are NA.
  if(length(y)>1) {
   if(sum(!is.na(y[2:length(y)])) != length(y)-1) {stop('recapture entry is not NA')}
  }
 }
 print('No problems detected')
}

#firstCapAge####
#Create vector of age at first capture.
firstCapAge = function(bands, captureAge, years) {

 allBands = unique(bands)

 for(i in 1:length(allBands)) {
  inds = which(bands == allBands[i])

  #Get ages
  ages = captureAge[inds]

  if(allBands[i] == '66429793') {ages[1]='Adult'}

  ages = rep(ages[1], length(ages))
  captureAge[inds] = ages
 }
```

```
 return(captureAge)

}

#Year at first capture.#####

firstCapYear = function(bands, years) {

 allBands = unique(bands)
 i=1
 for(i in 1:length(allBands)) {
  inds = which(bands == allBands[i])

  ys = years[inds]

  ys = rep(min(ys), length(ys))

  years[inds] = ys
 }

 return(years)
}

#Make capture history####
#Make capture history from mark-recapture data. Added June 11: three-dimensional array
#with first layer being capture history, second being x coord, third being y coord.


make_ch = function(bands, years, xcoords, ycoords) {

 bs = sort(unique(bands))
 firstYear = min(years)
 lastYear = max(years)
 yearVec = firstYear:lastYear
 arr = array(0, dim = c(length(bs),length(yearVec),3), dimnames = list(bs, yearVec, c('ch','x', 'y')))
 #Make capture history.

 for(i in 1:length(bs)) {
  ys = years[bands==bs[i]]
  east = xcoords[bands==bs[i]]
  north = ycoords[bands==bs[i]]
  arr[bs[i],as.character(ys),1] = 1
  arr[bs[i],as.character(ys),2] = east
  arr[bs[i],as.character(ys),3] = north
 }
 return(arr)
}

#Capture type ####
```

```
captureType = function(bands, years) {
 #List of bands
 ub = unique(bands)
 #Loop through unique bands. Note classification here is contingent on the filtered dataset, not
 #necessarily on age at first capture. So a ADULT-FEMALE first banded as juvenile, later seen as adult,
 #would be classified as "original" here when first seen as adult.

 types = rep(NA, length(bands))

 for(i in 1:length(ub)) {
  inds = which(bands == ub[i])
  ys = years[inds]
  t = types[inds]
  for(j in 1:length(ys)) {
   if(ys[j] == min(ys)) {t[j]='original'} else {t[j]='recapture'}
  }
  types[inds] = t
 }
 if(sum(is.na(types))>0) {stop('Function failed.')}
 return(types)
}
```

Code for Baker Simulation– Adult-Female banding

```
#########################################################################
#Adult-Female – banding data
#Load all packages
library(tidyverse)
library(readxl)
library(ggplot2)
library(dplyr)
library(xlsx)
library(grid)
library(gridExtra)
library(ggpubr)
library(dunn.test)
library(circular)
library(rgeos)
library(fitdistrplus)
library(MASS)
library(logspline)
require(sp)
require(rgdal)
require(maps)
require(GISTools)
require(raster)
```

```
library(vioplot)
library(binom)
library(dgof)
#library(openair)
library(marked)
library(Hmisc)
#library(R2ucare)
library(dplyr)
library(magrittr)
library(rgeos)

source('./code/SpatialCJSFunctions.R')
source('./code/BakerFunctions.R')

############################################################################################
#Baker analysis for ADULT-FEMALE birds using banding data only.

load('./data/Adult-Female.RData')

Adult-Female = femaleadult[[1]]

spatial_polygons = femaleadult[[2]]

proj = proj4string(spatial_polygons)

rm(femaleadult)


#############################################################################
#Simulation Code - Combined All Dispersals to Inform Simulations
set.seed(1)

#Set number of simulations to run per bird
NSim=10000


#Breeding females - Lognormal with 0's removed

mu = mean(log(Adult-Female@data$dispersalDist[Adult-Female@data$dispersalDist>.250]), na.rm=T)
sd = sd(log(Adult-Female@data$dispersalDist[Adult-Female@data$dispersalDist>.250]), na.rm=T)

#Dispersal probability: number moved >.250 divided by number that were resighted.
PDisperse.Females=sum(Adult-Female@data$dispersalDist>.250 & !is.na(Adult-
Female@data$dispersalDist)) /
 sum(!is.na(Adult-Female@data$dispersalDist))

#Start simulation
jj=1
#Initialize P vector, to contain probability the bird will remain inside study area.
Adult-Female@data$P = NA
```

```
for(jj in 1:nrow(Adult-Female)) {
 #Use SimLN function to simulate P (probability the bird remained in study area)
 Adult-Female@data$P[jj]=SimLN(NestPoint=Adult-Female[jj,], sps=spatial_polygons, NSim=NSim,
meanlog=mu, sdlog=sd, pDisperse=PDisperse.Females)
 #Print progress of for loop
 if(jj %% 100==0) print(jj)
}

#Visualize boxplot of P values across all birds
boxplot(Adult-Female@data$P)
boxplot(Adult-Female@data$P ~ Adult-Female@data$study)
summary(Adult-Female@data$P ~ Adult-Female@data$study)

#Survival = Total Observed/ Total Expected to Observe (if survived, accounting for dispersal).
#Total observed must account for missed years. I.e. if a bird was banded, not seen, then seen again,
#that bird survived two years, and this must be accounted for (rather than just saying it survived one year,
because it was seen in one subsequent years)

Adult-Female@data$gapYear = gapYear(Adult-Female) #Gap year will be NA for original capture, 0 if
resight was in consecutive years
#and 1 if one gap year, etc.

#Exclude birds banded in the final year of a study.
#Total years "observed" to have survived (even if gap year).
totalYearsSurvived = sum(Adult-Female@data$gapYear+1, na.rm=T) #add one so that recaptures with
no gap count for one, recaptures with one year gap count for two, etc.
#Total birds expected, not including birds banded in the last year of a project, accounting for dispersal.

#variance of poisson binomial is from https://en.wikipedia.org/wiki/Poisson_binomial_distribution
expVec = Adult-Female@data$P[Adult-Female@data$type == 'original' & !Adult-
Female@data$finalYear]
expectedBirds = sum(expVec)

Survival = totalYearsSurvived / expectedBirds

#Assessing uncertainty using bootstrapping.

SurvBootstrap = rep(NA, 1000)
for(i in 1:1000) {
 inds = sample(1:nrow(Adult-Female@data), size = nrow(Adult-Female@data), replace=T)
 df = Adult-Female@data[inds,]
 totYrSurv = sum(df$gapYear+1, na.rm=T) #add one so that recaptures with no gap count for one,
recaptures with one year gap count for two, etc.
 #Total birds expected, not including birds banded in the last year of a project, accounting for dispersal.

 #variance of poisson binomial is from https://en.wikipedia.org/wiki/Poisson_binomial_distribution
 eVec = df$P[df$type == 'original' & !df$finalYear]
 eBirds = sum(eVec)
 SurvBootstrap[i] = totYrSurv / eBirds
}
```

```
mean.Survival = Survival
sd.Survival = sd(SurvBootstrap)
CI.Survival = stats::quantile(SurvBootstrap, probs=c(0.025, 0.975))
```

Code for CJS

```
#Code is based on two blog posts:
#1) https://jamesepaterson.github.io/jamespatersonblog/2020-04-26_introduction_to_CJS.html
#2) https://jamesepaterson.github.io/jamespatersonblog/2020-05-20_gof_for_CJS

##################################################################################
##################################################################################
#Load all packages
library(tidyverse)
library(readxl)
library(ggplot2)
library(dplyr)
library(xlsx)
library(grid)
library(gridExtra)
library(ggpubr)
library(dunn.test)
library(circular)
library(rgeos)
library(fitdistrplus)
library(MASS)
library(logspline)
require(sp)
require(rgdal)
require(maps)
require(GISTools)
require(raster)
library(vioplot)
library(binom)
library(dgof)
#library(openair)
library(marked)
library(Hmisc)
library(R2ucare)
library(dplyr)
library(magrittr)
library(rgeos)

source('./code/SpatialCJSFunctions.R')
source('./code/BakerFunctions.R')

#
#######################################################################################################
#############################################
```

```
#CJS for ADULT-FEMALE birds using banding data.

load('./data/Adult-Female.RData')

Adult-Female = femaleadult[[1]]

spatial_polygons = femaleadult[[2]]

proj = proj4string(spatial_polygons)

rm(femaleadult)

#Create capture history.

ch = make_ch(bands=Adult-Female@data$band, years=Adult-Female@data$year, xcoords=Adult-
Female@data$easting, ycoords=Adult-Female@data$northing)

#pull out study areas as grouping variables
Adult-Femaletest = cbind(Adult-Female[[1]],Adult-Female[[2]])
Adult-Femaletest<-as.data.frame(Adult-Femaletest)
Adult-Femaletest<-Adult-Femaletest[!duplicated(Adult-Femaletest$V2),]
summary(Adult-Femaletest)


#Strip coordinates.
ch = ch[,,1]


#Collapse to character vectors.
caphist = rep(NA, nrow(ch))

for(i in 1:nrow(ch)) {
 caphist[i]=paste0(ch[i,], collapse="")
}

data = data.frame(ch=caphist, stringsAsFactors=F)

data<-cbind(data,Adult-Femaletest)
##########################################################################################
###############
##########################################################################################
######
# #Standard CJS Model
#View(data)
#head(data)
# #data preparation for cjs model
data <-as.data.frame(data)
names(data)[2] <- "study"
names(data)[3] <- "band"

#data$category <-as.factor(data$category)
```

```
head(data)
sum(is.na(data)) #check for NAs

#compute initial values for the parameters and
#find the MLEs with the selected optimization method(s).
model=crm(data)
model
model=cjs.hessian(model) #print the SE and confidence intervals
model

plogis(model$results$beta$Phi) #24% survival probability.
plogis(model$results$beta$p) #40% detection probability.
predict(model)

#predict(model,
   # newdata = data.frame(category = c("AdultFemale", "AdultMale","Juvenile")),
   # se = TRUE)

colnames(ch)

#The following code was taken from https://jamesepaterson.github.io/jamespatersonblog/2020-04-
26_introduction_to_CJS.html
#It is aimed at fitting all models and selecting the best using AIC.
#
# Step 1. Process data (and set grouping variables)
data$study<-as.factor(data$study)
data.proc=process.data(data, group="study")
data.ddl=make.design.data(data.proc)

#outline formulas for each parameter
#Phi.dot <- list(formula=~1) # ~1 is always a constant (or single estimate)
#Phi.study <- list(formula=~study)
#p.study <- list(formula=~study)

#model=crm(data.proc,data.ddl,model.parameters = list(Phi = Phi.study))
#
fit.test.cjs.models <- function(){
#
#  # Apparent survival (Phi) formula
 Phi.study <-list(formula=~study)
 #Phi.study.time <-list(formula=~study*time) # Just like in other linear models "*" includes main effects
and an interaction
 Phi.time <- list(formula=~time) # differs between discrete times
 #Phi.category <- list(formula=~category) # differs between males and females
 Phi.dot <- list(formula=~1) # constant survival
#
#  # Detection probability (p) formula
 p.study <- list(formula=~study) # differs between males and females
 p.time <- list(formula=~time) # one discrete estimate of p per capture event
 p.dot <- list(formula=~1) # constant detection
 #p.study.time <-list(formula=~study*time)
```

```
#
#  # Construct all combinations and put into one model table
 cml <- create.model.list(c("Phi","p")) # makes all possibile combinations of those parameter formulas
 results <- crm.wrapper(cml,
           data = data.proc,
            ddl = data.ddl,
            external = FALSE,
            accumulate = FALSE,
            hessian = TRUE)
 return(results)
 }
#
# # Run function
test.cjs.models <- fit.test.cjs.models()
# # Display model table
test.cjs.models
write.xlsx(test.cjs.models$model.table,file="ADULT-FEMALE_CJSModels.xlsx")
test.cjs.models[[2]]

#Top candidate model
predict(test.cjs.models[[2]])$Phi
Phi_by_category <- predict(test.cjs.models[[2]])$Phi# predict Phi kept constant

predict(test.cjs.models[[2]])$p
p_by_category <- predict(test.cjs.models[[2]])$p #predict p for all studies

#second candidate model
predict(test.cjs.models[[4]])$Phi
#Phi_by_category <- predict(test.cjs.models[[4]])$Phi


predict(test.cjs.models[[1]])$Phi
#p_by_category <- predict(test.cjs.models[[4]])$p

#non-zero value indicate model did not converge
#Can pull models out using the number from the table or the parameters
finalmodel<-test.cjs.models[[2]]
secondmodel<-test.cjs.models[[4]]
thirdmodel<-test.cjs.models[[1]]
#Because you're looking at the beta estimates, which are derived on the logit scale.
#For them to 'make sense', you need to 'back-transform' from logit -> real.
#logit2prob <- function(logit){
# odds <- exp(logit)
# prob <- odds / (1 + odds)
# return(prob)
#}

#finalmodel$results$beta$Phi
#logit2prob(finalmodel$results$beta$Phi)
#or use predict command
ADULT-FEMALE.CJS.estimates<-predict(finalmodel)
```

```
ADULT-FEMALE.CJS.estimates
ADULT-FEMALE.CJS.estimates2<-predict(secondmodel)
ADULT-FEMALE.CJS.estimates3<-predict(thirdmodel)

#The following code is from https://jamesepaterson.github.io/jamespatersonblog/2020-05-20_gof_for_CJS
#It is intended on conducting goodness of fit tests on the data.

#Run test 1
overall_CJS(ch, rep(1,nrow(ch)))
#H0: there is no strong evidence for lack-of-fit
ADULT-FEMALE.chat<-(8.48/19)
ADULT-FEMALE.chat
```

Code for Spatial CJS

```
library(readxl)
library(sp)
library(rgdal)
library(raster)
library(xlsx)

source('./code/SpatialCJSFunctions.R')

#Read data########################################################################################
#Spatial CJS - ADULT-FEMALE in Regina Plain, without PTT data incorporated.

#Load ADULT-FEMALE data.
load('./data/Adult-Female.RData')

Adult-Female = femaleadult[[1]]

spatial_polygons = femaleadult[[2]]

proj = proj4string(spatial_polygons)

rm(femaleadult)

#Make capture history.

ch = make_ch(bands=Adult-Female@data$band, years=Adult-Female@data$year,
xcoords=coordinates(Adult-Female)[,1], ycoords=coordinates(Adult-Female)[,2])

yearVec = min(Adult-Female$year):max(Adult-Female$year)


#Specify models############################
```

```
# Specify analyzing models

# sCJS-N with irregularly shaped study area
# June 11 2021 - directly replaced noccasions variable with d[i] to indicate bird-specific end-point of
# search (actually study-area specific endpoint, but applied to each bird).
sink("sCJSNg.mod")
cat("
  model {

  # Priors and constraints
  for (i in 1:nind){
  for (t in f[i]:(d[i]-1)){
  phi[i,t] <- mean.phi
  p[i,t] <- mean.p
  } #t
  } #i

  mean.phi ~ dunif(0,1)
  mean.p ~ dunif(0,1)

  for (i in 1:2){
  tau[i] <- pow(sigma[i], -2)
  sigma[i] ~ dunif(0, 50)
  }

  # Likelihood
  for (i in 1:nind){
  # Define latent state at first capture
  z[i,f[i]] <- 1

  for (t in (f[i]+1):d[i]){
  # State processes
  # Survival
  z[i,t] ~ dbern(phi[i,t-1] * z[i,t-1])

  # Dispersal
  G[i,t,1] ~ dnorm(G[i,t-1,1], tau[1])
  G[i,t,2] ~ dnorm(G[i,t-1,2], tau[2])

  # Observation process
  # Test whether the actual location is in- or outside the state-space.
  # Changed this so that it selects the appropriate study area based on the vector
  # sa.

  # sa[i] is value 1:5 defining study area.

  for (g in 1:ngrids[sa[i]]){
  inside[i,t,g] <- step(G[i,t,1]-grid.x.study.area[g,sa[i]]) * step(grid.x.study.area[g,sa[i]]+grid.size-G[i,t,1])
*
  step(G[i,t,2]-grid.y.study.area[g,sa[i]]) * step(grid.y.study.area[g,sa[i]]+grid.size-G[i,t,2])
  }
```

```
  r[i,t] <- sum(inside[i,t,1:ngrids[sa[i]]])
  Y[i,t] ~ dbern(p[i,t-1] * z[i,t] * r[i,t])
  } #t
  } #i
  }
  ",fill = TRUE)
sink()


#Create study areas##############################

#Grid study area.
grid.size = 5
grids = grid_study_area(sps=spatial_polygons, prj=proj, grid.size=grid.size)

# Matrix with grids and their min coordinates - the max is determined by grid.size.
# Matrix dimensions are i,j where i is max(ngrids), and study areas with <ngrids
# are assigned NA for the rest.

grid.x.study.area = grid_coordinates(grids, xy='x')
grid.y.study.area = grid_coordinates(grids, xy='y')

plot(unlist(grid.x.study.area), unlist(grid.y.study.area)) #Plot to check.

#Format Recapture data for JAGS####

#Need recapture data that matches theirs.

#Need dat$Y.in to record capture history of each individual by year.
#Need dat$G.in to record coordinates, first matrix is x coord, second is y coord, NA for not encountered.
#This should all be in UTMs, although km units for consistency.
#Need dat$f to be a vector stating in which year each individual was first captured.
#New: need dat$d to be a vector stating in which year searches were terminated for each individual (i.e.
each study area).
#Add: dat$sa to be a vector stating in which study area the individual was captured.


Y.in = ch[,,1]

G.in = ch[,,2:3]
G.in[G.in==0]=NA
plot(G.in[,,1], G.in[,,2])
plot(spatial_polygons, add=T) #looks good.

rm(ch)

#Create f, vector of year of first capture.
f = rep(NA, length = nrow(Y.in))

for(i in 1:nrow(Y.in)) {
 row = Y.in[i,] #Row
```

```
 firstCap=min(which(row>0))
 f[i]=firstCap
}
rm(list=c('row', 'firstCap'))

#Create d, vector of last year of searching. Done by study area.
#Same time, define sa, a vector indicating which study area to use for each data point.
d = rep(NA, length = nrow(Y.in))
sa = rep(NA, length = nrow(Y.in))

i=1
for(i in 1:nrow(Y.in)) {
 band = row.names(Y.in)[i]
 study = Adult-Female@data$study[Adult-Female@data$band == band][1] #Define study area based on
first location of capture.
 #On the basis of study variable, define last year of the study and the number (i.e. grid.x.study.area and
grid.y.study.area column order.)
 if(study == 'James') {
  sa[i] = 1
  maxyear = 2002
 }
 if(study == 'Regina Plain') {
  sa[i] = 2
  maxyear = 2002
 }
 if(study == 'Schmutz') {
  sa[i] = 3
  maxyear = 1993
 }
 if(study == 'Suffield') {
  sa[i] = 4
  maxyear = 2019
 }
 if(study == 'Wellicome') {
  sa[i] = 5
  maxyear = 2002
 }
 d[i] = which(colnames(Y.in) == as.character(maxyear))

 rm(list=c('maxyear', 'study'))
}

rm(list=c('i', 'band'))

table(sa)
table(d)

#Scale coordinates by minimum so they start at zero. This was needed in order for the code to run,
#after much trial and error.

plot(G.in[,,1], G.in[,,2])
```

```
points(grid.x.study.area, grid.y.study.area)

i=1
for(i in 1:nrow(G.in)) {
 S = sa[i]

 mins = c(min(grid.x.study.area[,S], na.rm=T), min(grid.y.study.area[,S], na.rm=T))

 G.in[i,,1] = G.in[i,,1] - mins[1]
 G.in[i,,2] = G.in[i,,2] - mins[2]
}

for(i in 1:ncol(grid.x.study.area)) {
 grid.x.study.area[,i] = grid.x.study.area[,i] - min(grid.x.study.area[,i], na.rm=T)
 grid.y.study.area[,i] = grid.y.study.area[,i] - min(grid.y.study.area[,i], na.rm=T)
}

#Check.
plot(grid.x.study.area, grid.y.study.area)
points(G.in[,,1], G.in[,,2], pch=20)

#Number of grid cells per study area.
ngrids=as.vector(sapply(grids, function(x) sum(values(x))))
apply(grid.x.study.area,2,function(x) sum(!is.na(x)))
apply(grid.y.study.area,2,function(x) sum(!is.na(x)))

# 2. Create data
dat <- list(Y.in = Y.in, G.in = G.in, f = f, d = d, sa=sa)

# 3. Bundle data
jags.data <- list(Y = dat$Y.in, G = dat$G.in, f = dat$f, d=dat$d, sa=dat$sa, nind = nrow(dat$Y.in),
grid.x.study.area = grid.x.study.area, grid.y.study.area = grid.y.study.area, grid.size = grid.size, ngrids =
ngrids)

# 4. Initial values
inits <- function(){list(mean.phi = runif(1,0,1), mean.p = runif(1,0,1),
          sigma = runif(2,0.01,2),
          z = known.state.cjs(dat$Y.in))}

# 5. Parameters monitored
parameters <- c("mean.phi", "mean.p", "sigma")

# 6. MCMC settings
ni <- 10000 #orig 10000
nt <- 1
nb <- 5000 #orig 5000
nc <- 2

# 7. Call JAGS from R
library(R2jags)
```

```
mN <- jags(jags.data, inits, parameters.to.save=parameters, "sCJSNg.mod", n.chains = nc, n.thin = nt,
n.iter = ni, n.burnin = nb, working.directory = getwd())
mN


#BUOW Survival Estimate Correction Analysis. ADULT-FEMALE banding data.
setwd("D:/BUOW Dispersal Distance/Chapter -DispersalSimulations")

######################################################################
######################################################################
#Baker Simulation
#Load all packages
library(tidyverse)
library(readxl)
library(ggplot2)
library(dplyr)
library(xlsx)
library(grid)
library(gridExtra)
library(ggpubr)
library(dunn.test)
library(circular)
library(rgeos)
library(fitdistrplus)
library(MASS)
library(logspline)
require(sp)
require(rgdal)
require(maps)
require(GISTools)
require(raster)
library(vioplot)
library(binom)
library(dgof)
#library(openair)
library(marked)
library(Hmisc)
#library(R2ucare)
library(dplyr)
library(magrittr)
library(rgeos)

source('./2021-07-19/2021-06-03_AllAnalysesTogether/code/SpatialCJSFunctions.R')
source('./2021-07-19/2021-06-03_AllAnalysesTogether/code/BakerFunctions.R')


########################################################################################
######################################
#Baker analysis for ADULT-FEMALE birds using tracking data only.
#NEW THIS TIME AROUND: Added detection probability parameter, drawn from
#spatial CJS.
```

```
load('./2021-07-19/2021-06-03_AllAnalysesTogether/data/Adult-Female.RData')

Adult-Female = femaleadult[[1]]

spatial_polygons = femaleadult[[2]]

proj = proj4string(spatial_polygons)

rm(femaleadult)

PTTData <- read.csv("./2021-07-19/2021-06-03_AllAnalysesTogether/data/PTTOwl_xyDistances.csv",
stringsAsFactors=F)


#LOAD Spatial CJS P estimate.
#NOTE: for the spatial CJS, we can simply use the monte carlo samples of p
#directly. No need to parametrize an approximation, then draw from that.

load("./2021-07-19/2021-06-03_AllAnalysesTogether/Adult-FemaleModelOutput.RData")

#Get Monte Carlo samples.
Ps <- mN$BUGSoutput$sims.matrix[,'mean.p']
#Plot to visualize.
plot(density(Ps))

Mean.P <- mN$BUGSoutput$mean$mean.p

#Thin to 1000 to match bootstrap below. Take every 10th sample.
Ps <- Ps[c(1:10000) %% 10 == 0]




################################################################################
#Simulation Code - Combined All Dispersals to Inform Simulations
set.seed(1)

#Set number of simulations to run per bird
NSim=10000


#Breeding females - Lognormal with 0's removed

mu = mean(log(PTTData$Distance..km.[PTTData$Distance..km.>.250]), na.rm=T)
sd = sd(log(PTTData$Distance..km.[PTTData$Distance..km.>.250]), na.rm=T)

#Dispersal probability: proportion moved >.250.
PDisperse.Females=sum(PTTData$Distance..km.>.250)/length(PTTData$Distance..km.)

#Start simulation
```

```
jj=1
#Initialize P vector, to contain probability the bird will remain inside study area.
Adult-Female@data$P = NA

for(jj in 1:nrow(Adult-Female)) {
 #Use SimLN function to simulate P (probability the bird remained in study area)
 Adult-Female@data$P[jj]=SimLN(NestPoint=Adult-Female[jj,], sps=spatial_polygons, NSim=NSim,
meanlog=mu, sdlog=sd, pDisperse=PDisperse.Females)
 #Print progress of for loop
 if(jj %% 100==0) print(jj)
}

#Visualize boxplot of P values across all birds
boxplot(Adult-Female@data$P ~ Adult-Female@data$study)

#Survival = Total Observed/ Total Expected to Observe (if survived, accounting for dispersal).
#Total observed must account for missed years. I.e. if a bird was banded, not seen, then seen again,
#that bird survived two years, and this must be accounted for (rather than just saying it survived one year,
because it was seen in one subsequent years)

Adult-Female@data$gapYear = gapYear(Adult-Female) #Gap year will be NA for original capture, 0 if
resight was in consecutive years
#and 1 if one gap year, etc.

#Exclude birds banded in the final year of a study.
#Total years "observed" to have survived (even if gap year).
totalYearsSurvived = sum(Adult-Female@data$gapYear+1, na.rm=T) #add one so that recaptures with
no gap count for one, recaptures with one year gap count for two, etc.
#Total birds expected, not including birds banded in the last year of a project, accounting for dispersal.
#New this time: expected birds is corrected for detection probability from spatial CJS.
expectedBirds = sum(Adult-Female@data$P[Adult-Female@data$type == 'original' & !Adult-
Female@data$finalYear]) * Mean.P
Survival = totalYearsSurvived / expectedBirds


#Assessing uncertainty using bootstrapping.

SurvBootstrap = rep(NA, 1000)
for(i in 1:1000) {
 inds = sample(1:nrow(Adult-Female@data), size = nrow(Adult-Female@data), replace=T)
 df = Adult-Female@data[inds,]
 totYrSurv = sum(df$gapYear+1, na.rm=T) #add one so that recaptures with no gap count for one,
recaptures with one year gap count for two, etc.
 #Total birds expected, not including birds banded in the last year of a project, accounting for dispersal.

 #variance of poisson binomial is from https://en.wikipedia.org/wiki/Poisson_binomial_distribution
 eVec = df$P[df$type == 'original' & !df$finalYear]
 #NEW: Add detection probability correction. In this case, only expect to see ~0.42 of all birds.
 eBirds = sum(eVec) * Ps[i]
 SurvBootstrap[i] = totYrSurv / eBirds
}
```

```
mean.Survival = Survival
sd.Survival = sd(SurvBootstrap)
CI.Survival = stats::quantile(SurvBootstrap, probs=c(0.025, 0.975))
plot(density(SurvBootstrap))

write.csv(data.frame(mean=mean.Survival, sd=sd.Survival, CI_Low=CI.Survival[1],
CI_High=CI.Survival[2]), 'Baker_TrackingResults_WithPSpatialCJS.csv', row.names=F)



#BUOW Survival Estimate Correction Analysis. ADULT-FEMALE banding data.
setwd("D:/BUOW Dispersal Distance/Chapter -DispersalSimulations")

########################################################################
########################################################################
#Baker Simulation
#Load all packages
library(tidyverse)
library(readxl)
library(ggplot2)
library(dplyr)
library(xlsx)
library(grid)
library(gridExtra)
library(ggpubr)
library(dunn.test)
library(circular)
library(rgeos)
library(fitdistrplus)
library(MASS)
library(logspline)
require(sp)
require(rgdal)
require(maps)
require(GISTools)
require(raster)
library(vioplot)
library(binom)
library(dgof)
#library(openair)
library(marked)
library(Hmisc)
#library(R2ucare)
library(dplyr)
library(magrittr)
library(rgeos)

source('./2021-07-19/2021-06-03_AllAnalysesTogether/code/SpatialCJSFunctions.R')
source('./2021-07-19/2021-06-03_AllAnalysesTogether/code/BakerFunctions.R')
```

```
##############################################################################
##################################
#Baker analysis for ADULT-FEMALE birds using tracking data only.
#NEW THIS TIME AROUND: Added detection probability parameter, drawn from
#spatial CJS.

load('./2021-07-19/2021-06-03_AllAnalysesTogether/data/Adult-Female.RData')

Adult-Female = femaleadult[[1]]

spatial_polygons = femaleadult[[2]]

proj = proj4string(spatial_polygons)

rm(femaleadult)

PTTData <- read.csv("./2021-07-19/2021-06-03_AllAnalysesTogether/data/PTTOwl_xyDistances.csv",
stringsAsFactors=F)


#LOAD CJS P estimate.
#NOTE: for the spatial CJS, we can simply use the monte carlo samples of p
#directly. No need to parametrize an approximation, then draw from that.

cjs <- read_xlsx("./2021-07-19/2021-06-03_AllAnalysesTogether/ADULT-
FEMALE_CJSOutput_Combined.xlsx")


meanlogis <- qlogis(cjs$p.estimate)
sdlogis <- (qlogis(cjs$p.estimate) - qlogis(cjs$p.lcl)) / 1.96

#The fact that the following gives zeroes shows that it is appropriate to use the logit scale here.
meanlogis - qlogis(cjs$p.lcl) + (meanlogis - qlogis(cjs$p.ucl))

#Clearly the above is how sd is calculated, since lcl matches the cjs$p.lcl values.
lcl <- meanlogis - 1.96*sdlogis
plogis(lcl) - cjs$p.lcl

#So we can work with a normal distribution on the logit scale, with mean = qlogis(cjs$p.estimate)
#and sd = sdlogis as above.

#Draw monte carlo samples. Transform to probability scale.
#One per study area, so a matrix with 5 columns.
set.seed(1)
Ps <- plogis(rnorm(n = 1000, mean = meanlogis, sd = sdlogis))


#Plot to visualize.
plot(density(Ps))
```

```
dev.off()

##############################################################################
#Simulation Code - Combined All Dispersals to Inform Simulations
set.seed(1)

#Set number of simulations to run per bird
NSim=10000


#Breeding females - Lognormal with 0's removed

mu = mean(log(PTTData$Distance..km.[PTTData$Distance..km.>.250]), na.rm=T)
sd = sd(log(PTTData$Distance..km.[PTTData$Distance..km.>.250]), na.rm=T)

#Dispersal probability: proportion moved >.250.
PDisperse.Females=sum(PTTData$Distance..km.>.250)/length(PTTData$Distance..km.)

#Start simulation
jj=1
#Initialize P vector, to contain probability the bird will remain inside study area.
Adult-Female@data$P = NA

for(jj in 1:nrow(Adult-Female)) {
 #Use SimLN function to simulate P (probability the bird remained in study area)
 Adult-Female@data$P[jj]=SimLN(NestPoint=Adult-Female[jj,], sps=spatial_polygons, NSim=NSim,
meanlog=mu, sdlog=sd, pDisperse=PDisperse.Females)
 #Print progress of for loop
 if(jj %% 100==0) print(jj)
}

#Visualize boxplot of P values across all birds
boxplot(Adult-Female@data$P ~ Adult-Female@data$study)

#Survival = Total Observed/ Total Expected to Observe (if survived, accounting for dispersal).
#Total observed must account for missed years. I.e. if a bird was banded, not seen, then seen again,
#that bird survived two years, and this must be accounted for (rather than just saying it survived one year,
because it was seen in one subsequent years)

Adult-Female@data$gapYear = gapYear(Adult-Female) #Gap year will be NA for original capture, 0 if
resight was in consecutive years
#and 1 if one gap year, etc.

#Exclude birds banded in the final year of a study.
#Total years "observed" to have survived (even if gap year).
totalYearsSurvived = sum(Adult-Female@data$gapYear+1, na.rm=T) #add one so that recaptures with
no gap count for one, recaptures with one year gap count for two, etc.
#Total birds expected, not including birds banded in the last year of a project, accounting for dispersal.
#New this time: expected birds is corrected for detection probability from spatial CJS.
expectedBirds = sum(Adult-Female@data$P[Adult-Female@data$type == 'original' & !Adult-
Female@data$finalYear]) * cjs$p.estimate
```

```
Survival = totalYearsSurvived / expectedBirds


#Assessing uncertainty using bootstrapping.

SurvBootstrap = rep(NA, 1000)
for(i in 1:1000) {
 inds = sample(1:nrow(Adult-Female@data), size = nrow(Adult-Female@data), replace=T)
 df = Adult-Female@data[inds,]
 totYrSurv = sum(df$gapYear+1, na.rm=T) #add one so that recaptures with no gap count for one,
recaptures with one year gap count for two, etc.
 #Total birds expected, not including birds banded in the last year of a project, accounting for dispersal.

 #variance of poisson binomial is from https://en.wikipedia.org/wiki/Poisson_binomial_distribution
 eVec = df$P[df$type == 'original' & !df$finalYear]
 #NEW: Add detection probability correction. In this case, only expect to see ~0.42 of all birds.
 eBirds = sum(eVec) * Ps[i]
 SurvBootstrap[i] = totYrSurv / eBirds
}

mean.Survival = Survival
sd.Survival = sd(SurvBootstrap)
CI.Survival = stats::quantile(SurvBootstrap, probs=c(0.025, 0.975))
plot(density(SurvBootstrap))

write.csv(data.frame(mean=mean.Survival, sd=sd.Survival, CI_Low=CI.Survival[1],
CI_High=CI.Survival[2]), 'Baker_TrackingResults_WithPCJS.csv', row.names=F)
```