

DISSERTATION

RESTORATION OF SCALED QUAIL TO HISTORIC RANGES IN THE ROLLING PLAINS

ECOREGION OF TEXAS

Submitted by

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ABSTRACT

RESTORATION OF SCALED QUAIL TO HISTORIC RANGES IN THE ROLLING PLAINS ECOREGION OF TEXAS

Scaled quail (*Callipepla squamata*) are a gallinaceous game bird native to the grasslands and deserts of the southwestern United States and northcentral Mexico experiencing range contraction and population decline due to habitat fragmentation and degradation. Once abundant in the Rolling Plains ecoregion of Texas dating back to the 1880's, scaled quail were locally extinct throughout most of the ecoregion by the late 1980's primarily due to brush encroachment and spatial aggregation of row crop agriculture. Despite state and federal landowner habitat restoration programs (e.g., Landowner Incentive Program, Environmental Quality Incentives Program) scaled quail populations in the Rolling Plains ecoregion failed to respond, likely because the same fragmentation that contributed to decline also prevented effective natural recolonization to restored habitats. Translocation of wild-caught quails to reestablish self-sustaining populations gained popularity during the 2000's, particularly due to success reestablishing northern bobwhites (*Colinus virginianus*) in fragmented habitats of the southeastern United States. However, many translocations in arid, western climates were either poorly documented or failed outright. Understanding factors that influence translocation outcomes and form best practices is critical for translocation to be used effectively as a management tool.

I examined long-term, seasonal survival in a population of scaled quail successfully reestablished on the Rolling Plains Quail Research Ranch in Fisher County, Texas in the context of drought

and demographics (Chapter 1). Competing hypotheses predict that scaled quail populations are either resistant to drought or that annual survival is negatively correlated with precipitation amounts. My findings supported the hypothesis that scaled quail are drought sensitive. Additionally, I found survival was lower during non-breeding season, for females, and adults. Scaled quail survival estimates reported here are the most comprehensive for the species and the longest-term study of a translocated scaled quail population to date.

I conducted a field experiment to test the effects of source population and variation in delayed release strategy (1–9 weeks) on mortality, dispersal, nest initiation, renesting rate, and nest survival of wild-caught, translocated scaled quail (Chapters 2 and 3). I trapped and translocated quail over 2 years (2016–2017) from source populations in the Edwards Plateau and Rolling Plains ecoregions to a large (>40,000 ha), contiguous release site in Knox County, Texas. Data were analyzed using two multi-state mark-recapture models with state uncertainty to incorporate uncertainty in the process of observing location and nest initiation in radio-marked birds. The framework I used to model reproductive processes is a novel method for obtaining estimates of nest initiation and renesting rate (Chapter 3). I found that scaled quail translocated within the Rolling Plains were more likely to exhibit philopatry to the release site, but that source population did not influence reproduction. Quail with longer holding times had higher mortality, but lower dispersal rates. Additionally, increased length of holding time decreased renesting effort. Yearlings were more likely to initiate nests than adults and the probability of renesting was lower during drought conditions.

Finally, I compiled estimated demographics from chapters 1–3 to inform a matrix population model (MPM) that compared asymptotic and transient dynamics under wet and drought

conditions (Chapter 4). While traditional MPM analyses focus on asymptotic dynamics, transient dynamics are more relevant for modeling short-term dynamics in translocated or unstable populations. My findings showed divergence between transient and asymptotic dynamics, with asymptotic projections potentially overestimating population growth by 14%. Asymptotic growth rates were most sensitive to renesting rate changes, while transient growth rates were affected by changes in hatchability and renesting rates.

The results from my research will inform management decisions and I summarize my recommendations in Chapter 5. I suggest managers avoid initiating translocations in years projected to have drought conditions. Improved accuracy of El Niño–Southern Oscillation cycle-based long-range forecasts has made predictions a useful tool for managers considering translocation. Even so, translocated populations can persist long-term in drought conditions despite the negative impacts to survival and reproduction. Longer holding times for translocated scaled quail result in lower dispersal but higher mortality and lower renesting rates, presenting a decision tradeoff for managers. Managers can hold scaled quail on the release site (up to 9 weeks) when limiting dispersal is a priority (e.g., when in habitats surrounded by a high degree of fragmentation) or holding birds makes the translocation more feasible. However, when considering all factors a holding time of 2–3 weeks is ideal (Chapter 5). The Edwards Plateau is a suitable source site for translocations in the Rolling Plains. Managers should consider transient dynamics when modeling populations where short-term outcomes are relevant such as translocation. By doing so, I show that prioritizing the translocation of yearlings, the stage class with the highest reproductive value, can result in a 16% larger population after one year compared to translocating only adults.

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$$\Psi_{AC}(\text{year}) + \Psi_{AC}(\text{ranch}) + \Psi_{AC}(\text{release}) + \Psi_{BD}(\text{year}) + \Psi_{BA}(\text{year}) + \Psi_{BA}(\text{ranch}) + \Psi_{BA}(\text{age}) + \Psi_{BA}(\text{source}) + \Psi_{AB}(\text{year}) + \Psi_{AB}(\text{ranch}) + \Psi_{AB}(\text{release}) + \Psi_{AB}(\text{trend}) + \delta_{u|A}(\cdot) + \delta_{u|B}(\cdot). \dots\dots\dots 50$$

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CHAPTER 1. DROUGHT AND SEASONALITY INFLUENCE SURVIVAL IN AN AUGMENTED POPULATION OF SCALED QUAIL

Native grasslands are a threatened biome in North America and the projected increase of drought frequency and intensity will further fragment grasslands. Grassland-associated species, such as scaled quail (*Callipepla squamata*), are vulnerable to fragmentation, but may benefit from translocation programs to reintroduce locally extinct or augment remnant populations. My objectives were to evaluate the influence of drought, seasonality, age, and sex on long-term survival in a population of scaled quail augmented via translocation in the Southern Great Plains. Competing hypotheses surrounding drought predict that scaled quail populations are resistant to drought, versus that survival is negatively correlated with precipitation amount. Scaled quail translocation efforts will benefit from clarifying influences of drought on survival. Scaled quail were translocated to a depopulated private property in Fisher County, Texas. Founding individuals and the subsequent population were monitored via band-recapture for 6 years post release. I found survival was negatively correlated with drought severity. Survival was lower during non-breeding season, for female, and for adult scaled quail. My findings support hypotheses that scaled quail are drought sensitive. Yet, translocated populations can persist under moderate drought conditions and benefit from favorable weather conditions at the outset of reintroduction or augmentation. My findings also highlight the need for seasonal and year-round survival estimates including both sexes and age classes to inform conservation decisions.

INTRODUCTION

Native grasslands are the most threatened biome in North America (Hoekstra et al. 2004). Anthropogenic activities such as row crop agriculture, energy development, and mineral extraction caused the loss of >50% of grasslands, and fragmentation of the rest, in the Great Plains (Samson et al. 2004, Zhu et al. 2011). Consequently, North American grassland birds declined more severely than any other avian guild (Brennan and Kuvlesky 2005, Rosenberg et al. 2019). Remaining grasslands are critical for conservation. Yet, seasonal weather patterns strongly influence the quality of remnant habitats, and thus demographics of grassland birds (Dreitz et al. 2012, Skagen and Adams 2012). Precipitation promotes vegetation growth that provides cover and food, but its effects are mediated by temperature (Gorzo et al. 2016) with droughts being intensified by hot temperatures (Cheng et al. 2019). Anthropogenic climate change is expected to increase drought frequency and intensity in the future (Schubert et al. 2004, Livneh and Hoerling 2016).

Although drought is historically common to the Great Plains, it now acts on a heavily fragmented landscape (Clark et al. 2002). Species that evolved shifting their distributions in response to a landscape mosaic of varying habitat quality are limited by remnant patches available (Wilson et al. 2018). Highly mobile migratory species can avoid poor quality habitat by dispersing long distances, but less mobile, non-migratory species, such as gallinaceous grassland birds, are more vulnerable (Bateman et al. 2015, Tanner et al. 2017) and local extinction resulting from environmental stochasticity is more likely in such small, isolated populations (Hanski 1998). One potential management action is to ‘rescue’ isolated populations of gallinaceous grassland birds that are unable to recover on their own through translocation (Carrlson et al. 2014, Mathews et

al. 2016, Downey et al. 2017). Translocation is the process of moving animals from source to release sites for the purposes of reintroducing a locally extinct population or augmenting a remnant population (Griffith 1989).

Translocation has become an increasingly common conservation tool, despite low success rates often accompanied by poor monitoring (Seddon et al. 2014). Obtaining vital rate estimates that encompass the full life cycle of founding individuals and their offspring is critical to a comprehensive assessment of translocation success (Servanty et al. 2014). Furthermore, understanding how an extrinsic factor, such as seasonal weather, regulates vital rates is crucial because nascent populations are particularly vulnerable (Fischer and Lindenmayer 2000).

Weather is uncontrollable, but translocation protocols and management activities can be adapted to mitigate effects of weather (Heffelfinger et al. 1999, Flanders-Wanner et al. 2004).

Information collected year-round and for multiple years is needed to evaluate seasonal weather effects, yet most studies are limited to breeding season survival of translocated individuals in the short-term (i.e., 1st year) and do not evaluate the subsequent larger population of residents and descendants (Downey et al. 2017, Gruber-Hadden et al. 2016, Ruzicka et al. 2017).

I studied a population of Arizona scaled quail (*Callipepla squamata pallida*; hereafter scaled quail), a gallinaceous grassland bird native to the Southern Great Plains, augmented via translocation. My goal was to understand the influence of drought, seasonality, and demographic categories on long-term survival. Scaled quail populations declined sharply since the 1980s, particularly in the Rolling Plains ecoregion of Texas (Gould 1975, Peterson 2001, Sauer et al. 2017). Brush encroachment and spatial aggregation of cropland in the Rolling Plains ecoregion are contributing factors (Rho et al. 2015). Brush encroachment reduces the quality of habitats,

while large tracts of cropland further isolate habitat fragments (Guthery et al. 2001, Rho et al. 2015). Translocation is gaining popularity with state wildlife agencies to re-establish scaled quail in isolated fragments, yet little is known concerning the effects of weather or non-breeding season demographics (Silvy et al. 2007, Zornes and Bishop 2009).

Several studies have found evidence for an influence of weather on scaled quail population dynamics, specifically adequate spring-summer precipitation and moderate temperatures which are favorable for reproduction (Campbell et al. 1973, Leyva-Espinosa 2000, Bridges et al. 2001, Silvy et al. 2007). However, scaled quail abundance has been less closely linked to drought conditions than a sympatric quail species, northern bobwhite (*Colinus virginianus*; Lusk et al. 2007). Northern bobwhite survival and reproduction are negatively correlated with strength of drought conditions (Hernández et al. 2005, Tri et al. 2016). Scaled quail are thought to be more drought resistant than northern bobwhites because of the aridity of their native range (Schemnitz 1964, Giuliano et al. 1999, Silvy et al. 2007). Yet, several studies anecdotally attribute annual variation in survival to an increase in vegetative cover due to precipitation (Lerich 2002, Pleasant et al. 2006). These conflicting conclusions call for an empirical evaluation of scaled quail survival in relation to weather fluctuations.

Scaled quail survival outside of breeding season is largely unknown. Campbell et al. (1973) reported annual, but not seasonal, estimates of survival. Other studies reporting scaled quail survival have only focused on breeding season (Pleasant et al. 2006, Rollins et al. 2009, Gonzalez 2015, Ruzicka et al. 2017). Northern bobwhites often experience lower survival during non-breeding season due to increased predation that occurs during raptor migration (Terhune et al. 2007). Scaled quail are vulnerable to raptor predation as well and may exhibit a similar

decrease during non-breeding season (Rollins and Carroll 2001, Rollins et al. 2009). Reduced cover and food resources are two mechanisms by which drought can increase vulnerability to predation (Bridges et al. 2001). Thus, the influence of drought on survival may manifest more intensively during periods of peak predator abundance (i.e., non-breeding season). Whereas, studies evaluating abundance, which is driven by reproduction, have concluded that breeding season drought conditions are most influential (Campbell et al. 1973, Leyva-Espinosa 2000, Bridges et al. 2001, Silvy et al. 2007).

Demographic categories are an important source of variation in survival for avian species (Martin 1995). Both age and sex are known to influence survival in quails. Sub-adult quail can be distinguished from adults during their first winter and breeding seasons (Smith and Cain 1984). Northern bobwhite (Terhune et al. 2007) and scaled quail (Campbell et al. 1973, Ruzicka et al. 2017) adults tend to survive at a higher rate than sub-adults during this period. The few studies that evaluated sex effects indicate higher survival in male quail attributed to the cost of reproduction for females (Campbell et al. 1973, Terhune et al. 2007).

Here I use a 6-year capture-recapture dataset to estimate survival in an augmented scaled quail population on an isolated property actively managed for quail. A remnant population of scaled quail was present in the year prior to initiating translocations. My objectives were to evaluate the influence of drought, seasonality (i.e., non-breeding versus breeding season), age, and sex on survival in the context of a translocated population. I hypothesized that drought would have a weak negative effect that was more pronounced during the non-breeding season and that survival during non-breeding season would be lower than during the breeding season. I predicted survival

would be lower in sub-adults versus adults and in females versus males due to costs of reproduction.

METHODS

Study Area

The Rolling Plains Quail Research Ranch (RPQRR) in Fisher County, Texas is a 1900-ha ranch owned by a non-profit organization, the Rolling Plains Quail Research Foundation. RPQRR is dedicated to quail management, ecological research, and outreach. RPQRR historically supported northern bobwhites and scaled quail. RPQRR employs a variety of extensive quail abundance surveys year-round (e.g., call counts, helicopter counts, roadside counts, and trapping). Staff detected only two scaled quail during intensive trapping the year prior to translocation, thus augmentation of the scaled quail population was warranted.

The vegetation and topography were typical of the Rolling Plains ecoregion within clay-loam soil types characterized by gently undulating terrain interspersed with cropland and mesquite (*Prosopis glandulosa*)-dominated grasslands (Rollins 2007). RPQRR soils were comprised of Paducah loam, Miles sandy loam, Latom-Vernon complex, Woodward clay-loam, and Wichita clay loam types (NRCS 2016). Average annual rainfall in Fisher County was 56 cm and snowfall averaged 5 cm annually. RPQRR had a high diversity of grasses, forbs, and shrubs. Dominant grass species were silver bluestem (*Bothriochloa saccharoides*), sideoats grama (*Bouteloua curtipendula*), purple threeawn (*Aristida purpurea*), and Texas wintergrass (*Nasella leucotricha*). Common forb species were western ragweed (*Ambrosia psilostachya*), annual sunflower (*Helianthus annuus*), croton (*Croton* spp.), Illinois bundleflower (*Desmanthus illinoensis*),

basketflower (*Centaurea americana*), and filaree (*Erodium* spp.). Shrub species included mesquite, lotebush (*Ziziphus obtusifolia*), algerita (*Mahonia trifoliata*), catclaw acacia (*Acacia greggii*), catclaw mimosa (*Mimosa pellita*), elbow-bush (*Forestiera pubescens*), littleleaf sumac (*Rhus microphylla*), skunkbush sumac (*R. trilobata*), live oak (*Quercus virginiana*), netleaf hackberry (*Celtis laevigata* var. *reticulata*), and wolfberry (*Lycium barbarum*).

Field Methods

RPQRR staff trapped scaled quail from private properties in the western Edwards Plateau ecoregion during February and March 2013–2014. Staff also translocated individuals from Muleshoe National Wildlife Refuge located in the High Plains ecoregion in March 2014. Translocation efforts were timed such that individuals would be released at the start of breeding season. Staff pre-baited 25–50 locations on each property for two weeks prior to trapping. Scaled quail were trapped using a collapsible walk-in wire funnel trap baited with grain sorghum (*Sorghum bicolor*; Gooden 1953, Ruzicka et al. 2016). Quail were weighed, banded (aluminum size 7 butt-end band; National Band and Tag Co., Newport, KY), and classified by age and sex. Age was determined using primary covert feathers and individuals were classified as either adult (>1 year) or sub-adult (<1 year; Smith and Cain 1984). Scaled quail were transported in plastic gamebird carriers (GQF Manufacturing Company Inc., Savannah, GA) to RPQRR within 24 hours where they were transferred to a holding pen (Surrogator™, Wildlife Management Technologies, Wichita, KS). Quail were held 4 weeks prior to release to minimize dispersal off-site (Ruzicka et al. 2017). Staff conducted fall (November/December) and spring (February/March) trapping from 2013–2019 at RPQRR. The property was trapped at an intensity of 1 trap per 6 ha for 5 days. All quail were held and handled in accordance with the protocol

approved by Texas A&M University Institutional Animal Care and Use Committee (AUP#2009-57).

Weather Variables

I downloaded monthly precipitation and temperature data at a resolution of 20-km² from the PRISM Climate Group for each month from 2013–2019 (<http://prism.oregonstate.edu>, accessed 1 August 2020). I downloaded monthly standardized precipitation evapotranspiration index (SPEI) data at a resolution of 100-km² (<https://spei.csic.es/index.html>, accessed 1 August 2020). SPEI is a temporally and spatially multi-scalar drought index that addresses shortcomings of the self-calibrated Palmer Drought Severity Index (Vicente-Serrano et al. 2010, Wells et al. 2004) . SPEI incorporates data on precipitation, temperature, and potential evapotranspiration (Beguería et al. 2014).

Data Analysis

I used a Cormack-Jolly-Seber (CJS) model implemented in Program MARK to evaluate the influence of drought, season, age, and sex on apparent survival (hereafter survival; φ) of banded scaled quail. I evaluated capture probability (p) on season, age, sex, and average temperature. Temperature and season of trapping influence p for northern bobwhites (Ruzicka et al. 2016). I averaged temperature over each 5-day trapping occasion. I defined breeding season as the period between 1 March and 31 October trapping (8 months) and non-breeding season as the period between 1 November and 28 February (4 months). Because the intervals between trapping occasions were uneven, I rescaled time intervals in Program MARK so that estimates of φ would be per month and comparable between seasons. I averaged SPEI to describe the intensity of

drought conditions during seasonal intervals. I used an all possible combinations approach to model selection, whereby I ran all additive combinations of variables in the global model (256 models; Doherty et al. 2012). I then calculated cumulative AIC_c weight for each variable and interpreted a final predictive model that included every variable with cumulative weight >0.5 (Barbieri and Berger 2004). I derived estimates of annual survival by multiplying breeding and non-breeding season estimates for comparison to other studies. I obtained an estimate of average annual survival (ϕ^{12}) from the null model. Standard error was calculated using the Delta method (Powell 2007).

RESULTS

RPQRR staff translocated 14 scaled quail (7 male, 7 female) in 2013 and 74 (38 male, 36 female) in 2014. The sub-adult to adult ratio of translocated individuals was 3:1. Staff captured 822 non-translocated individuals and recaptured 30 translocated individuals from November 2013–November 2019. Non-translocated individuals could have been from an undetected remnant population, immigrants, or descendants of translocated birds. Most resident scaled quail were first captured as sub-adults (n = 596). More resident males (n = 465) were captured than resident females (n = 357). The final predictive model based on cumulative weights >0.5 was ϕ (drought + season + age + sex) p (season + age + sex + temp) (Table 1.1–1.2).

Average annual survival was 0.28 (SE = 0.02). However, survival varied greatly as a function of the variables I evaluated. I found a strong negative effect of drought on ϕ ($\beta = 2.21$, SE = 0.26; Table 1.3, Figure 1.1). Monthly SPEI ranged from severe drought (-2) to very wet (1.7), while seasonally averaged values varied from -0.86 to 0.55. I found strong effects of season ($\beta = -2.49$, SE = 0.92) and moderate effects of age ($\beta = -0.60$, SE = 0.20) and sex ($\beta = 0.33$, SE = 0.18;

Figure 1.2). Monthly survival varied from 0.98 (SE = 0.01) to 0.74 (SE = 0.03). Annual survival ranged from 0.03 (SE = 0.01) to 0.71 (SE = 0.02) for adults and 0.11 (SE = 0.04) to 0.83 (SE = 0.04) for sub-adults. Survival was highest during breeding season, for sub-adults, and for males. Monthly survival for an adult female during non-breeding season was 0.75 (SE = 0.06) compared to 0.95 (SE = 0.02) for a sub-adult male during breeding season (Table 1.4). Season ($\beta = -1.06$, SE = 0.20), sex ($\beta = 0.56$, SE = 0.23), and temperature ($\beta = -0.09$, SE = 0.04) influenced capture probability (Figure 1.3). Capture probabilities were highest during fall capture, for males, and when temperatures were cooler.

DISCUSSION

This study is the most comprehensive analysis of scaled quail survival in the Southern Great Plains since Campbell et al. (1973) and the longest survival study of a translocated scaled quail population (Ruzicka et al. 2017, Yancey 2019). Survival varied greatly over 6 years and was influenced by drought, season, age, and sex. I found a negative effect of drought on survival largely due to the response during two years — one with severe drought and one with very wet conditions. Both years produced estimates of annual survival that were outside the range of survival reported in the limited literature for resident scaled quail (0.10–0.64; Campbell et al. 1978, Rollins et al. 2009). Survival of adult scaled quail (0.03) under severest drought conditions was lower than previously reported estimates, while sub-adult survival was comparable (0.11). Only Ruzicka et al. (2017) reported estimates of breeding season survival in a failed translocation effort that were as low or lower (0.00–0.33). However, a <10-year study on a stable northern bobwhite population in the Southeastern United States observed annual survival rates as low as 0.05 (SE = 0.03; Pollock et al. 1989). Conversely, survival in the wettest conditions for

both adults (0.71) and sub-adults (0.83) were the highest observed rates of annual survival for scaled quail. I am not aware of higher survival rates for northern bobwhites. My results are contradictory to the literature suggesting that scaled quail are insensitive to drought (Schemnitz 1964, Giuliano et al. 1999), but support conclusions that variation in survival between years was a result of precipitation (Lerich 2002, Pleasant et al. 2006).

I note that estimates reported here are apparent survival and do not separate true mortality from the probability that an individual dispersed off site. Most estimates of scaled quail survival in the literature derive from radio-telemetry studies where true survival was estimated. This difference should be kept in mind when making comparisons as my survival estimates would likely be lower as compared to estimates derived from telemetry data. Campbell et al. (1973) reported apparent survival and, consequently, their estimates of annual survival are some of the lowest reported prior to this study. The authors also reported unpredictable mass dispersal events in 2 of the 6 years of their study. I did not observe mass dispersal off the study area in a sample radio-marked for a different study and do not think dispersal was likely given the isolation of the population. However, I cannot rule out the possibility that the low apparent survival I observed was in part due to dispersal. Regardless, population impacts in an isolated habitat are equivalent whether the loss is due to mortality or dispersal.

I found that monthly non-breeding season survival was lower than breeding season survival. Similar survival differences between breeding and non-breeding season survival occur in northern bobwhite populations (Terhune et al. 2007). Raptors are common quail predators and the temporary spike in raptor abundance during their annual migration in the southern U.S. may explain seasonal increase in quail mortality (Rollins and Carroll 2001, Turner et al. 2014).

Both age and sex influenced survival. Sub-adult scaled quail exhibited higher survival than adults. Many studies have found higher survival in adults versus sub-adults for scaled quail (Campbell et al. 1973, Ruzicka et al. 2017) and northern bobwhites (Terhune et al. 2007, Downey et al. 2017) or no difference between age classes (Pollock et al. 1989, Burger et al. 1995, Pleasant et al. 2006, Terhune et al. 2010). Life history theory predicts that fast lived species with short life expectancies should exhibit lower sub-adult survival relative to adults or, at least, equal survival among age classes (Charnov 1986, Martin 1995). Thus, my results are anomalous. One explanatory factor may be high parasite occurrence in the Rolling Plains ecoregion relative to other regions (Olsen 2014, Dunham et al. 2016). Quail parasite surveys on the study area found high prevalence and intensity of pathogenic parasites that increased with quail age (Bruno et al. 2015, Villarreal et al. 2016). Despite parasite pathogenicity, no studies have yet linked quail survival to parasite infection (Olsen et al. 2016). Parasites do negatively impact survival and reproduction in other gallinaceous bird species (Cattadori et al. 2005).

I observed higher survival in males compared to females. Campbell et al. (1973) reported higher survival in scaled quail males as have several studies on northern bobwhites (Pollock et al. 1989, Terhune et al. 2007). Previous studies have reported an increase in hen mortality that corresponded with the start of nesting season (Lerich 2002, Pleasant et al. 2006, Gonzalez 2015). Although both males and females share brood tending duties, lower female survival is likely due to the female investment in laying eggs and vulnerability in incubating a clutch (Martin 1995).

Average annual survival (0.28) was slightly higher than estimates of survival in stable populations of scaled quail (0.17–0.22; Campbell et al. 1973) and northern bobwhites (0.13–0.21; Pollock 1989). My findings provide evidence that translocated populations, despite being

small and isolated, can benefit if weather conditions are favorable at the outset of reintroduction or augmentation and can persist despite drought conditions. Although my results are limited to a single population, the strength of the relationship between drought and survival is concerning given that climate change is projected to increase the frequency of drought years. Scaled quail are predicted to lose a significant portion of their range due to climate change in the next 30 years (Tanner et al. 2017). This loss will occur in areas where abundances are currently highest and habitats most connected (Tanner et al. 2017).

Additional habitat loss and greater drought frequency will place greater importance on population restoration tools such as translocation and successful mitigation of drought impacts in small populations. My findings highlight the need for year-round survival estimates to inform effective conservation decisions. Low survival during non-breeding season may represent a previously unaddressed weak link for scaled quail populations. Future research should emphasize questions concerning non-breeding season survival, specifically factors that influence it and management strategies to bolster it.

Table 1.1. Model set evaluating the influence of drought, season, age, and sex on apparent survival (ϕ) and the influence of season, age, sex, and temperature (temp) on capture probability (p) of scaled quail (*Callipepla squamata*) in Fisher County, Texas, USA, 2013–2019. All possible combinations of the variables were included in the model set (256 models). Only models with Akaike’s corrected information criterion (AIC_c) weight >0.00 and the null model are shown.

Models	AIC _c	ΔAIC _c	AIC _c Weight	Model Likelihood	k ¹	Deviance
$\phi(\text{drought} + \text{season} + \text{age} + \text{sex}) \text{ p}(\text{season} + \text{sex} + \text{temp})$	1814.21	0.00	0.28	1.00	9	1796.06
$\phi(\text{drought} + \text{season} + \text{age}) \text{ p}(\text{season} + \text{sex} + \text{temp})$	1815.27	1.06	0.16	0.59	8	1799.15
$\phi(\text{drought} + \text{season} + \text{age} + \text{sex}) \text{ p}(\text{season} + \text{age} + \text{sex} + \text{temp})$	1815.28	1.07	0.16	0.59	10	1795.08
$\phi(\text{drought} + \text{season} + \text{age}) \text{ p}(\text{season} + \text{age} + \text{sex} + \text{temp})$	1815.73	1.51	0.13	0.47	9	1797.57
$\phi(\text{drought} + \text{season} + \text{age} + \text{sex}) \text{ p}(\text{season} + \text{sex})$	1817.46	3.24	0.05	0.20	8	1801.33
$\phi(\text{drought} + \text{season} + \text{age} + \text{sex}) \text{ p}(\text{season} + \text{age} + \text{sex})$	1817.87	3.65	0.04	0.16	9	1799.71
$\phi(\text{drought} + \text{season} + \text{age} + \text{sex}) \text{ p}(\text{season} + \text{temp})$	1818.24	4.03	0.04	0.13	8	1802.12
$\phi(\text{drought} + \text{season} + \text{age}) \text{ p}(\text{season} + \text{age} + \text{sex})$	1818.37	4.15	0.03	0.13	8	1802.24
$\phi(\text{drought} + \text{season} + \text{age}) \text{ p}(\text{season} + \text{sex})$	1818.70	4.49	0.03	0.11	7	1804.60
$\phi(\text{drought} + \text{season} + \text{age} + \text{sex}) \text{ p}(\text{season} + \text{age} + \text{temp})$	1819.79	5.58	0.02	0.06	9	1801.64
$\phi(\text{drought} + \text{season}) \text{ p}(\text{season} + \text{age} + \text{sex} + \text{temp})$	1820.92	6.71	0.01	0.03	8	1804.80
$\phi(\text{drought} + \text{season} + \text{age} + \text{sex}) \text{ p}(\text{season})$	1821.17	6.96	0.01	0.03	7	1807.07
$\phi(\text{drought} + \text{season} + \text{age}) \text{ p}(\text{season} + \text{age} + \text{sex} + \text{temp})$	1821.27	7.05	0.01	0.03	9	1803.11
$\phi(\text{drought} + \text{season} + \text{age} + \text{sex}) \text{ p}(\text{season} + \text{sex} + \text{temp})$	1822.18	7.96	0.01	0.02	9	1806.05
$\phi(.) \text{ p}(.)$	1924.58	110.36	0	0	2	1920.57

¹Number of parameters

Table 1.2. Akaike’s corrected information criterion (AIC_c) cumulative variable weights from a candidate model set (256 models) that included all possible combinations of the global model evaluating the influence of drought, season, age, and sex on apparent survival (ϕ) and the influence of season, age, sex, and temperature (temp) on capture probability (p) of scaled quail (*Callipepla squamata*) in Fisher County, Texas, USA, 2013–2019.

Parameter	Weight
$\phi(\text{drought})$	1.00
$\phi(\text{season})$	1.00
$\phi(\text{age})$	0.97
$\phi(\text{sex})$	0.63
$p(\text{season})$	1.00
$p(\text{age})$	0.42
$p(\text{sex})$	0.93
$p(\text{temp})$	0.81

Table 1.3. Variable beta (β) values with associated standard errors (SE), 95% lower (LCI) and upper (UCI) confidence interval of apparent survival (ϕ) and capture probability (p) of scaled quail (*Callipepla squamata*) in Fisher County, Texas, USA, 2013–2019.

Parameter	β	SE	LCI	UCI
ϕ (drought)	2.21	0.26	1.70	2.72
ϕ (season)	2.49	0.92	-4.29	-0.68
ϕ (age)	-0.60	0.20	-0.99	-0.21
ϕ (sex)	0.33	0.18	-0.03	0.68
p(season)	-1.06	0.18	-1.41	-0.71
p(sex)	0.56	0.23	0.12	1.01
p(temp)	-0.09	0.04	-0.16	-0.01

Table 1.4. Estimates of monthly apparent survival (ϕ) with associated standard errors (SE), 95% lower (LCI) and upper (UCI) confidence interval limits of scaled quail (*Callipepla squamata*) in Fisher County, Texas, USA, 2013–2019. Breeding season was defined as 1 March–31 October and non-breeding season was 1 November–28 February.

Season	Age	Sex	Estimate	SE	LCI	UCI
Breeding	Adult	Female	0.88	0.04	0.79	0.93
		Male	0.91	0.02	0.86	0.95
	Sub-adult	Female	0.93	0.04	0.81	0.97
		Male	0.95	0.02	0.87	0.98
Non-breeding	Adult	Female	0.75	0.06	0.61	0.85
		Male	0.81	0.05	0.69	0.90
	Sub-adult	Female	0.84	0.03	0.77	0.88
		Male	0.88	0.02	0.84	0.92

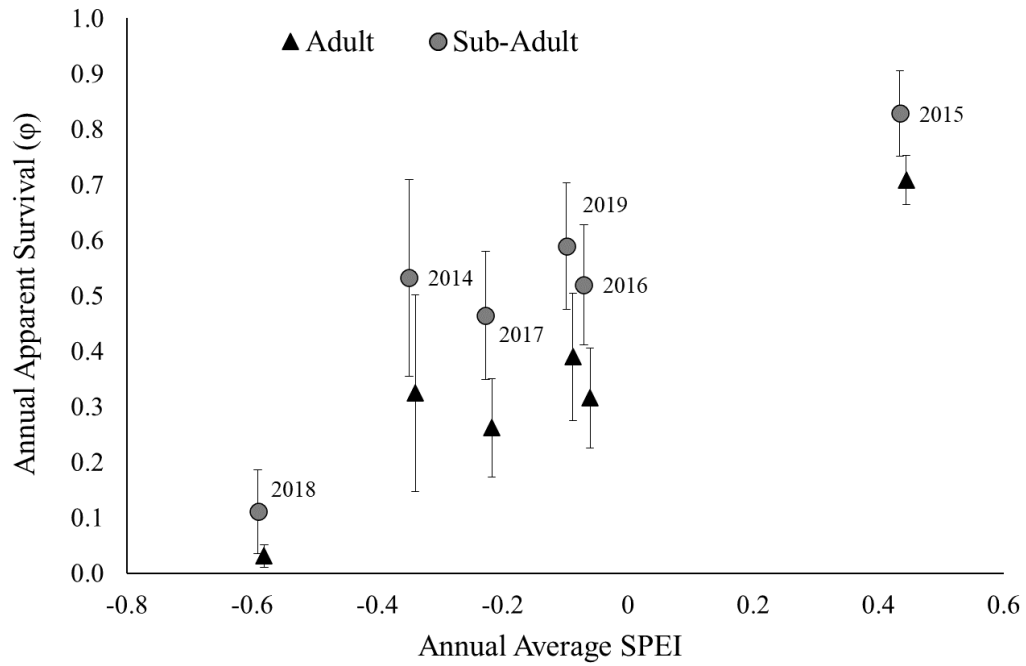


Figure 1.1. The relationship between annual apparent survival (ϕ) of scaled quail (*Callipepla squamata*) and annual average standardized precipitation evapotranspiration index (SPEI) in Fisher County, Texas, USA, 2013–2019.

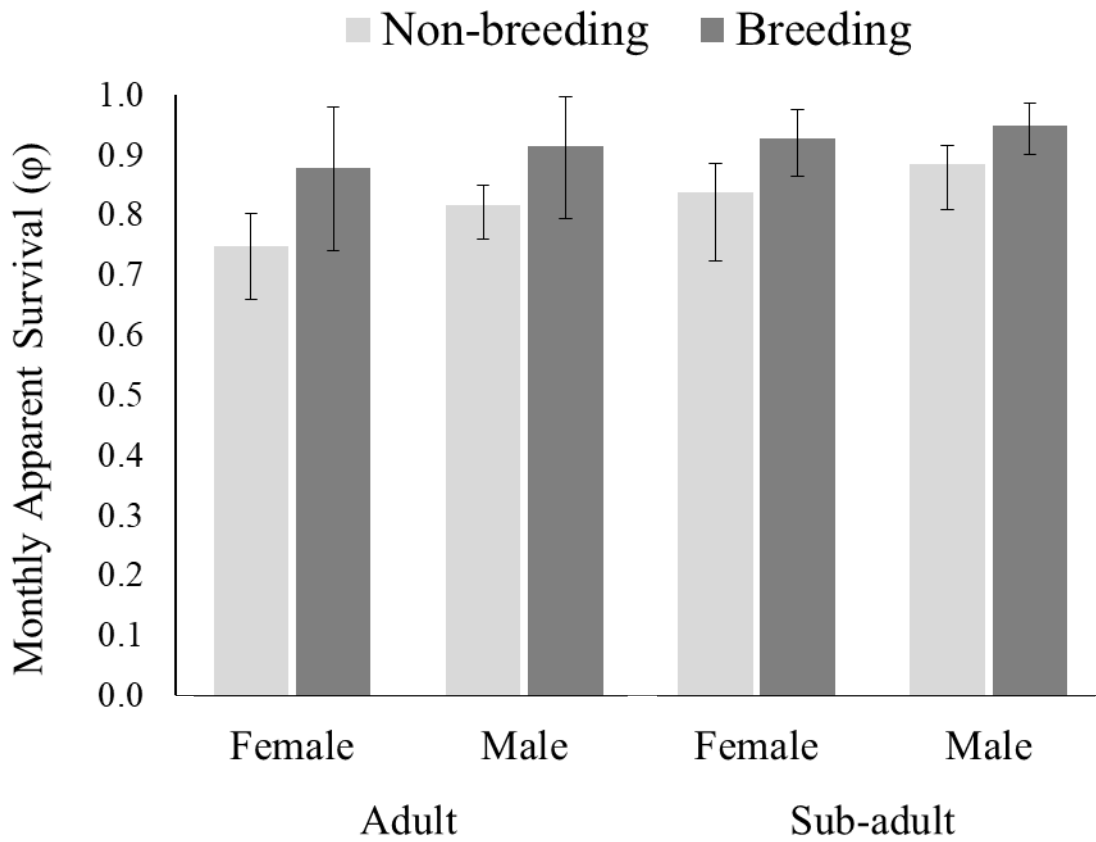


Figure 1.2. Monthly apparent survival (ϕ) of scaled quail (*Callipepla squamata*) in Fisher County, Texas, USA, 2013–2019. Breeding season was defined as 1 March–31 October and non-breeding season was 1 November–28 February.

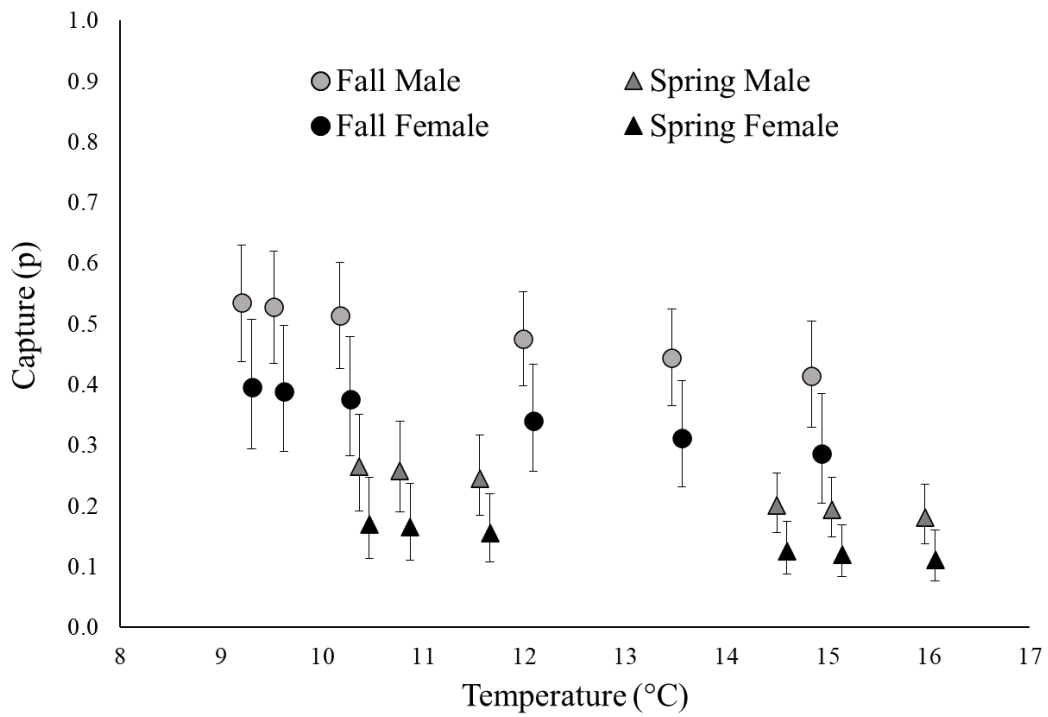


Figure 1.3. Capture probability (p) of scaled quail (*Callipepla squamata*) in Fisher County, Texas, USA, 2013–2019. Fall trapping occurred November–December. Spring trapping occurred February–March.

CHAPTER 2. LONGER HOLDING TIMES DECREASE DISPERSAL BUT INCREASE MORTALITY OF TRANSLOCATED SCALED QUAIL

Scaled quail (*Callipepla squamata*) decline caused by habitat loss and fragmentation has increased interest in translocation to reestablish populations. Yet factors determining translocation success are poorly understood. I tested hypotheses concerning the influence of source population and variation in delayed release strategy (1–9 weeks) on mortality and dispersal of wild-caught, translocated scaled quail. I trapped and translocated quail over 2 years (2016–2017) from source populations in the Edwards Plateau and Rolling Plains ecoregions to a large contiguous (>40,000 ha) release site in Knox County, Texas. I evaluated mortality and dispersal of translocated females as a function of source population, holding time prior to release, age, release location, and year using a multi-state mark-recapture model with state uncertainty. I found that scaled quail translocated within the Rolling Plains were more likely to exhibit philopatry to the release site. Quail with longer holding times had higher mortality, but lower dispersal rates. The Edwards Plateau is a suitable source site for translocation in the Rolling Plains. The reduced dispersal but higher mortality of translocated scaled quail associated with longer holding times creates a decision tradeoff for managers.

INTRODUCTION

The Anthropocene is characterized by an increasing number of species needing conservation (Scott et al. 2010) and managers need a wide range of tools. Translocating individuals to reintroduce populations, reinforce remnant populations, or establish populations in new areas is a common, yet intensive and expensive management action (Converse et al. 2013, Seddon et al.

2014, Armstrong et al. 2015). Translocation is the physical process of moving animals from source to release site(s) and can be critical for populations that lack the ability to rebound through natural processes (IUCN/SSC 2013). For example, inverse density dependence, or Allee effects, can manifest in small, isolated populations. Under inverse density dependence demographic rates decline as abundance declines (Dennis 1989). Mechanistically, demographic rates may decline due to the inability of animals to find mates, genetic inbreeding, or less effective group defenses. Remnant populations can disappear without an influx of new individuals. Thus, translocation can be essential where barriers to natural immigration exist (Houde et al. 2015).

Translocation success is typically defined as the establishment of a self-sustaining population (Griffith 1989). Across taxa, translocations are more successful when the species is native, wild-caught, an early breeder with large clutch or litter size, and released in high quality habitat (Griffith 1989). Taxa characteristics address which species are the best candidates for translocation, but questions remain about protocols to best translocate those species (Armstrong and Seddon 2008). Despite an increase in translocation studies, overall success rates remain low prompting a push toward a unification of protocols to increase the probability of success (Fischer and Lindenmayer 2000, Seddon et al. 2007).

Grassland birds are the most imperiled of North American birds and, as such, have been the focus of numerous translocation efforts (Snyder et al. 1999, Rosenberg et al. 2019). Scaled quail (*Callipepla squamata*) are a declining grassland species native to the southern Great Plains and are the species I focus on here. Loss of grass-dominated rangelands to croplands have fragmented quail habitat and prevented effective recolonization (Rho et al. 2015). Scaled quail

are capable of dispersing long distances (Campbell and Harris 1965), but costs of dispersal are high in fragmented habitat (Clobert et al. 2001, Bonte et al. 2012). Additionally, the loss of the irruptive population growth that is characteristic of healthy quail populations indicates that populations are below minimum thresholds where inverse density dependence may manifest (Dennis 2002, Lusk et al. 2007, Silvy et al. 2007). Even weak inverse density dependence can impact populations of species with highly variable vital rates, such as a quail (Dennis et al. 2016).

Populations of several quail species have been re-established using translocation. Northern bobwhites (*Colinus virginianus*) translocated in the mesic southeastern U.S. survived and reproduced similarly to residents, ultimately demonstrating population increase (Terhune et al. 2006). Translocation outcomes in more xeric environments are varied. Scott et al. (2013) found lower survival of translocated northern bobwhite compared to a non-translocated population. Downey (2017) observed moderate survival and reproductive effort but was unable to document a population-level effect. Translocations of mountain quail (*Oreortyx pictus*) resulted in similar ambiguity (Pope and Crawford 2004, Stephenson et al. 2011). Translocation of quail is effective in some circumstances, but factors influencing success are still unclear and likely to vary among species and locations. Two such factors are source population and release strategy.

Selecting a source population from habitat like release sites is beneficial (Houde et al. 2015). Pre-release experiences may convey survival advantages in a new environment if source and release sites are similar (Frair et al. 2007, Troy et al. 2013). Individuals are often translocated from multiple sources to a single release site, yet few studies have compared vital rates of individuals between source populations (Troy et al. 2013). The Rolling Plains and Edwards

Plateau ecoregions represent 2 distinct populations of Arizona scaled quail (*Callipepla squamata pallida*) in Texas (Baccus and Eiteneer 2007, Rollins 2007). Populations are declining in the Rolling Plains while Edwards Plateau populations are stable or increasing despite being in proximity (Sauer et al. 2017). As such, the Edwards Plateau is a desirable source for translocations to the Rolling Plains, however translocating a non-native sub-species and/or individuals from outside the ecoregion may result in low survivability. Liu et al. (2000) observed lower survival for northern bobwhites translocated from the South Texas Plains ecoregion to the Piney Woods ecoregion compared to individuals translocated within the Piney Woods. Chestnut-bellied scaled quail (*Callipepla squamata castanogastris*) from the South Texas Plains ecoregion are not a suitable source for reestablishing populations in the Rolling Plains ecoregion due to high dispersal, low survival, and inherent differences in habitat preference between subspecies (Yancey 2019). The Edwards Plateau could provide a stable source of the native subspecies with lower financial and logistical costs.

Release strategies can be categorized broadly as immediate or delayed release, but many specific techniques exist in addition to length of holding time (Moseby et al. 2014, Batson et al. 2015a), including supplemental feeding and holding location (i.e., on or off site). Past translocations of northern bobwhite have used both immediate (Terhune et al. 2005, Downey 2015) and delayed release ranging from 48 hours to 4 months (Stephenson et al. 2011, Scott et al. 2013). A 4-week delayed release of scaled quail resulted in higher apparent survival compared to an immediately release group (Ruzicka et al. 2017). Acevedo et al. (2023) found that holding Gambel's quail (*Callipepla gambelii*) prior to release reduced losses. Quails may benefit from a delayed release for several reasons. Social species with small home ranges benefit from delayed release because site fidelity is increased by building social relationships and reducing homing instincts to source

areas (Moseby et al. 2014) and several studies identified the need to release quail in groups to promote these social relationships (Scott et al. 2013, Downey et al. 2017). A delayed release is logistically more feasible for group releases because capturing wild quails is time and labor intensive, particularly when multiple source sites are used. The delayed release strategy allows flexibility for handling and forming groups. Testing translocation techniques for an individual species is critical because best practices for translocation are species specific (Wolf et al. 1998, Moseby et al. 2014).

My objective was to test hypotheses concerning mortality and dispersal of translocated, wild-caught scaled quail as a function of source ecoregion and a delayed release treatment in the Rolling Plains of Texas. Specifically, I compared quail sourced from within the Rolling Plains and from the Edwards Plateau, as well as a 1–9 week delayed release treatment that varied by 1 week intervals. I hypothesized that individuals translocated from within the same ecoregion would outperform individuals from outside the ecoregion and that longer delayed release holding times would reduce dispersal post-release.

METHODS

Study Area

The release area was made up of 5 privately owned ranches in the South Wichita River Basin in the Rolling Plains ecoregion and Knox County, Texas, USA (Figure 2.1). The area encompassed >40,000 ha of contiguous rangeland. Two ranches (designated as ranch 1 and 2 to protect anonymity of the owners) were my primary cooperators and exclusive release sites. These ranches were 16,000 and 7,200 ha, respectively. Both sites were managed similarly for cattle and

wildlife. Habitat management included the use of chaining and prescribed burns to reduce redberry juniper (*Juniperus pinchotii*) density and grazing to promote native bunchgrasses. Both ranches extensively restored native grasslands prior to this study. Ranch 1 was leased for private hunting of deer and turkey, while ranch 2 was reserved for landowner hunting. Both ranches maintained deer feeders, but not quail feeders and engaged in feral hog population control primarily through aerial gunning or trapping. Hunting for scaled quail had not occurred on either site within 10 years prior to the beginning of the study owing to low quail abundance and did not occur during this study (2016–2017). Scaled quail were common to abundant in Knox County prior to ~ 1988 (Rollins 2007).

The larger monitoring area contained 3 distinct cover types delineated by elevation and soils: upland, badlands, and river bottom. The upland composed approximately 30% of the release area and was typical of gently rolling red prairie within the Rolling Plains (Griffith et al. 2007). Primary soils were Tillman and Wichita clay-loams (NRCS 2016) and elevation was approximately 485–500 m above sea level. Most of the upland was converted to croplands (wheat and cotton), but rangelands existed with a diversity of grasses and shrubs, including little bluestem (*Schizachyrium scoparium*), Texas wintergrass (*Stipa leucotricha*), sideoats grama (*Bouteloua curtipendula*), purple threeawn (*Aristida purpurea*), redberry juniper, honey mesquite (*Prosopis glandulosa*), netleaf hackberry (*Celtis laevigata*), western soapberry (*Sapindus saponaria*), and lotebush (*Ziziphus obtusifolia*). Badlands occurred from 485–425 m in elevation and consisted of 90% Knoco-Badland complex soil series (NRCS 2016). Badlands composed approximately 60% of the release area. This habitat was characterized by a high percentage of bare ground and steep slopes with sparse grasses and intermixed shrubs. Common species included blue grama (*B. gracilis*), buffalo grass (*Bouteloua dactyloides*), tobosa grass

(*Pleuraphis mutica*), ephedra (*Ephedra spp.*), redberry juniper, honey mesquite, lotebush, algerita (*Mahonia trifoliolata*), tasajillo (*Cylindropuntia leptocaulis*), and prickly pear (*Opuntia spp.*). River bottom elevation ranged from 425–415 m, composed approximately 10% of the release area, and consisted of Mangum and Vernon clays that supported a mosaic of honey mesquite and saltgrass (*Distichlis spicata*) monocultures and ephemeral wetlands. Other species included invasive saltcedar (*Tamarix spp.*), pecan, elm, cottonwoods, hackberry, and big bluestem. Average precipitation and snowfall in Knox County were 58 cm and 12 cm, respectively.

I sourced wild scaled quail from 8 private ranches with stable quail populations in the western Edwards Plateau and Rolling Plains ecoregions. These ranches were managed for wildlife and/or cattle grazing. The western Edwards Plateau is a transition zone between live oak (*Quercus virginiana*) savannas and desert ranging in elevation between 30 and 900 m (Griffith et al. 2007). The terrain was characterized by flat to gently rolling plateaus and rocky, calciferous soils. Dominant soil series included Ector gravelly loam, Kavett silty clay, and Tarrant cobbly clay. Average rainfall is 40–55 cm and snowfall events are rare. Rolling Plains source ranches were similar in plant species composition and soils to the upland habitat on the release site.

Field Methods

I trapped quail on source sites during February and March 2016–2017. My goal was to translocate 400 individuals per year (200 from each ecoregion). Limits on the number of quail translocated from each source property were designated by the landowners and ranged from 25–100 individuals per property. I used standard walk-in wire funnel traps baited with grain sorghum (*Sorghum bicolor*) to capture quail (Gooden 1953, Ruzicka et al. 2016). Trap sites were pre-

baited 2–4 weeks prior to trapping on each property. I held groups of 15–20 quail in plastic gamebird carriers (GQF Manufacturing Company Inc., Savannah, GA) covered with a black sheet to reduce stress and stocked with food and water. Quail were weighed, banded (aluminum size 7 butt-end band; National Band and Tag Co., Newport, KY), and classified by age and sex. Five to 6 females >150 g were selected from each group to be fitted with a 6 g necklace style radio-transmitter (American Wildlife Enterprises, Monticello, FL) or approximately 50% of the released females. I fitted radios to only females for 2 reasons: 1) these data were also intended to model reproduction for Chapter 3 and 2) males and females pair-up for breeding, thus collaring both males and females would not result in independent samples. Transmitters emitted both live and mortality signals. Collar life span was a maximum of 7-9 months. The collar transmission range was approximately 1 km, however there was a high degree of variation in the distance collars could transmit based on the conditions on the ground. No movement for 12 hours triggered a mortality signal. Quail were transported to release sites within 48 hours of capture.

I designated 1 release point on each primary cooperating ranch. Each quail group was assigned randomly to be released on either ranch 1 or 2. Upon arrival, the group was introduced to a holding pen on site (Surrogator™, Wildlife Management Technologies, Wichita, KS). The holding pens were placed approximately 200 m apart (i.e., within hearing distance, but not within sight of each other). I stocked the holding pens with 22.6 kg of a mixture of grain sorghum and a commercially available poultry layer ration. Groups were held for their assigned delayed release treatment and the delay varied by one-week intervals from 4–8 weeks in 2016 and 1–9 weeks in 2017. I replicated the delayed release treatments for each source population and on each release site such that there were 20 treatment groups (10 per site) in 2016 and 36 treatment groups (18 per site) in 2017.

I released groups together in late morning by standing behind the holding pens to open the large gate. I used this method so that the group could flush together, like a wild free covey reacting to a threat. I coordinated trapping efforts so that all treatment groups could be released over a 10–15-day period in April despite holding times that varied by as much as 8 weeks. Thus, I standardized on a similar release date at the cost of having holding times for groups being correlated with capture date (e.g., long holding times could not be assigned to late-captured coveys). Delayed release treatments were duplicated at each release point and for each source ecoregion.

I monitored mortality status (i.e., whether the quail was alive or dead) of radio-marked quail daily during breeding season (10 Apr–15 Aug; 131 days). I obtained 2 types of observations: 1) mortality status and location were both known, and 2) only mortality status was known. The latter observations resulted when I was able to detect a signal from a high point but did not obtain an accurate location. I homed in on and then circled each quail approximately 3 times per week to obtain accurate location information, although the number of locations recorded varied due to weather conditions, site access, and distance dispersed. I kept at least 30 m away from hens to avoid disturbing any nesting activity or pushing hens to new locations. When birds were moving in response to researcher monitoring, I made larger arcs (100–250 m) around their location. I recorded locations in UTM coordinates using a handheld GPS unit (Garmin International Inc., Olathe, KS).

Data Analysis

I treated dispersal as a binary factor by designating whether an individual was inside or outside of its respective core release area. Core release areas were defined by a 2-km buffer surrounding

both release points. My choice of the 2 km distance to assess dispersal was based on 2 factors: 1) previous studies classified quail that travelled >2 km straight line distance within a single season as dispersers (Townsend et al. 2003, Downey et al. 2017) and 2) this 2-km buffer creates an area (1,300 ha) approximately equal to the preferred habitat size for initiating a translocation (1,400 ha) as defined by Texas Parks and Wildlife Department (Connolly et al. 2008). Thus, my core release area definition has direct management implications.

I used a multi-state mark-recapture model with state uncertainty (MSMR-SU) to evaluate the effects of source ecoregion and release strategy because it provided the flexibility to model daily mortality and dispersal probabilities simultaneously (Kendall et al. 2003, Pradel 2005, Conn and Cooch 2009, Kendall et al. 2012). Individuals must be alive to disperse; therefore, combining these 2 parameters into a single model where the probability of an individual dispersing is conditional on it being alive reduces potential biases in dispersal found in other studies (Townsend et al. 2003, Downey et al. 2017). The MSMR-SU also provided a framework for incorporating observations of individuals that were alive but without an exact location (e.g., dispersal status was unknown). Including additional mortality information improves estimate precision (Kendall et al. 2012).

I considered individuals to be in 1 of 4 true states (Figure 2.2): A) alive and inside their respective core area, B) alive and outside their respective core area, C) dead inside, or D) dead outside (Devineau et al. 2010). Individuals could be observed in any of the 4 true states or 1 unknown event (u). I classified an individual as unknown when I knew the individual was alive, but its location was uncertain (i.e., true state was either A or B). I assumed that dead states (C and D) were observed reliably. The general MSMR-SU models allow for the estimation of 4

types of parameters: detection in each true state (p), survival in each true state (S), transition probabilities between true states (Ψ), and the probability of being classified as unknown given true state (δ) (Kendall et al. 2012). In my application, I fixed 2 of these parameters; I assumed $p = 1$ for all states because all animals used in this analysis were radio-marked. Additionally, I modeled mortality inside (Ψ_{AC}) and outside the core area (Ψ_{BD}) explicitly through transition parameters, thus the survival parameters were redundant, and I fixed survival to 1 for all live states (A, B) and 0 for all dead states (C, D). I constrained all transitions out of dead states to zero, so that once an individual was discovered dead it could not be resurrected. I modeled dispersal as the probability of an individual leaving the core area (Ψ_{AB}) independently from the probability that an individual returned (Ψ_{BA}). Probabilities of individuals surviving and staying inside or outside the release area (Ψ_{AA} and Ψ_{BB}) were obtained through subtraction. I encountered issues with model convergence when I modeled the probability of transitioning from alive inside to dead outside (Ψ_{AD}) and alive outside to dead inside (Ψ_{BC}), thus I fixed those parameters to zero. Ψ_{AD} was then defined as $\Psi_{AB} \times \Psi_{BD}$ and likewise, $\Psi_{BC} = \Psi_{BA} \times \Psi_{AC}$. This model was implemented using the Hidden Markov Model module of Program MARK (White and Burnham 2009).

I evaluated the influence of source population (source), release treatment (release), age of individual (either adult or sub-adult; age), release ranch (ranch), and year (year) for each transition parameter. I also included a time trend (trend) variable or time since release for parameters Ψ_{AB} and Ψ_{AC} to allow for a linear increase or decrease that might occur in mortality and dispersal over time. I considered a quadratic effect early in the analysis, but again encountered issues with convergence when the squared terms were included in the global model. I used a 2-step, all-plausible combinations approach to model selection with Akaike's

information criterion corrected for small sample size (AIC_C) (Doherty et al. 2012, Bromaghin et al. 2013, Morin et al. 2020). For the first step, I constructed a balanced set of all additive models, including a constant model, for each of the 4 transition parameters (Ψ), while holding all other parameters constant (i.e., 4 separate model sets; Table 2.1–2.4). I considered only additive models because including interactions caused estimation problems. I calculated cumulative variable weights (w_i) for the variables in each model set (Table 2.5). Variable and parameters combinations with cumulative $w_i > 0.5$ were retained for the second step of modeling (Barbieri and Berger 2004). In the second modeling step, I built a balanced model set of all additive combinations of each variable and parameter combination with $w_i > 0.5$. My predictive model contained all variables with cumulative $w_i > 0.5$ from the final model set (Table 2.6). I report beta estimates as well as breeding season (i.e., monitoring period) mortality probabilities and odds ratios where appropriate. I calculated standard errors for breeding season estimates using the Delta method in the *msm* package in R (Jackson 2011, www.r-project.org).

RESULTS

I trapped and translocated 888 scaled quail from 2016–2017. Of those, 220 were radio-marked hens (132 juveniles, 80 adults). In 2016, I experienced flooding on release ranch 2 that resulted in the mortality of 1 treatment group: 6-week delayed release sourced from the Rolling Plains ecoregion. I censored the radio-marked individuals in that group ($n = 6$) as well as 1 individual that died of unknown causes during the holding period and 1 individual that died of radio-collar entanglement during the holding period. I did not observe any individuals transition from inside the core area to dead outside (Ψ_{AD}) or alive outside to dead inside (Ψ_{BC}) within 1 time step, thus I believe my simplification of the model (i.e., fixing these parameters to 0) was valid. In total, I

recorded 8,437 telemetry observations (5,308 mortality status only; 3,129 locations). Source, release, ranch, and year were important variables in the preliminary modeling steps (Tables 2.1–5). My final prediction model based on cumulative weights was $\hat{\Psi}_{AC}(\text{release} + \text{ranch} + \text{year}) \hat{\Psi}_{AB}(\text{release} + \text{ranch} + \text{year}) \hat{\Psi}_{BA}(\text{source} + \text{ranch}) \hat{\Psi}_{BD}(\cdot) \hat{\delta}_{u|A}(\cdot) \hat{\delta}_{u|B}(\cdot)$ (Tables 2.6 and 2.7).

Mortality inside the core area was 3.4 times greater ($\beta = 1.22$, $SE = 0.27$) in 2017 compared to 2016. On average, breeding season (131 days) mortality inside the core area was 0.29 ($SE = 0.06$) in 2016 and 0.70 ($SE = 0.06$) in 2017. I did not find a difference in mortality outside the core area by year, but this may be due to small sample size. The direction and magnitude of the effect of year on mortality outside of the core area agreed with the effect I detected inside the core area despite large confidence intervals. Only 19 of all 101 mortalities occurred outside the core area. Mortality rate for the breeding season given an individual was outside the core area was 0.50 ($SE = 0.08$). Similarly, dispersal out of the core area was 1.8 times greater ($\beta = 0.57$, $SE = 0.21$) in 2017 compared to 2016. Delayed release treatment affected mortality inside and dispersal out of the core area (Figure 2.3). Daily mortality probability increased ($\beta = 0.08$, $SE = 0.05$), while dispersal decreased ($\beta = -0.07$, $SE = 0.04$) as length of holding time increased. When extrapolated over the entire monitoring period, mortality probability increased by 0.02 on average for each additional week the birds were held. While the probability of dispersal decreased by 0.03 on average for each additional week held. Thus, birds held for 9 weeks incurred a 0.15 increase in mortality probability over the entire monitoring period, but the probability that the birds did not leave the release area was increased by 0.27. Optimal holding time for delayed release occurred when the probability that an individual survived and stayed in the core area ($\hat{\Psi}_{AA}$) was maximized. Due to the disproportionate influence of year on mortality versus dispersal, the optimal holding time was >8 weeks (longest treatment) in 2016 and 8 weeks

in 2017. The additional per week supply cost (<\$10) of holding scaled quail is negligible once the investment is made in purchasing holding units (~ \$2000 each). I also incurred additional costs of roughly 1–2 hours per day of labor for checking and troubleshooting 20–36 holding pens.

I found evidence for an influence of release ranch on mortality inside and dispersal out of the core area. Mortality was 1.8 times greater ($\beta = 0.58$, SE = 0.26) on release ranch 2 compared to release ranch 1; however, dispersal was 0.6 times less ($\beta = 0.42$, SE = 0.20; Figure 2.4). Release ranch also influenced the probability that an individual would return to the core area. Individuals released on ranch 1 were 2.8 times more likely ($\beta = -1.02$, SE = 0.31) to return to that location, despite higher initial dispersal. Additionally, the probability that an individual returned to its respective release ranch was influenced weakly by the source population (Figure 2.5).

Individuals translocated within the Rolling Plains ecoregion were 1.5 times more likely ($\beta = -0.44$, SE = 0.28) to return than individuals translocated from the Edwards Plateau.

DISCUSSION

My primary goal was to refine best practices for scaled quail translocation protocols by identifying the optimal delayed release strategy and testing for effects of source population. I found the optimal holding time was a balance between increased mortality and decreased dispersal as the length of holding time increased. Other studies of wild avian translocations also found a negative effect of delayed release on survival (Richardson et al. 2015), while mammals have generally exhibited a positive response (Bright and Morris 1994, Letty et al. 2000). Why wild mammals and birds would exhibit different responses to captivity is unclear; however, the most likely mechanism for a deleterious response is the stress associated with the translocation

process (Dickens et al. 2010). Stress can have cumulative impacts on the physiology of wild animals and increased holding time may prolong those effects (Dickens et al. 2010, Richardson et al. 2015).

My findings that longer release holding times decrease dispersal also coincide with research in other disparate species such as lizards (Knox et al. 2017, Miller et al. 2019), small mammals (Bright and Morris 1994, Letty et al. 2000, Matějů et al. 2012), and wolves (Fritts et al. 2001), as well as previous research comparing immediate to delayed release for scaled quail (Ruzicka et al. 2017). Confining animals may allow them to become more familiar with environmental features of the release site and develop a preference for the site (Stamps and Swaisgood 2007).

Additionally, confinement provides an opportunity to develop social bonds and to perceive the habitat as occupied by conspecifics (de Milliano et al. 2016). I observed calling between individuals in different pens on the release ranches. Communication may have contributed to the perception that the habitat was occupied by conspecifics and, thus, was high quality (Martin et al. 2017). I also observed coveys of individuals released from the same holding pen travelling together prior to pairing-up.

My results indicated that the optimum holding time was ≥ 8 weeks but was mediated by year effects. In my study, the difference in mortality and dispersal between years was the largest effect and is likely attributable to the weather conditions. Weather is highly influential for quail populations. Links between annual fall abundance of scaled quail and spring-summer weather patterns (e.g., precipitation and temperature) are well-documented (Campbell et al. 1973, Leyva-Espinosa 2000, Bridges et al. 2001, Lusk et al. 2007, Silvy et al. 2007). The direct influence of weather on vital rates is less documented, although, Tri et al. (2016) found survival of northern

bobwhite to be negatively correlated with drought severity. Several studies of scaled quail have observed large differences in mortality among years attributed anecdotally to weather patterns (Lerich 2002, Pleasant et al. 2006). Cool and wet weather predominated the spring and summer of 2016 producing ideal conditions on my study site. However, 2017 was hotter and drier with Knox County experiencing 22 weeks of moderate to severe drought conditions from March–August (National Drought Mitigation Center 2018). These drought conditions were correlated with an increase in mortality and dispersal rates. The disproportionately greater increase in mortality shifted the optimum holding time from >9 weeks under ideal conditions to 8 weeks in drought conditions.

My estimates of mortality for translocated scaled quail were comparable to previously reported mortality of non-translocated scaled quail, although breeding season mortality varies widely. Rollins et al. (2009) summarized estimates of breeding season mortality ranging from 0.20–0.78 and averaging 0.48 in 5 populations. Mortality reported here was lower than a previous scaled quail translocation in the Rolling Plains ecoregion. Ruzicka et al. (2017) observed mortality of 0.92 in sub-adults and 0.78 in adults. Unlike Ruzicka et al. (2017), I did not find any differences between age classes.

I found that source population weakly influenced the probability that scaled quail would return to the release site. Birds that were translocated from sources in the Rolling Plains ecoregion (i.e., similar habitats) were more likely to return to their respective release locations given that they had already dispersed. The tendency to return may be an artifact of those birds exhibiting more exploratory behavior of their new habitat versus homing behavior in birds that were from the Edwards Plateau (i.e., dissimilar habitats). Numerous studies have documented exploratory and

homing behavior in translocated animals and most have hypothesized that these behaviors were driven by habitat preferences and perceptions (Fritts et al. 2001, Dickens et al. 2009, Kesler et al. 2012). Homing behavior is thought to be an indication of habitat unsuitability at the release site (Dickens et al. 2009).

I did not find an effect of source population on mortality in contrast to other studies on northern bobwhites (Liu et al. 2000) and scaled quail (Yancey 2019) in Texas, but in concurrence with a study on mountain quail in Idaho (Troy et al. 2013). Yancey (2019) translocated individuals that were a different subspecies (*C. s. castanogastris*) than the naturally occurring subspecies on the release site. I translocated individuals within the geographic range of Arizona scaled quail (*C. squamata pallida*). The lack of a source population effect on mortality or dispersal suggests translocating the subspecies is more important than habitat differences.

Despite selecting properties in proximity with similar habitats and management, I found that the release ranch influenced probabilities of mortality, dispersal, and return. One unforeseen factor in the placement of the holding pens on the release ranch 2 may have contributed to the higher mortality observed on that site. Holding pens were in closer proximity to anthropogenic features (e.g., ranch headquarters, shop). Scaled quail tend to have an affinity for using anthropogenic structures on the landscape as cover (Silvy et al. 2007). I observed radio-marked birds frequently in the vicinity of buildings and vehicles which may have created an ecological trap on this site. My results concerning dispersal and return are less intuitive. Birds were slightly more likely to disperse away from release ranch 1, however they were also more likely to return. The tendency to return may indicate that the habitat surrounding the release area was less suitable. A priority

research need is understanding fine-scale habitat preferences of scaled quail in the Rolling Plains ecoregion.

MANAGEMENT IMPLICATIONS

Long holding times (e.g., >8 weeks) may act to reduce post-release dispersal in species where dispersal is a liability to translocation success. However, lower dispersal rates should be weighed against potentially higher mortality rates. I found that scaled quail benefit from a delayed release of at least 9 weeks in years with ideal weather conditions. Conversely, I don't recommend translocating scaled quail during drought conditions, as I observed a 3-fold increase in mortality likely influenced by drought. Long range forecasting using the El Nino–Southern Oscillation (ENSO) cycle has improved in recent decades (L'Heureux et al. 2017). The ENSO cycle has a strong influence over weather patterns in the Southwestern U.S., thus predictions by the Climate Prediction Center (NWS NOAA; <https://www.cpc.ncep.noaa.gov>) may be a useful tool for managers when deciding whether to initiate a translocation. My results suggest that populations in the Edwards Plateau are suitable sources for scaled quail translocation efforts in the Rolling Plains ecoregion. I found the source population was not an important factor when using different populations of the native subspecies.

Table 2.1. Model results from the first modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), year, and time trend (trend) on translocated scaled quail (*Callipepla squamata*) dispersal (Ψ_{AB}) using a multistate mark-recapture model with state uncertainty, in Knox County, Texas, USA, 2016–2017. Individuals could be described in 1 of 4 true states: alive inside the release area A), alive outside the release area B), dead inside the release area C), and dead outside the release area D), thus transitions in the model described dispersal (Ψ_{AB}), mortality inside release area (Ψ_{AC}), return (Ψ_{BA}), and mortality outside release area (Ψ_{BD}). Alive individuals could also be assigned as unknown (u) if their location relative to the release area was unknown. δ ($\delta_{u|A}$, $\delta_{u|B}$) parameters describe the probability of an unknown status to an individual given its true state was either A or B. All other transitions (Ψ_{AC} , Ψ_{BA} , Ψ_{BD}) were held constant (.) while focusing on Ψ_{AB} . The top model AIC is 17,895.10.

Model	ΔAIC_c^a	w_i^b	L^c	k^d	Deviance
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{ranch} + \text{year} + \text{trend})$	0.00	0.16	1.00	10	17,875.08
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{ranch} + \text{year} + \text{trend})$	0.74	0.11	0.69	9	17,877.82
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{ranch} + \text{year})$	1.07	0.09	0.59	9	17,878.15
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{age} + \text{ranch} + \text{year} + \text{trend})$	1.57	0.07	0.46	11	17,874.64
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{ranch} + \text{year})$	1.82	0.06	0.40	8	17,880.91
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{ranch} + \text{year} + \text{trend})$	1.83	0.06	0.40	11	17,874.90
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{ranch} + \text{year} + \text{trend})$	2.50	0.04	0.29	10	17,877.57
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{age} + \text{ranch} + \text{year})$	2.62	0.04	0.27	10	17,877.70
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{age} + \text{ranch} + \text{year} + \text{trend})$	2.73	0.04	0.26	10	17,877.81
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{ranch} + \text{year})$	2.89	0.04	0.24	10	17,877.97
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{year} + \text{trend})$	3.28	0.03	0.19	9	17,880.36
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{age} + \text{ranch} + \text{year} + \text{trend})$	3.41	0.03	0.18	12	17,874.48
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{ranch} + \text{year})$	3.58	0.03	0.17	9	17,880.66
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{age} + \text{ranch} + \text{year})$	3.81	0.02	0.15	9	17,880.90
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{year} + \text{trend})$	3.85	0.02	0.15	8	17,882.94
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{year})$	4.34	0.02	0.11	8	17,883.42
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{age} + \text{ranch} + \text{year})$	4.46	0.02	0.11	11	17,877.54
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{age} + \text{ranch} + \text{year} + \text{trend})$	4.49	0.02	0.11	11	17,877.56
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{age} + \text{year} + \text{trend})$	4.80	0.01	0.09	10	17,879.88
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{year})$	4.94	0.01	0.08	7	17,886.03
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{year} + \text{trend})$	5.10	0.01	0.08	10	17,880.18

$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{age} + \text{ranch} + \text{year})$	5.57	0.01	0.06	10	17,880.65
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{year} + \text{trend})$	5.65	0.01	0.06	9	17,882.73
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{age} + \text{year})$	5.85	0.01	0.05	9	17,882.93
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{age} + \text{year} + \text{trend})$	5.85	0.01	0.05	9	17,882.93
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{year})$	6.16	0.01	0.05	9	17,883.24
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{age} + \text{year} + \text{trend})$	6.65	0.01	0.04	11	17,879.72
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{year})$	6.75	0.01	0.03	8	17,885.83
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{age} + \text{year})$	6.94	0.00	0.03	8	17,886.03
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{age} + \text{year} + \text{trend})$	7.65	0.00	0.02	10	17,882.73
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{age} + \text{year})$	7.69	0.00	0.02	10	17,882.77
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{age} + \text{year})$	8.75	0.00	0.01	9	17,885.83
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{age} + \text{ranch} + \text{trend})$	17.24	0.00	0.00	9	17,894.33
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{ranch} + \text{trend})$	17.50	0.00	0.00	8	17,896.58
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{age} + \text{ranch} + \text{trend})$	18.11	0.00	0.00	10	17,893.19
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{age} + \text{ranch})$	18.26	0.00	0.00	8	17,897.35
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{ranch})$	18.52	0.00	0.00	7	17,899.61
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{age} + \text{ranch})$	19.12	0.00	0.00	9	17,896.20
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{age} + \text{ranch} + \text{trend})$	19.20	0.00	0.00	10	17,894.28
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{ranch} + \text{trend})$	19.32	0.00	0.00	9	17,896.41
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{ranch} + \text{trend})$	19.45	0.00	0.00	9	17,896.53
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{age} + \text{ranch} + \text{trend})$	20.10	0.00	0.00	11	17,893.18
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{age} + \text{ranch})$	20.22	0.00	0.00	9	17,897.31
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{ranch})$	20.34	0.00	0.00	8	17,899.43
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{ranch})$	20.47	0.00	0.00	8	17,899.56
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{age} + \text{ranch})$	21.11	0.00	0.00	10	17,896.18
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{ranch} + \text{trend})$	21.28	0.00	0.00	10	17,896.36
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{age} + \text{trend})$	21.62	0.00	0.00	8	17,900.71
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{trend})$	22.06	0.00	0.00	7	17,903.15
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{ranch})$	22.30	0.00	0.00	9	17,899.39

$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{age} + \text{trend})$	22.42	0.00	0.00	9	17899.51
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{age})$	22.64	0.00	0.00	7	17,903.73
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\cdot)$	23.08	0.00	0.00	6	17,906.18
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{age})$	23.42	0.00	0.00	8	17,902.51
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{age} + \text{trend})$	23.60	0.00	0.00	9	17,900.68
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release} + \text{trend})$	23.84	0.00	0.00	8	17,902.93
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{trend})$	24.02	0.00	0.00	8	17,903.11
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{age} + \text{trend})$	24.42	0.00	0.00	10	17899.50
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{age})$	24.62	0.00	0.00	8	17,903.71
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{release})$	24.86	0.00	0.00	7	17,905.95
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source})$	25.05	0.00	0.00	7	17,906.14
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{age})$	25.42	0.00	0.00	9	17,902.50
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release} + \text{trend})$	25.82	0.00	0.00	9	17,902.90
$\Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AB}(\text{source} + \text{release})$	26.84	0.00	0.00	8	17,905.92

^a Akaike's corrected information criterion

^b Akaike weights

^c Model likelihood

^d Number of parameters

Table 2.2. Model results from the first modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), year, and time trend (trend) on translocated scaled quail (*Callipepla squamata*) mortality (Ψ_{AC}) using a multistate mark-recapture model with state uncertainty. Individuals could be described in one of four true states: alive inside the release area (A), alive outside the release area (B), dead inside the release area (C), and dead outside the release area (D), thus transitions in the model described dispersal (Ψ_{AB}), mortality inside release area (Ψ_{AC}), return (Ψ_{BA}), and mortality outside release area (Ψ_{BD}). Alive individuals could also be assigned as unknown (u) if their location relative to the release area was unknown. δ ($\delta_{u|A}$, $\delta_{u|B}$) parameters describe the probability of an unknown status to an individual given its true state was either A or B. All other transitions (Ψ_{AB} , Ψ_{BA} , Ψ_{BD}) were held constant (.) while focusing on Ψ_{AC} . The top model AIC is 17,887.42.

Model	ΔAIC_c^a	w_i^b	L^c	k^d	Deviance
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{ranch} + \text{year})$	0.00	0.15	1.00	9	17,869.40
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{ranch} + \text{year})$	0.74	0.10	0.69	8	17,872.15
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{ranch} + \text{year} + \text{trend})$	0.96	0.09	0.62	10	17,868.36
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{age} + \text{ranch} + \text{year})$	1.53	0.07	0.46	10	17,868.93
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{ranch} + \text{year} + \text{trend})$	1.76	0.06	0.42	9	17,871.15
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{ranch} + \text{year})$	1.82	0.06	0.40	10	17,869.22
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{ranch} + \text{year})$	2.49	0.04	0.29	9	17,871.89
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{age} + \text{ranch} + \text{year} + \text{trend})$	2.53	0.04	0.28	11	17,867.92
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{age} + \text{ranch} + \text{year})$	2.73	0.04	0.25	9	17,872.13
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{ranch} + \text{year} + \text{trend})$	2.74	0.04	0.25	11	17,868.13
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{year})$	3.17	0.03	0.20	8	17,874.58
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{age} + \text{ranch} + \text{year})$	3.37	0.03	0.19	11	17,868.76
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{ranch} + \text{year} + \text{trend})$	3.42	0.03	0.18	10	17,870.81
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{year})$	3.73	0.02	0.15	7	17,877.14
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{age} + \text{ranch} + \text{year} + \text{trend})$	3.74	0.02	0.15	10	17,871.13
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{year} + \text{trend})$	4.31	0.02	0.12	9	17,873.71
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{age} + \text{ranch} + \text{year} + \text{trend})$	4.32	0.02	0.12	12	17,867.71
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{age} + \text{ranch} + \text{year})$	4.48	0.02	0.11	10	17,871.88
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{age} + \text{year})$	4.66	0.01	0.10	9	17,874.06
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{year} + \text{trend})$	4.86	0.01	0.09	8	17,876.27
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{year})$	4.99	0.01	0.08	9	17,874.39

$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{age} + \text{ranch} + \text{year} + \text{trend})$	5.40	0.01	0.07	11	17,870.79
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{year})$	5.52	0.01	0.06	8	17,876.93
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{age} + \text{year})$	5.73	0.01	0.06	8	17,877.14
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{age} + \text{year} + \text{trend})$	5.83	0.01	0.05	10	17,873.22
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{year} + \text{trend})$	6.09	0.01	0.05	10	17,873.49
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{age} + \text{year})$	6.50	0.01	0.04	10	17,873.89
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{year} + \text{trend})$	6.59	0.01	0.04	9	17,875.99
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{age} + \text{year} + \text{trend})$	6.86	0.00	0.03	9	17,876.26
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{age} + \text{year})$	7.52	0.00	0.02	9	17,876.92
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{age} + \text{year} + \text{trend})$	7.63	0.00	0.02	11	17,873.02
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{age} + \text{year} + \text{trend})$	8.59	0.00	0.01	10	17,875.98
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{age} + \text{ranch})$	17.30	0.00	0.00	8	17,888.70
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{ranch})$	17.59	0.00	0.00	7	17,891.00
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{age} + \text{ranch})$	18.16	0.00	0.00	9	17,887.56
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{age} + \text{ranch} + \text{trend})$	19.04	0.00	0.00	9	17,888.43
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{age} + \text{ranch})$	19.26	0.00	0.00	9	17,888.65
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{ranch} + \text{trend})$	19.39	0.00	0.00	8	17,890.80
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{ranch})$	19.42	0.00	0.00	8	17,890.82
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{ranch})$	19.54	0.00	0.00	8	17,890.94
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{age} + \text{ranch} + \text{trend})$	19.95	0.00	0.00	10	17,887.35
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{age} + \text{ranch})$	20.15	0.00	0.00	10	17,887.54
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{age} + \text{ranch} + \text{trend})$	20.98	0.00	0.00	10	17,888.37
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{ranch} + \text{trend})$	21.25	0.00	0.00	9	17,890.65
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{ranch} + \text{trend})$	21.33	0.00	0.00	9	17,890.73
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{ranch})$	21.38	0.00	0.00	9	17,890.78
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{age})$	21.53	0.00	0.00	7	17,894.94
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{age} + \text{ranch} + \text{trend})$	21.93	0.00	0.00	11	17,887.32
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\cdot)$	22.02	0.00	0.00	6	17,897.43
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{age})$	22.33	0.00	0.00	8	17,893.73

$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{ranch} + \text{trend})$	23.20	0.00	0.00	10	17,890.60
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{age} + \text{trend})$	23.31	0.00	0.00	8	17894.71
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{age})$	23.51	0.00	0.00	8	17,894.91
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release})$	23.82	0.00	0.00	7	17,897.22
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{trend})$	23.86	0.00	0.00	7	17,897.27
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source})$	23.98	0.00	0.00	7	17,897.39
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{age} + \text{trend})$	24.16	0.00	0.00	9	17893.56
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{age})$	24.32	0.00	0.00	9	17,893.72
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{age} + \text{trend})$	25.28	0.00	0.00	9	17,894.68
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{release} + \text{trend})$	25.68	0.00	0.00	8	17,897.08
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release})$	25.79	0.00	0.00	8	17,897.19
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{trend})$	25.82	0.00	0.00	8	17,897.22
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{age} + \text{trend})$	26.15	0.00	0.00	10	17,893.54
$\Psi_{AB}(\cdot) \Psi_{BA}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{AC}(\text{source} + \text{release} + \text{trend})$	27.65	0.00	0.00	9	17,897.04

^a Akaike's corrected information criterion

^b Akaike weights

^c Model likelihood

^d Number of parameters

Table 2.3. Model results from the first modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), year, and time trend (trend) on translocated scaled quail (*Callipepla squamata*) probability of return to release area (Ψ_{BA}) using a multistate mark-recapture model with state uncertainty. Individuals could be described in one of four true states: alive inside the release area (A), alive outside the release area (B), dead inside the release area (C), and dead outside the release area (D), thus transitions in the model described dispersal (Ψ_{AB}), mortality inside release area (Ψ_{AC}), return to release area (Ψ_{BA}), and mortality outside release area (Ψ_{BD}). Alive individuals could also be assigned as unknown (u) if their location relative to the release area was unknown. δ ($\delta_{u|A}$, $\delta_{u|B}$) parameters describe the probability of an unknown status to an individual given its true state was either A or B. All other transitions (Ψ_{AB} , Ψ_{AC} , Ψ_{BD}) were held constant (.) while focusing on Ψ_{BA} . The top model AIC is 19,491.07.

Model	ΔAIC_c^a	w_i^b	L^c	k^d	Deviance
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{age} + \text{ranch} + \text{year})$	0.00	0.27	1.00	10	19,471
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{age} + \text{ranch} + \text{year})$	0.04	0.26	0.98	9	19,473.1
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{release} + \text{age} + \text{ranch} + \text{year})$	1.03	0.16	0.60	10	19,472.1
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{release} + \text{age} + \text{ranch} + \text{year})$	1.23	0.15	0.54	11	19,470.3
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{ranch} + \text{year})$	3.73	0.04	0.16	9	19,476.8
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{ranch} + \text{year})$	4.28	0.03	0.12	8	19,479.3
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{age} + \text{year})$	5.19	0.02	0.07	9	19,478.2
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{age} + \text{year})$	5.43	0.02	0.07	8	19,480.5
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{release} + \text{ranch} + \text{year})$	5.69	0.02	0.06	10	19,476.7
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{release} + \text{ranch} + \text{year})$	6.20	0.01	0.05	9	19,479.2
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{release} + \text{age} + \text{year})$	6.42	0.01	0.04	9	19,479.5
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{release} + \text{age} + \text{year})$	6.43	0.01	0.04	10	19,477.5
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{year})$	9.55	0.00	0.01	8	19,484.6
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{year})$	10.37	0.00	0.01	7	19,487.4
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{release} + \text{year})$	11.53	0.00	0.00	9	19,484.6
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{release} + \text{year})$	12.30	0.00	0.00	8	19,487.4
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{release} + \text{ranch})$	45.79	0.00	0.00	9	19,518.8
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{ranch})$	46.32	0.00	0.00	8	19,521.4
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{release} + \text{ranch})$	46.81	0.00	0.00	8	19,521.9

$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{release} + \text{age} + \text{ranch})$	47.62	0.00	0.00	10	19,518.7
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{ranch})$	48.02	0.00	0.00	7	19,525.1
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{age} + \text{ranch})$	48.32	0.00	0.00	9	19,521.4
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{release} + \text{age} + \text{ranch})$	48.56	0.00	0.00	9	19,521.6
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{age} + \text{ranch})$	50.02	0.00	0.00	8	19,525.1
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{release})$	51.59	0.00	0.00	8	19,526.7
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source})$	52.11	0.00	0.00	7	19,529.2
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{release})$	52.69	0.00	0.00	7	19,529.7
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{release} + \text{age})$	53.36	0.00	0.00	9	19,526.4
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\cdot)$	53.83	0.00	0.00	6	19,532.9
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{source} + \text{age})$	54.11	0.00	0.00	8	19,529.2
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{release} + \text{age})$	54.34	0.00	0.00	8	19,529.4
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BA}(\text{age})$	55.83	0.00	0.00	7	19,532.9

^a Akaike's corrected information criterion

^b Akaike weights

^c Model likelihood

^d Number of parameters

Table 2.4. Model results from the first modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), year, and time trend (trend) on translocated scaled quail (*Callipepla squamata*) mortality (Ψ_{BD}) using a multistate mark-recapture model with state uncertainty. Individuals could be described in one of four true states: alive inside the release area (A), alive outside the release area (B), dead inside the release area (C), and dead outside the release area (D), thus transitions in the model described dispersal (Ψ_{AB}), mortality inside release area (Ψ_{AC}), return (Ψ_{BA}), and mortality outside release area (Ψ_{BD}). Alive individuals could also be assigned as unknown (u) if their location relative to the release area was unknown. δ ($\delta_{u|A}$, $\delta_{u|B}$) parameters describe the probability of an unknown status to an individual given it's true state was either A or B. All other transitions (Ψ_{AC} , Ψ_{AB} , Ψ_{BA}) were held constant (.) while focusing on Ψ_{BD} . The top model AIC is 19,543.12.

Model	ΔAIC_c^a	w_i^b	L^c	k^d	Deviance
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{year})$	0.00	0.13	1.00	7	19,529.11
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{year})$	0.14	0.12	0.93	8	19,527.24
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{ranch} + \text{year})$	1.63	0.06	0.44	8	19,528.73
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\cdot)$	1.79	0.05	0.41	6	19,532.90
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{ranch} + \text{year})$	1.81	0.05	0.40	9	19,526.91
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{release} + \text{year})$	1.92	0.05	0.38	8	19,529.02
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source})$	1.93	0.05	0.38	7	19,531.03
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{age} + \text{year})$	1.96	0.05	0.37	8	19,529.07
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{age} + \text{year})$	2.03	0.05	0.36	9	19,527.13
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{release} + \text{year})$	2.07	0.04	0.35	9	19,527.17
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{age})$	2.62	0.03	0.27	8	19,529.72
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{age})$	2.84	0.03	0.24	7	19,531.94
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{ranch})$	3.32	0.02	0.19	7	19,532.43
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{release} + \text{ranch} + \text{year})$	3.56	0.02	0.17	9	19,528.65
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{ranch})$	3.56	0.02	0.17	8	19,530.66
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{age} + \text{ranch} + \text{year})$	3.58	0.02	0.17	9	19,528.68
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{age} + \text{ranch} + \text{year})$	3.69	0.02	0.16	10	19,526.78
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{release})$	3.75	0.02	0.15	7	19,532.85
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{release} + \text{ranch} + \text{year})$	3.75	0.02	0.15	10	19,526.84
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{release} + \text{age} + \text{year})$	3.84	0.02	0.15	9	19,528.94
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{release})$	3.88	0.02	0.14	8	19,530.98

$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{release} + \text{age} + \text{year})$	3.88	0.02	0.14	10	19,526.97
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{age} + \text{ranch})$	4.17	0.02	0.12	9	19,529.27
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{age} + \text{ranch})$	4.31	0.01	0.12	8	19,531.41
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{release} + \text{age})$	4.61	0.01	0.10	9	19,529.71
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{release} + \text{age})$	4.84	0.01	0.09	8	19,531.94
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{release} + \text{ranch})$	5.27	0.01	0.07	8	19,532.37
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{release} + \text{age} + \text{ranch} + \text{year})$	5.46	0.01	0.07	10	19,528.55
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{release} + \text{ranch})$	5.50	0.01	0.06	9	19,530.59
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{release} + \text{age} + \text{ranch} + \text{year})$	5.54	0.01	0.06	11	19,526.63
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{source} + \text{release} + \text{age} + \text{ranch})$	6.16	0.01	0.05	10	19,529.25
$\Psi_{AB}(\cdot) \Psi_{AC}(\cdot) \Psi_{BA}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot) \Psi_{BD}(\text{release} + \text{age} + \text{ranch})$	6.31	0.01	0.04	9	19,531.40

^a Akaike's corrected information criterion

^b Akaike weights

^c Model likelihood

^d Number of parameters

Table 2.5. Akaike’s corrected information criterion (AIC_c) cumulative variable weights from the first model sets in a multistate mark-recapture model with state uncertainty to describe mortality and dispersal of translocated scaled quail (*Callipepla squamata*) in Knox County, Texas, USA, 2016–2017. Weights in boldface type indicate variables with cumulative weight >0.5 and that were retained to the second round of modeling. Individuals could be described in 1 of 4 true states: alive inside the release area (A), alive outside the release area (B), dead inside the release area (C), and dead outside the release area (D), thus transitions in the model described dispersal (Ψ_{AB}), mortality inside release area (Ψ_{AC}), return (Ψ_{BA}), and mortality outside release area (Ψ_{BD}). NA indicates variable was not used to model parameter.

Parameters	Source	Release	Age	Ranch	Year
Ψ_{AB}	0.29	0.60	0.30	0.83	0.99
Ψ_{AC}	0.29	0.60	0.30	0.83	0.99
Ψ_{BA}	0.60	0.28	0.32	0.97	0
Ψ_{BD}	0.49	0.28	0.32	0.31	0.67

Table 2.6. Model results from the second step of the modeling strategy evaluating the effect of year, delayed release treatment (release), age, source population (source), release ranch (ranch), and time trend (trend) on scaled quail (*Callipepla squamata*) mortality (Ψ_{AC} , Ψ_{BD}) and dispersal (Ψ_{AB} , Ψ_{BA}) using a multistate mark-recapture model with state uncertainty. Only models with AIC_c weight >0 reported. Full model set included all permutations of the global model: $\Psi_{AC}(\text{year}) + \Psi_{AC}(\text{ranch}) + \Psi_{AC}(\text{release}) + \Psi_{BD}(\text{year}) + \Psi_{BA}(\text{year}) + \Psi_{BA}(\text{ranch}) + \Psi_{BA}(\text{age}) + \Psi_{BA}(\text{source}) + \Psi_{AB}(\text{year}) + \Psi_{AB}(\text{ranch}) + \Psi_{AB}(\text{release}) + \Psi_{AB}(\text{trend}) + \delta_{u|A}(\cdot) + \delta_{u|B}(\cdot)$. The top model AIC was 17,865.69.

Model	ΔAIC_c^a	w_i^b	L^c	k^d	Deviance
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot)$ $\delta_{u A}(\cdot) \delta_{u B}(\cdot)$	0.00	0.02	1.00	14	17,837.64
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch})$ $\Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	0.52	0.02	0.77	15	17,836.15
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot)$ $\delta_{u B}(\cdot)$	0.52	0.02	0.77	13	17,840.16
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	0.74	0.02	0.69	13	17,840.38
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{ranch}) \Psi_{BD}(\text{year}) \delta_{u A}(\cdot)$ $\delta_{u B}(\cdot)$	1.07	0.01	0.59	14	17,838.70
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot)$ $\delta_{u A}(\cdot) \delta_{u B}(\cdot)$	1.13	0.01	0.57	15	17,836.76
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year} + \text{trend}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch})$ $\Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	1.13	0.01	0.57	15	17,836.76
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot)$ $\delta_{u A}(\cdot) \delta_{u B}(\cdot)$	1.14	0.01	0.56	15	17,836.77
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\text{year}) \delta_{u A}(\cdot)$ $\delta_{u B}(\cdot)$	1.26	0.01	0.53	14	17,838.89
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{ranch} + \text{year}) \Psi_{BA}(\text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	1.29	0.01	0.52	12	17,842.94
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch})$ $\Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	1.63	0.01	0.44	16	17,835.26
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch})$ $\Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	1.66	0.01	0.44	16	17,835.28
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year} + \text{trend}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch})$ $\Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	1.66	0.01	0.44	16	17,835.29

$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{ranch} + \text{year}) \Psi_{BA}(\text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.51	0.01	0.28	13	17,842.16
$\Psi_{AB}(\text{ranch} + \text{year} + \text{trend}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.76	0.01	0.25	14	17,840.39
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year} + \text{trend}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.78	0.01	0.25	17	17,834.39
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year} + \text{trend}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.78	0.01	0.25	17	17,834.39
$\Psi_{AB}(\text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{ranch}) \Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.82	0.01	0.24	13	17,842.46
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{ranch}) \Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.82	0.01	0.24	15	17,838.45
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.83	0.01	0.24	16	17,836.45
$\Psi_{AB}(\text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.85	0.01	0.24	14	17,840.48
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year} + \text{trend}) \Psi_{AC}(\text{release} + \text{ranch}) \Psi_{BA}(\text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.89	0.01	0.24	15	17,838.52
$\Psi_{AB}(\text{release} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.90	0.01	0.23	12	17,844.55
$\Psi_{AB}(\text{ranch} + \text{year}) \Psi_{AC}(\text{release} + \text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.95	0.01	0.23	14	17,840.59
$\Psi_{AB}(\text{release} + \text{ranch} + \text{year} + \text{trend}) \Psi_{AC}(\text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\cdot) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.96	0.01	0.23	15	17,838.59
$\Psi_{AB}(\text{ranch} + \text{year}) \Psi_{AC}(\text{ranch} + \text{year}) \Psi_{BA}(\text{source} + \text{ranch}) \Psi_{BD}(\text{year}) \delta_{u A}(\cdot) \delta_{u B}(\cdot)$	2.98	0.01	0.23	13	17,842.62

^a Akaike's corrected information criterion

^b Akaike weights

^c Model likelihood

^d Number of parameters

Table 2.7. Akaike’s corrected information criterion (AIC_c) cumulative variable weights from the final (second step) model set in a multistate mark-recapture model with state uncertainty to describe mortality and dispersal of translocated scaled quail (*Callipepla squamata*) in Knox County, Texas, USA, 2016–2017. Weights in boldface type indicate variables that were included in the final model. Individuals could be described in 1 of 4 true states: alive inside the release area (A), alive outside the release area (B), dead inside the release area (C), and dead outside the release area (D), thus transitions in the model described dispersal (Ψ_{AB}), mortality inside release area (Ψ_{AC}), return (Ψ_{BA}), and mortality outside release area (Ψ_{BD}). NA indicates variable was not used to model parameter.

Parameters	Variables				
	Ranch	Release	Source	Trend	Year
Ψ_{AB}	0.76	0.71	NA	0.36	0.96
Ψ_{AC}	0.84	0.58	NA	NA	0.99
Ψ_{BA}	0.98	NA	0.59	NA	0.34
Ψ_{BD}	0.31	NA	NA	NA	0.43

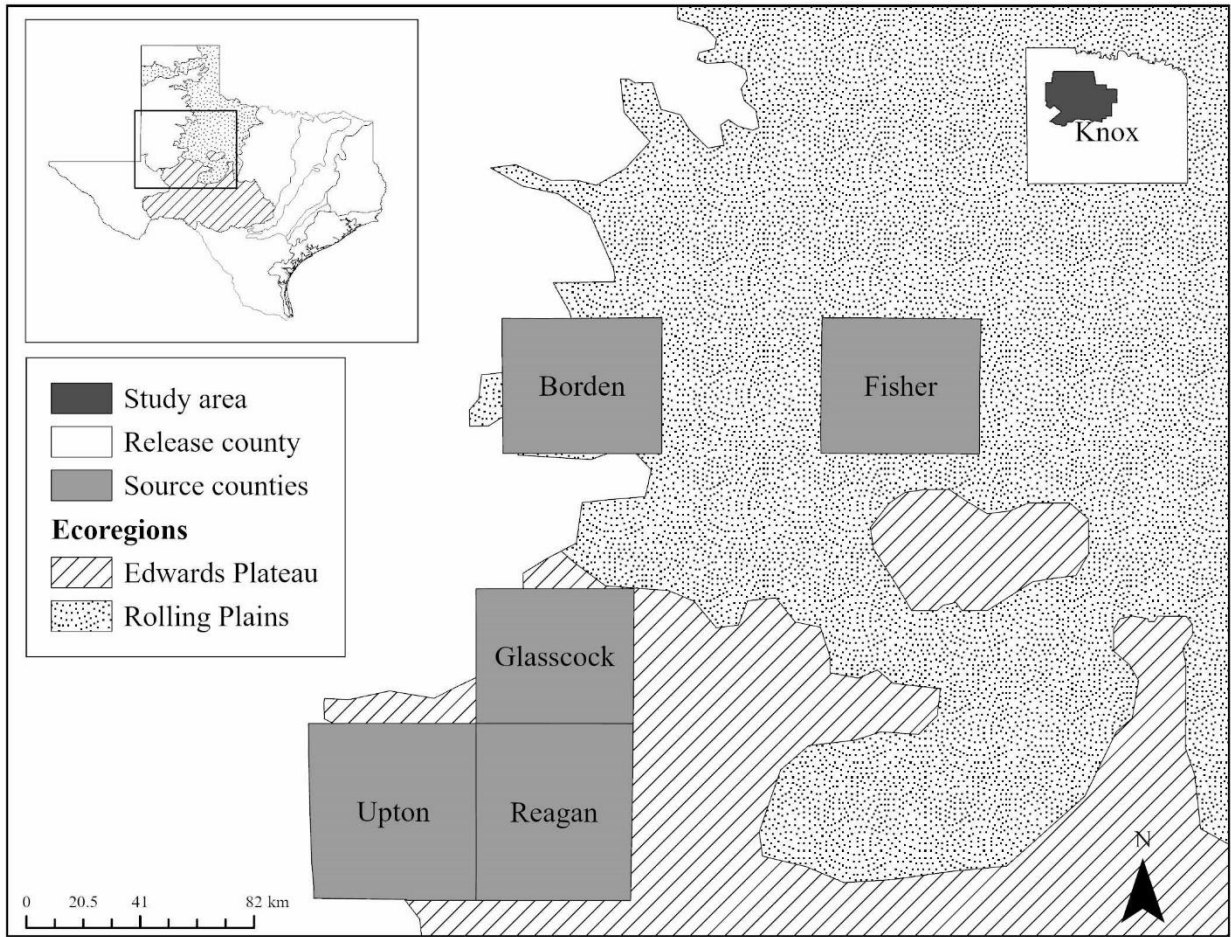


Figure 2.1. Source sites in relation to release area in Knox County, Texas, USA and ecoregions. Scaled quail (*Callipepla squamata*) were translocated in 2016–2017.

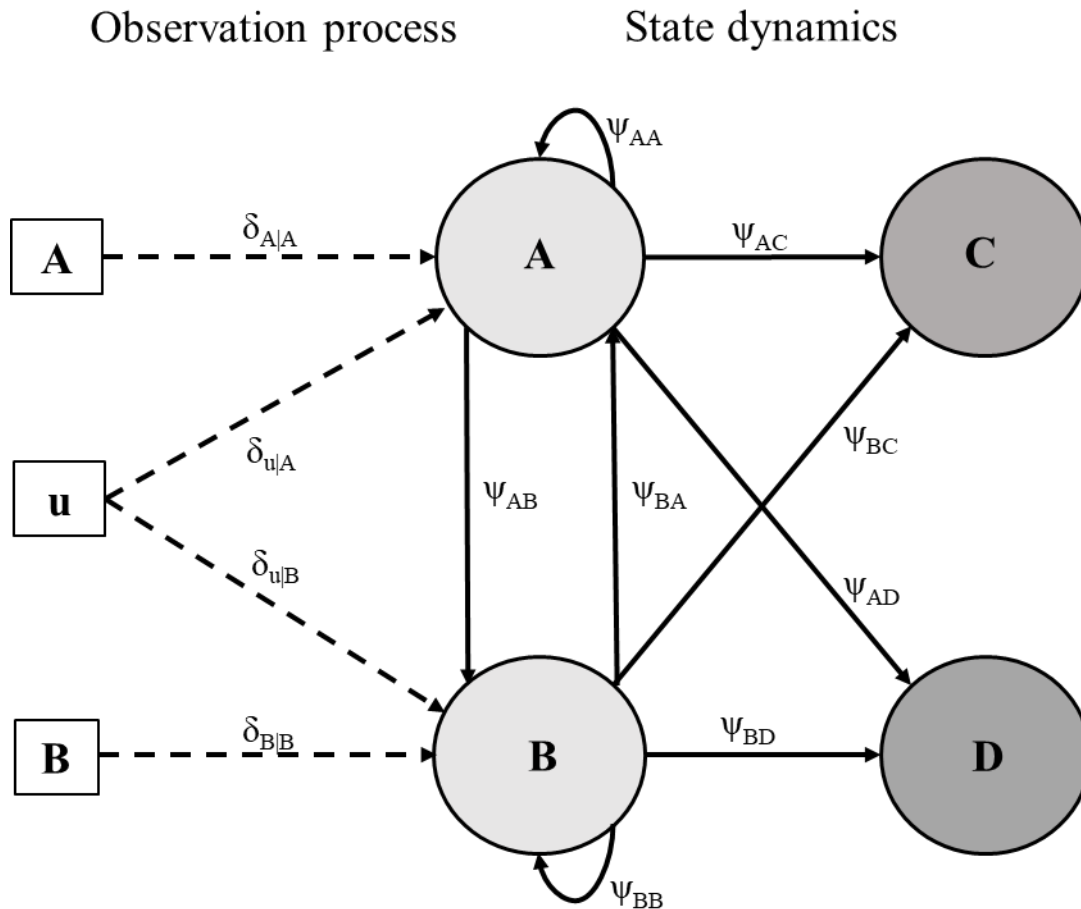


Figure 2.2. Mark-recapture multistate model with state uncertainty (MSMR-SU) used to model mortality and dispersal of scaled quail (*Callipepla squamata*) translocated to Knox County, Texas, USA, 2016–2017. Individuals could be in 1 of 4 true states (denoted by circles): A) alive and inside the core release area, B) alive and outside the core release area, C) dead inside the core release area, or D) dead outside the core release area. Allowable transitions between states are given by the solid arrows. True states and transitions describe the state dynamics. The observation process was also modeled to account for uncertainty that arose when an individual was known to be alive but its location was not known (i.e., observed as an event, u). Parameters $\delta_{A|A}$ and $\delta_{B|B}$ describe the probability of observing an individual in state A or B given that it was truly in that state. Potential observations of individuals given true state are described by dashed arrows.

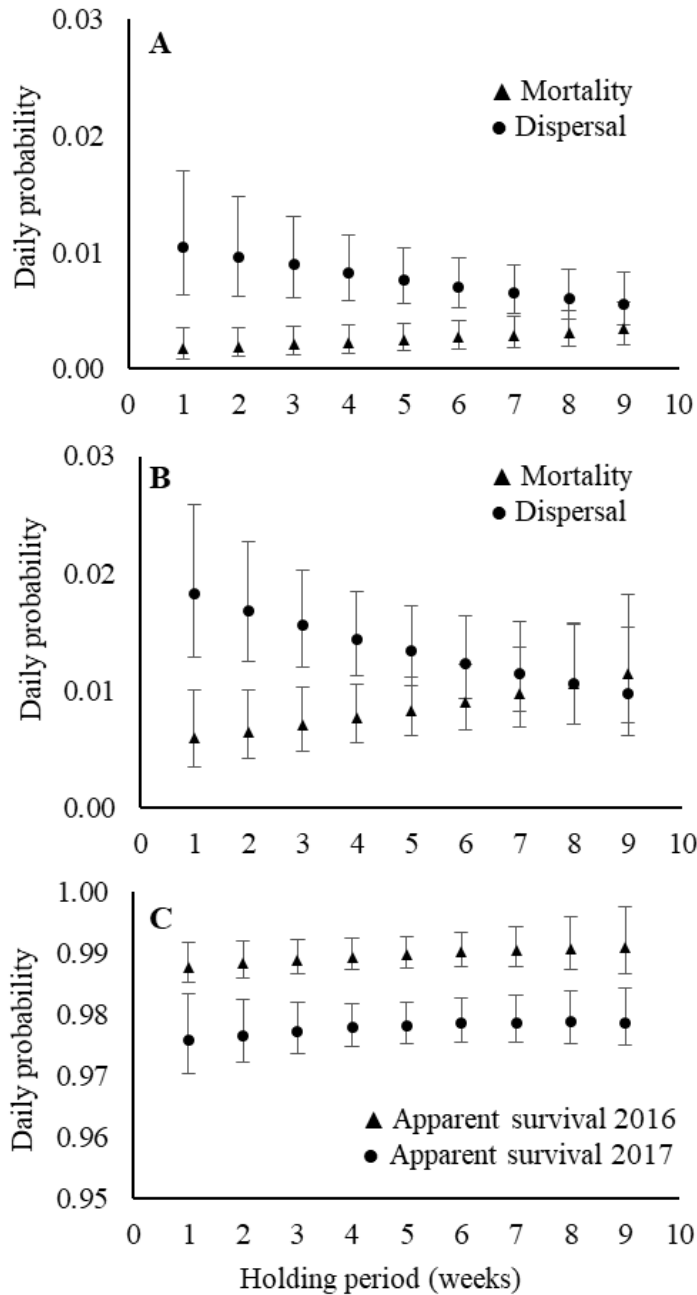


Figure 2.3. Estimated transition probabilities of translocated scaled quail (*Callipepla squamata*) between live and dead states (Ψ_{AC} ; i.e., mortality) and inside to outside the core release area (Ψ_{AB} ; i.e., dispersal) in A) 2016, B) 2017, and C) probability of the individuals surviving and remaining in the core release area (Ψ_{AA}) as a function of delayed release holding period in Knox County, Texas, USA, 2016–2017.

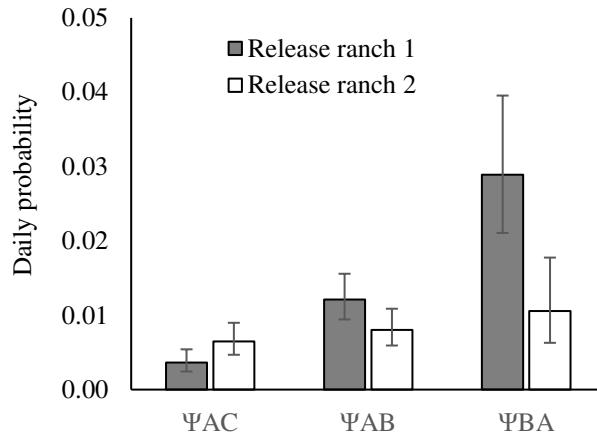


Figure 2.4. Estimated transition probabilities of translocated scaled quail (*Callipepla squamata*) between live and dead states (Ψ_{AC} ; i.e., mortality), inside to outside the core release area (Ψ_{AB} ; i.e., dispersal), and outside to inside the core release area (Ψ_{BA} ; i.e., return) compared between release ranches located in Knox County, Texas, USA, 2016–2017.

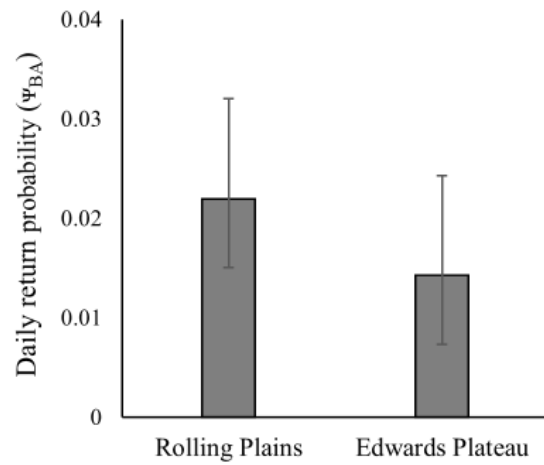


Figure 2.5. Estimated transition probabilities of translocated scaled quail (*Callipepla squamata*) from outside to inside the core release area (Ψ_{BA} ; i.e., return) as a function of the source population ecoregion (i.e., Rolling Plains or Edwards Plateau) in Knox County, Texas, USA, 2016–2017.

CHAPTER 3. EFFECTS OF RELEASE STRATEGY, SOURCE POPULATION, AND AGE ON REINTRODUCED SCALED QUAIL REPRODUCTION

Translocation is one strategy to reestablish populations of scaled quail (*Callipepla squamata*). Initial reproductive success post-translocation is critical for establishing short-lived species such as quail, but factors influencing reproductive success are poorly understood. I evaluated the effect of source population and variation in delayed release strategy (1–9 weeks) on nest initiation and nest survival of wild-caught, translocated scaled quail. I trapped and translocated scaled quail over two years (2016-2017) from source populations in the Edwards Plateau and Rolling Plains ecoregions of Texas to a large contiguous (>40,000 ha) release site in Knox County, Texas. I used a multi-state mark-recapture model with state uncertainty to test for effects of release treatment, source population, age, release location, and year on nest initiation and survival. I found that increased length of holding time decreased renesting effort. Yearlings were more likely to initiate nests than adults and the probability of renesting was lower during the year with drought conditions. There was no effect of source population on any of the parameters I evaluated. Future scaled quail reintroduction efforts will benefit from prioritizing translocation of yearlings.

INTRODUCTION

The number of threatened species is growing globally due to anthropogenic impacts (Gaston 2005). Habitat loss and fragmentation continue to be major contributors to the biodiversity crisis (Butchart et al. 2010, Tilman et al. 2017). As such, conservationists are increasingly turning to restoration of habitats and animal populations (Török and Helm 2017, Hale et al. 2019).

Translocation is a valuable tool for reestablishing animal populations in restored habitats where barriers to natural recolonization exist (Griffith 1989, Seddon 2010). Yet many translocation programs still suffer from low success rates despite a >100-year history of translocation research (Kleiman 1989, Fischer and Lindenmayer 2000).

Calls to improve translocation efficacy point to inadequate monitoring and a lack of methods testing (Sarrazin and Barbault 1996, Hein 1997, Seddon et al. 2007). Most translocations remain largely descriptive and, though monitoring has improved, it often ignores key vital rates (Armstrong and Seddon 2008, Hale et al. 2019). A large number of strategies (e.g., release strategy, selection of founding population) can be employed to improve vital rates and, thus, translocation success (Batson et al. 2015b). Studies designed to test effects of strategies on demographic performance should improve success of future translocations (Nichols and Williams 2006).

Fecundity is one metric of long-term translocation success (e.g., establishing a self-sustaining population) particularly in species on the “fast” end of the fast-slow continuum of life histories (Griffith 1989, Oli 2004, Baxter et al. 2009). Translocated animals with low annual adult survival must reproduce quickly to establish a self-sustaining population. For these species, fecundity has a disproportionate impact on population growth and is often one of the most labile vital rates (Saether and Bakke 2000). Yet, few studies evaluate vital rates that contribute to fecundity (Hale et al. 2019).

Fecundity is often difficult to measure empirically because of partial observability, misclassification of breeding state, and/or low detection of animals (Etterson et al. 2011). Obtaining unbiased estimates of reproductive vital rates is challenging because many individuals

die during the breeding season (Dobson and Oli 2007). Individuals must survive to reproduce; therefore, seasonal reproductive rates are conditional on seasonal survival. Some studies account for high mortality bias by only calculating reproductive rates for individuals that survived an entire breeding season (Hernández et al. 2005, Scott et al. 2013, Downey et al. 2017). However, excluding certain individuals can bias reproductive estimates, as those likely to survive the breeding season are often the fittest and most fecund, leading to incomplete accounting of reproduction. High rates of reproductive failure present an additional challenge because reproductive events (e.g., litters, nests) are available for detection for a short time (Peron et al. 2014, Blomberg et al. 2015). Thus, some failed reproductive events are undetected, producing bias in estimates of reproductive success and negative bias in the number of nesting attempts (Peron et al. 2014).

Multi-state mark-recapture (MSMR) models are analytical tools developed to estimate population parameters (Lebreton and Pradel 2002) and can account for bias in reproductive rates resulting from partial observability. Reproductive vital rates can be estimated conditional on the individual being alive, while also allowing for imperfect detection, unobservable states, and state uncertainty (Kendall et al. 2003, Lebreton et al. 2009, Kendall et al. 2012). Explicitly modeling uncertainty in the observation process improves precision and accuracy of parameter estimates (Conn and Cooch 2009). MSMR models have been applied when aspects of reproduction were difficult to monitor, including misclassification of reproductive status (Kendall et al. 2004), individuals that skip breeding resulting in unobserved states (Converse et al. 2009), or when the stage at which nest failure occurred was uncertain (Setash et al. 2020). Here I present an application of a MSMR model with state uncertainty (MSMR-SU) to test hypotheses concerning

the effects of translocation strategies on reproduction of scaled quail (*Callipepla squamata*), a grassland bird with a fast life history.

Grassland bird species in North America have experienced precipitous declines largely from loss, fragmentation, and degradation of grassland habitats (Rosenberg et al. 2019). Many gallinaceous grassland birds, such as prairie grouse (*Tympanuchus* spp.), sage-grouse (*Centrocercus* spp.), and quails (Odontophoridae), are candidates for translocation (Carrlson et al. 2014, Martin et al. 2017, Ebenhoch et al. 2019, Mathews et al. 2019) and also tend to exhibit relatively fast life histories (Gaillard et al. 1989). Scaled quail (*Callipepla squamata*) are one such species that have declined throughout their native range in the southwestern U.S. as a result of brush encroachment and spatial aggregation of mono-crop agriculture (Rho et al. 2015). Translocation as a population restoration tool has been the focus of recent research and management discussion for scaled quail (Zornes and Bishop 2009, Ruzicka et al. 2017, Yancey 2019). Scaled quail populations exhibit large annual variation in survival, fecundity, and abundance (Lusk et al. 2007, Silvy et al. 2007). Their life histories are defined by low annual survival (~25%) which is balanced by high reproductive potential (Silvy et al. 2007).

Choice of release strategy, source population, and selection of age class are common translocation strategies manipulated to improve translocation success (Batson et al. 2015a, Houde et al. 2015). Although benefits from refining these translocation strategies are typically framed in terms of survival and movements for a particular species, all three may influence reproduction (Chapter 2). Delayed release strategies (i.e., holding translocated animals prior to release) have been used successfully for many species to acclimatize individuals, decrease movement, and increase site fidelity (Batson et al. 2015a, Tetzlaff et al. 2019). Most avian

translocations have employed an immediate release strategy, including translocations of northern bobwhites (Terhune et al. 2007, Baxter et al. 2009, Kaler et al. 2010, Gruber-Hadden et al. 2016, Downey et al. 2017). However, a delayed release can be beneficial for some gallinaceous species (Rodgers 1992, Snyder et al. 1999). Delayed release allows social species with small home ranges, e.g., many gallinaceous species, to benefit by developing social relationships prior to release (Moseby et al. 2014). This may confer benefits for a species, such as scaled quail, whose reproductive strategy involves forming pair bonds. Experimental studies on scaled quail found that a 4-week holding period was effective at reducing scaled quail dispersal off site compared to immediate release (Ruzicka et al. 2017) and that increased holding time resulted in a tradeoff between increased mortality and decreased dispersal (Chapter 2). Longer holding times reduced mortality of Gambel's quail (*Callipepla gambelii*) (Acevedo et al. 2023). No studies have addressed the impacts of a delayed release on quail or other gallinaceous species reproduction.

Selecting a source population from a similar habitat to the release area may confer advantages in reproduction if pre-release experiences translate to the new environment (Frair et al. 2007, Houde et al. 2015). Chestnut-bellied scaled quail (*Callipepla squamata castanogastris*) translocated from the South Texas Plains ecoregion to the Rolling Plains ecoregion, where the Arizona subspecies (*C. squamata pallida*) is native, exhibited poor survival and reproduction (Yancey 2019). No studies have evaluated reproduction of quail translocated within their native range, but from dissimilar habitat types. Stress is known to disrupt avian reproduction and may be heightened for individuals less familiar with the release area habitat even if they are native (Wingfield 1984, Dickens and Bentley 2014).

First-time breeders in avian species often have lower reproductive success (Martin 1995) and an age effect could be exacerbated in translocated individuals due to the stress associated with the translocation process (Dickens et al. 2010). Translocated adult sage grouse and wild turkey (*Meleagris gallopavo*) hens are more successful breeders than yearling birds (Lopez et al. 2000, Duvuvuei et al. 2017), although they exhibit relatively slower life histories than scaled quail. Pleasant et al. (2006) found that yearling scaled quail had lower nest success than adults during the first year of their study, but equivalent nest success to adults in the following year.

I used an MSMR-SU model to estimate the effect of release strategy, source population, and age on nesting propensity, renesting propensity, and nest survival of translocated Arizona scaled quail hens in the Rolling Plains ecoregion of Texas. Specifically, my objectives were to determine the effect of a 1–9-week delayed release, compare quail sourced from the Rolling Plains and the Edwards Plateau ecoregions, and compare adults to yearlings. I hypothesized that translocated quail with longer holding times would exhibit increased reproductive performance because they would have the opportunity to form pair bonds prior to release. Further, I hypothesized individuals from within the Rolling Plains would outperform those from the Edwards Plateau, and adults would outperform juveniles in all metrics. Understanding how translocation strategies effect scaled quail reproductive performance post-release will help guide reintroduction protocols in scaled quail and similar species.

METHODS

Study area

The release site encompassed >40,000 ha of contiguous rangeland owned by a cooperative of 5 private ranches in the South Wichita River Basin of Knox County, Texas, USA. I selected this study area based on the quantity, quality, and interconnectedness of habitat and because scaled quail were common to abundant in Knox County prior to about 1988 and the degradation of the habitat through brush encroachment (Rollins 2007). Management on all properties integrated for-profit cattle ranching with goals that included the promotion of deer (*Odocoileus* spp.), wild turkey (*Meleagris gallopavo*) and quail. All properties had deer feeders, but not quail feeders, and engaged in population control of feral swine (*Sus scrofa*). Hunting for scaled quail did not occur within the last 10 years prior to the study because of low populations and did not occur during this study. Landowners engaged in extensive management to restore native grasslands (e.g., brush removal via chaining, native plant seeding, and sustainable grazing management practices) at these locations approximately 6 years prior to this study. I released scaled quail at two locations approximately 8 km apart, centrally located within this larger study area. I caught wild scaled quail on 6 private ranches in the western Edwards Plateau and Rolling Plains ecoregions. Scaled quail populations in the western Edwards Plateau have been stable or increasing since 1966, while Rolling Plains populations decreased during that same period (Sauer et al. 2017). All source sites supported viable populations. For more information on the habitat at release and source sites see Chapter 2.

Field Methods

I translocated quail during February and March 2016–2017. Limits on the number of quail translocated from each source site were determined by the landowners and were based on current population and size of the area trapped. I removed 25–100 individuals per site using standard walk-in wire funnel traps (Gooden 1953, Ruzicka et al. 2016). All quail were weighed, banded (aluminum size 7 butt-end band; National Band and Tag Co., Newport, KY), classified by age and sex, and sorted into 20 groups of 18–20 quail. I grouped individuals caught together when possible. I randomly selected five to six females >150 g from each group (i.e., 50% of released females) and fitted them with 6 g necklace style radio-transmitters (American Wildlife Enterprises, Monticello, FL). I radioed only females to ensure that I could follow the reproductive process and that sample sizes were adequate. The transmitters were equipped with a mortality switch that was activated after 12 hours of no movement. Collar life span was a maximum of 7–9 months. I transported quail in plastic gamebird carriers (GQF Manufacturing Company Inc., Savannah, GA) stocked with food and water and covered with a black sheet to reduce stress. All quail were held in a well-ventilated area and transported to the release site within 48 hours of capture.

Each quail group was assigned randomly to one of two central release points (see description above). Groups were introduced to a holding pen in the field (Surrogator™, Wildlife Management Technologies, Wichita, KS) stocked with 25 kg of a mixture of grain sorghum and a commercially available layer ration. Holding pens were positioned on each release site approximately 200 m apart and set in an approximate circle. I chose this approach so that quail held in each pen could hear other quail vocalizing. The length of holding time varied from 4–8

weeks in 2016 and 1–9 weeks in 2017 by 1-week intervals. The specific holding time for the group was determined by the capture date. I replicated the delayed release treatments for each source population on each release ranch such that there were 20 treatment groups (10 per ranch) in 2016 and 36 treatment groups (18 per ranch) in 2017. I coordinated trapping efforts so that treatment groups could be released over a 10–15-day period in April despite holding times that varied by as much as 8 weeks. I chose to standardize on a similar release date at a cost of having holding times for groups correlated with capture date (i.e., coveys captured first received the longest holding times).

I monitored the mortality status of radio-marked quail daily post-release for the entirety of the breeding season (10 Apr–15 Aug; 131 days). I located each hen visually to determine breeding state (e.g., non-breeding, nesting, failed nester, or brooding) approximately 3 times per week. I defined non-breeding as not actively incubating a nest or having previously hatched a nest on the day the hen was observed. The number of observations varied due to weather, site access, and dispersal distance of the individual. These observations were collected from 10 am–4 pm. Scaled quail typically take two off-nest bouts each day, thus I attempted to time my monitoring to coincide with the time that would result in the highest probability of observing a hen incubating a nest if she had initiated one (Carroll et al. 2018). I defined nest initiation as the start of incubation because I was unable to reliably observe the egg laying stage. Once I discovered a hen incubating a nest, I collected information on clutch size while hens were on recess from incubation during early morning or evening hours. I considered a hen to have hatched a nest if at least one eggshell remaining in the nest indicated signs of pipping or I observed the hen with chicks. Hens were considered failed nesters if all eggs in the nest were destroyed or missing, and the hen was no longer incubating nor observed with chicks. I was

careful to avoid flushing nesting or brooding hens or disturbing the vegetation surrounding the nest. I trapped and handled all birds in accordance with the approval of Texas Parks and Wildlife Department (Scientific permit no. SPR-0690–152) and the Agriculture Animal Care and Use Committee (AACUC) at Texas A&M University (AUP # 2016–003A).

Data Analysis

I constructed a multi-state mark-recapture model with state uncertainty (MSMR-SU) to model daily transitions among breeding states conditional on a hen being alive. I considered hens to be in one of five biological states at time t : non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D) (Figure 3.1). I estimated two parameter types: transition among states (Ψ) and the probability of being classified as unknown given the true state (δ) (Kendall et al. 2012). I explicitly modeled mortality as a transition to a dead state (D) because the data were known fate (I could observe the death); thus I fixed the redundant survival (S) parameters to 1 in live states (A, N, F, and B) and $S = 0$ for dead state (D) (i.e., censored after death). I assumed detection (p) = 1 for all states because all hens were radio-collared, though the monitoring intervals were uneven.

I defined nesting propensity (Ψ_{AN}) as the probability that a hen transitioned from non-breeding (A) to nesting (N). Once a hen had a nest fail, I considered her to be a failed nester for the remainder of the breeding season or until she initiated another nest, therefore I fixed transitions Ψ_{NA} and Ψ_{FA} to 0. Renesting propensity (Ψ_{FN}) was the probability that a failed nester transitioned back into a nesting state. I defined daily nest survival (Ψ_{NN}) as the probability that a hen remained in a nesting state. The probability of nest success was calculated as $\hat{\Psi}_{NN}^{23}$ to account

for a 23-day average incubation period (Schemnitz et al. 2009). If a hen successfully hatched a nest, I considered her to be in a brooding state for the remainder of the breeding season or until she died. I did not observe any hens reneating after a successful hatch. I considered a 6th biologically relevant state, failed brooders, in initial stages of model building. Inclusion of this state would have allowed us to estimate brood survival as the transition from brooding to failed brooder; however, I did not collect enough brood observation data to estimate this transition due to poor detection of chicks.

I assumed that hens could begin nesting immediately because I released hens at the beginning of breeding season. Although I attempted to monitor hens during the time of day when they would be most likely to be incubating nests, nest initiation was uncertain until I made an observation of a hen incubating a nest. Given that I had observed a non-nesting hen (e.g., feeding, walking, or running), I could never be certain that non-nesting (A or F) was her true state. I incorporated this observational uncertainty in nest initiation by allowing for two “events” in my model framework (Pradel 2005).

Hens observed not nesting were assigned event 1 which allowed for one of three potential realities: observed not nesting given truly not nesting $\delta_{1|A}$, observed not nesting given nesting but currently on an off-bout $\delta_{1|N}$, or observed not nesting, but had previously initiated and failed an unobserved nest, thus was truly a failed nester $\delta_{1|F}$. Event 2 designated observations of hens with known previous nest failures. Similarly, failed nesters could be observed not nesting and were truly not nesting $\delta_{2|F}$, or observed not nesting, but were truly nesting and on an off-bout $\delta_{2|N}$. I assumed that I could document nest failures and successes without error due to eggshell evidence and presence/absence of a brood (Burger et al. 1995). I implemented the model in Program

MARK using maximum likelihood estimation and Akaike's information criterion corrected for small sample size (AIC_C) for model selection (White and Burnham 2009).

I used a three-step modeling process. To determine the basic model structure, I first developed a limited model set to test for evidence of differing mortality rates conditional on reproductive state. My model set included models to test the following hypotheses: 1) mortality differed by state ($\Psi_{AD} \neq \Psi_{ND} \neq \Psi_{FD} \neq \Psi_{BD}$), 2) mortality was equivalent across states ($\Psi_{AD} = \Psi_{ND} = \Psi_{FD} = \Psi_{BD}$), 3) mortality in non-breeding or failed breeder states was different from nesting or brooding states ($\Psi_{AD} = \Psi_{FD} \neq \Psi_{ND} = \Psi_{BD}$), 4) mortality in non-breeding state differed ($\Psi_{AD} \neq \Psi_{FD} = \Psi_{ND} = \Psi_{BD}$), 5) mortality in failed nester state differed ($\Psi_{FD} \neq \Psi_{AD} = \Psi_{ND} = \Psi_{BD}$), 6) mortality in nesting state differed ($\Psi_{ND} \neq \Psi_{AD} = \Psi_{FD} = \Psi_{BD}$), and 7) mortality in brooding state differed ($\Psi_{BD} \neq \Psi_{AD} = \Psi_{FD} = \Psi_{ND}$). The delta parameters were held constant in each model. Two delta parameters ($\delta_{2|N}$ and $\delta_{1|F}$) were fixed to low (<0.0001) constant probabilities to aid in model convergence because the estimated daily probability for those parameters was indistinguishable from 0. I used the top model describing state-specific mortality (Table 3.1) to evaluate more complex relationships between the reproductive parameters and variables.

I used an all-combinations approach to model selection to evaluate evidence for the effects of translocation strategy on reproduction and mortality (Doherty et al. 2012, Bromaghin et al. 2013, Morin et al. 2020). I constructed a balanced set of all additive models plus a constant model for each parameter (e.g., mortality, nesting propensity, re-nesting propensity, and nest success) in turn, while holding all other parameters constant (i.e., 4 separate model sets; Table 3.2–3.5). Additive models included all combinations of release treatment (release), source population (source), age, release ranch (ranch), and year variables. I include only additive models because

interactions caused issues with model convergence. Although I focused on reproduction, I also modeled mortality as a function of the variables to provide more accurate estimates of reproductive parameters because reproduction was conditional on a hen being alive. For a full analysis and discussion of mortality in the population studied here see Chapter 2.

I then calculated cumulative variable weights (w_i) for the variables in each model set (Table 3.6). Variable and parameter combinations with cumulative $w_i > 0.5$ were retained for the third step of modeling (Barbieri and Berger 2004). In the third step, I built a balanced model set of all additive combinations of each variable and parameter combination with $w_i > 0.5$ (Table 3.7). I interpreted estimates from a predictive model containing all variables with cumulative $w_i > 0.5$ in the final model set. I report predictor coefficient estimates as well as breeding season (i.e., monitoring period) probabilities and odds ratios where appropriate because daily probabilities are often small and difficult to interpret biologically. I approximated standard errors for breeding season estimates using the Delta method in the `msm` package in R (Jackson 2011, www.r-project.org).

RESULTS

I trapped and translocated 888 scaled quail (450 females, 443 males) from 2016-2017. Of those, 220 were radio-marked hens (138 yearlings, 82 adults). I experienced flooding on one release site in 2016 that resulted in the mortality of the Rolling Plains 6-week delayed release treatment group. I censored the radio-marked individuals in that group ($n = 6$), 1 individual that died of unknown causes in the holding pen, and 1 individual that died of radio-collar entanglement. Hens produced 101 nests (2016 = 50, 2017 = 51) with an average of 11 eggs per clutch (SD = 2.18) in the first nest, an average of 8 eggs per clutch (SD = 2.35) in the second nest, and 43 broods

(2016 = 27, 2017 = 16; apparent nest success = 43%). The most common nesting substrate was redberry juniper (*Juniperus pinchotii*; Appendix 1). Nests were initiated from May–August in 2016 and May–July in 2017. The average date of first nest initiation was 6 June in 2016 and 9 June in 2017. Date of first nest initiation was not correlated with release treatment of the hen ($r = 0.06$). In total, I recorded 3,129 observations of reproductive state. I did not find evidence that mortality differed by breeding state (Table 3.1). Release, ranch, and year were important variables in the preliminary modeling steps (Tables 3.2–3.6). My final predictive model based on cumulative weights was $\hat{\Psi}_{AN}(\text{age}) \hat{\Psi}_{FN}(\text{release} + \text{year}) \hat{\Psi}_{NN}(\cdot) \hat{\Psi}_{NB}(\cdot) \hat{\Psi}_{AD} = \hat{\Psi}_{ND} = \hat{\Psi}_{FD} = \hat{\Psi}_{BD}(\text{release} + \text{ranch} + \text{year}) \hat{\delta}_{1|A}(\cdot) \hat{\delta}_{1|N}(\cdot) \hat{\delta}_{1|F}(\cdot)$ (Tables 3.7 and 3.8).

Nesting propensity was 1.5 times greater ($\beta_{\hat{\Psi}_{AN}(\text{age})} = -0.44$, SE = 0.12) in yearling hens compared to adults (Figure 3.2). Over the entire monitoring interval, the probability that a yearling initiated a nest was 0.81 (SE = 0.01) and the probability that an adult initiated a nest was 0.66 (SE = 0.03). Release treatment affected re-nesting propensity, but no other reproductive parameters (Figure 3.3). For each additional week of holding time, the probability that a hen would re-nest was 1.3 times less likely ($\beta_{\hat{\Psi}_{FN}(\text{release})} = -0.31$, SE = 0.13). This effect was mediated by a strong difference in re-nesting propensity between years. Hens were 3.5 times more likely ($\beta_{\hat{\Psi}_{FN}(\text{year})} = -1.27$, SE = 0.67) to nest again following a failure in 2016 compared to 2017. Given that a hen had initiated then failed a nest and assuming average release treatment, the probability that she would re-nest was 0.67 (SE = 0.01) in 2016 and 0.26 (SE = 0.20) in 2017 across the entire breeding season. I found that source population did not affect any of the reproductive parameters, nor did I find an effect of any variables on nest survival. Daily nest survival was 0.94 (SE = 0.01) and nest success, assuming a 23-day incubation, was 0.24 (SE =

0.03). The probability that a hen did not have a nest and was observed not nesting was 0.99 ($\beta_{\delta_{1|A}} = 7.25$, SE = 0.99) for hens that had not previously nested and 0.86 ($\beta_{\delta_{2|F}} = 1.78$, SE = 0.15) for hens that had previously failed a nest on any given observation day. The probability that a hen truly had a nest, but was observed off-nest was 0.04 ($\beta_{\delta_{1|N}} = -3.29$, SE = 0.26) on any given observation day.

DISCUSSION

My goal was to obtain unbiased estimates of translocated scaled quail reproduction to evaluate the effect of delayed release strategy, source population, and age. The MSMR-SU model allowed us to estimate nesting propensity, renesting propensity, and nest survival conditional on hen survival in a single model, while also accounting for nesting status uncertainty. I was able to describe nuanced effects of translocation strategies on reproductive performance. The estimates of nesting and renesting propensity reported here are the first for scaled quail.

I found that longer delayed release holding time decreased reproductive performance by reducing renesting propensity but did not affect initial nesting propensity. This effect contradicted my hypothesis that a delayed release would be beneficial for reproduction because of the social bonds formed in holding. A negative effect of delayed release may be attributable to accumulated stress during the holding period. Translocation is inherently stressful for individuals and chronic stress from a lengthy holding period has the potential to negatively impact physical condition (Letty et al. 2007, Dickens et al. 2010). Longer holding times reduced dispersal of translocated scaled quail, but increased mortality (Chapter 2). I attributed the increase in mortality to stress incurred during the translocation and holding period.

Individuals also incur physiological stress from initiating breeding (Hanssen et al. 2005). In my study, detrimental effects of holding period did not manifest until hens were faced with the decision of initiating a second nest. Carryover effects, or events in previous time periods that produce a sub-lethal impact on performance in subsequent time periods, can influence an individual's decision to breed (Rubenstein 2007, Harrison et al. 2011). Grandmont et al. (2023) experimentally manipulated time in captivity of female greater snow geese (*Anser caerulescens*) prior to breeding season and found that as holding time increased, breeding propensity declined. Birds incur significant energetic costs during egg-laying and incubation (Guillemette and Pelletier 2022). Thus, reduced renesting propensity in translocated scaled quail may be due to the combined carryover effects of a lengthy holding period and the cost of producing a first nest.

I do not attribute reduction in renesting propensity with longer holding period to later release date or a reduced length of nesting season because I attempted to control for release date in my trapping schedule. I note that release dates varied by 10-15 days each year such that birds with longer holding times tended to be released later in the season, though there was some variation. However, the release treatment was not correlated with nest initiation date meaning that hens with longer holding times did not have a later start to nesting season on average.

The difference in renesting propensity between years is most likely attributable to differences in weather patterns. The link between reproductive success of scaled quail and annual spring-summer weather patterns is well established (Campbell et al. 1973, Lerich 2002, Pleasant et al. 2006, Gonzalez 2015). My study site experienced cool and wet weather throughout spring and summer of 2016. However, 2017 was characterized by 22 weeks of moderate to severe drought conditions throughout March-August (National Drought Mitigation Center, U.S. Department of

Agriculture and National Oceanic and Atmospheric Association; droughtmonitor.unl.edu). For many species, reproductive phenology is heavily influenced by environmental variables (Visser et al. 2010). I observed a decrease in overall breeding season length and markedly decreased effort in the drought year.

I did not find an effect of source population on any of the reproductive rates I evaluated.

Potentially, the lack of effect could be because I translocated individuals within their native range, whereas Yancey et al (2019) translocated non-native subspecies. Northern bobwhites (*Colinus virginianus texanus*) in Texas translocated outside of their native range also exhibited poor reproduction when compared to translocated individuals of the native subspecies (*Colinus virginianus mexicanus* and *Colinus virginianus taylori*; Nedbal et al. 1997, Palarski et al. 2023).

Reproduction of native sage-grouse translocated from disparate populations and habitats was unaffected by source population (Baxter et al. 2008). However, non-native mountain quail (*Oreortyx pictus eremophilus*) subspecies performed similarly in both reproduction and survival to native translocated individuals (*O. pictus pictus*). Regardless, my findings indicate that differences in habitat between ecoregions are relatively inconsequential for scaled quail in terms of source populations (Gould 1975). Thus, the Edwards Plateau ecoregion is a suitable source for translocation efforts in the Rolling Plains.

My findings that yearling scaled quail were more likely to initiate nests than adults in both years contradicted studies of sage-grouse and wild turkeys (Lopez et al. 2000, Duvuvuei et al. 2017). Though I cannot say with certainty why scaled quail would differ from other gallinaceous species, higher nest propensity in yearling birds may be related to their faster life history strategy relative to sage-grouse and turkeys. Individuals with a short lifespan have more incentive to

reproduce earlier in life (Stearns 1992). However, life history strategy does not fully explain why yearlings would be more likely to initiate nests. Behavioral flexibility, or the ability to change preferences based on changing circumstances, may be an explanation for the pattern I observed (Wright et al. 2010, Logan 2016, Beever et al. 2017). Younger individuals tend to be more behaviorally flexible and outperform older individuals when translocated (Roth and Krochmal 2015, Berger-Tal and Saltz 2016, van Toor et al. 2017). Translocated yearling mountain quail survived at a greater rate than adults, which would support a behavioral flexibility hypothesis, although the authors attributed this effect to differences in boldness between the two age groups (Troy et al. 2013).

Nest success was unaffected by the tested variables; however, the small sample size might have limited detection of treatment differences. My estimated nest success (24%) was lower than the apparent hatching rate of found nests (43%) indicating that nests failed before I were able to detect them (Jehle et al. 2004). Apparent hatch rate was comparable or lower than what Pleasant et al. (2006) reported for resident scaled quail in the southern High Plains ecoregion (e.g., 64% and 44%). Given that a hen was truly nesting, my probability of observing the hen off-nest was 0.04 per observation despite protocols to monitor hens for nests only during the time of day when they were most likely to be on the nest. Not accounting for that daily observation error likely would have resulted in a 19% bias in estimated nesting success. This finding highlights the necessity of using a model, such as MSMR-SU, that can capture error arising from the observation process even when using data from radio-marked individuals.

Biases or violations of assumptions in radio-telemetry arising from imperfect detection or observation of states are often unaddressed in studies, yet many powerful analytical tools exist to

account for these biases (Devineau et al. 2014). Radio-telemetry datasets are often rich in information (O'Toole et al. 2021). Recognizing when biases are problematic for a particular dataset and/or question, then using an appropriate analytical framework to account for the bias will insure that inferences from radio-telemetry studies provide useful management recommendations (Devineau et al. 2014). I urge future radio-telemetry based studies, particularly in fast-lived species, to consider and account for biases unique to their study species, location, and/or questions.

MANAGEMENT IMPLICATIONS

Delayed release may decrease reproductive output in translocated scaled quail. However, a delayed release is often logistically more feasible for group releases of social species because capturing wild animals is time- and labor-intensive and can reduce dispersal off site (Chapter 2). When deciding on release strategy at the outset of a translocation, weighing potential costs and benefits at each stage of the animal's life cycle will improve the chance of success.

Prioritizing the translocation of yearling scaled quail to increase reproductive output can be an effective strategy. Scaled quail populations are usually composed primarily of yearlings in years when they are most abundant on source sites. Thus, timing translocations for years with the highest abundances will de facto result in translocated populations dominated by juvenile birds if the source population is sampled randomly, and it will alleviate impacts to the source population (Verdon et al. 2021). The El Niño–Southern Oscillation cycle has strong influence over drought patterns in the Southwestern U.S. and predictive capability has improved in recent years making predictions by the Climate Prediction Center (NWS NOAA; <https://www.cpc.ncep.noaa.gov>) a

useful tool for practitioners to predict if release site conditions will be favorable when deciding whether to initiate a translocation on a given year (L'Heureux et al. 2017).

Table 3.1. Model results from a first modeling step to determine basic model structure by testing for evidence of differing mortality rates conditional on reproductive state in translocated scaled quail (*Callipepla squamata*). Hens were considered to be in one of five biological states: non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D), thus transitions in the model described mortality in non-breeding (Ψ_{AD}), nesting (Ψ_{ND}), reneating propensity (Ψ_{FN}), and mortality outside release area (Ψ_{BD}). Hens observed not nesting were assigned event 1 which allowed for one of three potential realities: observed not nesting and was truly not nesting ($\delta_{1|A}$) observed not nesting, but did have a nest and was temporarily off the nest ($\delta_{1|N}$), or observed not nesting, but had previously initiated and failed an unobserved nest, thus was truly a failed nester ($\delta_{1|F}$). Hens with known previous nest failures were assigned event 2 which allowed for observations where failed nesters were observed not nesting and were truly not nesting ($\delta_{2|F}$), or observed not nesting, but were truly nesting ($\delta_{2|N}$). Two delta parameters ($\delta_{2|N}$ and $\delta_{1|F}$) were fixed to low (<0.0001) constant probabilities to aid in model convergence. The corrected Akaike's information criterion (AIC_c) for the top model was 4697.31.

Model	ΔAIC_c	w_i^1	L^2	k^3	Deviance
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\cdot) \Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	0.00	0.55	1.00	8	4683.27
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}(\cdot) \Psi_{BD}(\cdot) \Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	3.26	0.11	0.20	9	4682.51
$\Psi_{AD}=\Psi_{FD}=\Psi_{BD}(\cdot) \Psi_{ND}(\cdot) \Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	3.62	0.09	0.16	9	4682.87
$\Psi_{AD}=\Psi_{ND}=\Psi_{BD}(\cdot) \Psi_{FD}(\cdot) \Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	3.68	0.09	0.16	9	4682.92
$\Psi_{AD}=\Psi_{FD}(\cdot) \Psi_{ND}=\Psi_{BD}(\cdot) \Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	3.89	0.08	0.14	9	4683.14
$\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\cdot) \Psi_{AD}(\cdot) \Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	4.02	0.07	0.13	9	4683.27
$\Psi_{AD}(\cdot) \Psi_{ND}(\cdot) \Psi_{FD}(\cdot) \Psi_{BD}(\cdot) \Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	6.76	0.02	0.03	11	4681.98

¹ Akaike weights

² Model likelihood

³ Number of parameters

Table 3.2. Model results from a second modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), and year on translocated scaled quail (*Callipepla squamata*) reproductive parameters. Hens were considered to be in one of five biological states: non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D), thus transitions in the model described mortality in non-breeding (Ψ_{AD}), nesting (Ψ_{ND}), reneesting propensity (Ψ_{FN}), and mortality outside release area (Ψ_{BD}). Hens observed not nesting were assigned event 1 which allowed for one of three potential realities: observed not nesting and was truly not nesting ($\delta_{1|A}$) observed not nesting, but did have a nest and was temporarily off the nest ($\delta_{1|N}$), or observed not nesting, but had previously initiated and failed an unobserved nest, thus was truly a failed nester ($\delta_{1|F}$). Hens with known previous nest failures were assigned event 2 which allowed for observations where failed nesters were observed not nesting and were truly not nesting ($\delta_{2|F}$), or observed not nesting, but were truly nesting ($\delta_{2|N}$). Two delta parameters ($\delta_{2|N}$ and $\delta_{1|F}$) were fixed to low (<0.0001) constant probabilities to aid in model convergence. All other transitions (Ψ_{AN} , Ψ_{FN} , Ψ_{NN}) were held constant (.) while focusing on $\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$. The corrected Akaike's information criterion (AIC_c) for the top model was 4398.66.

Model	ΔAIC_c	w_i^1	L^2	k^3	Deviance
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{release} + \text{year})$	0.00	0.26	1.00	11	4372.54
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{year})$	1.58	0.12	0.45	10	4376.14
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{source} + \text{release} + \text{year})$	1.90	0.10	0.39	12	4372.42
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{ranch} + \text{release} + \text{year})$	1.95	0.10	0.38	12	4372.47
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{release} + \text{year})$	2.29	0.08	0.32	10	4376.85
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{ranch} + \text{year})$	2.72	0.07	0.26	11	4375.26
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{source} + \text{year})$	3.47	0.05	0.18	11	4376.01
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{ranch} + \text{source} + \text{release} + \text{year})$	3.83	0.04	0.15	13	4372.33
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{year})$	3.88	0.04	0.14	9	4380.45
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{source} + \text{release} + \text{year})$	4.19	0.03	0.12	11	4376.73
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{release} + \text{year})$	4.20	0.03	0.12	11	4376.74
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{ranch} + \text{source} + \text{year})$	4.56	0.03	0.10	12	4375.08

$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{year})$	4.95	0.02	0.08	10	4379.51
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{source} + \text{year})$	5.77	0.01	0.06	10	4380.33
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{source} + \text{release} + \text{year})$	6.07	0.01	0.05	12	4376.59
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{source} + \text{year})$	6.79	0.01	0.03	11	4379.33
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch})$	20.70	0.00	0.00	9	4397.28
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{ranch})$	21.90	0.00	0.00	10	4396.45
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{release})$	22.19	0.00	0.00	10	4396.75
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{source})$	22.64	0.00	0.00	10	4397.19
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{ranch} + \text{release})$	22.77	0.00	0.00	11	4395.31
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\cdot)$	23.52	0.00	0.00	8	4402.11
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{ranch} + \text{source})$	23.87	0.00	0.00	11	4396.41
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{source} + \text{release})$	24.13	0.00	0.00	11	4396.67
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{ranch} + \text{source} + \text{release})$	24.77	0.00	0.00	12	4395.29
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age})$	24.87	0.00	0.00	9	4401.44
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{release})$	24.89	0.00	0.00	9	4401.46
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{source})$	25.47	0.00	0.00	9	4402.05
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{release})$	25.68	0.00	0.00	10	4400.24
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{source} + \text{release})$	26.84	0.00	0.00	10	4401.40
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{source})$	26.85	0.00	0.00	10	4401.41
$\Psi_{AN}(\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{age} + \text{source} + \text{release})$	27.68	0.00	0.00	11	4400.22

¹ Akaike weights

² Model likelihood

³ Number of parameters

Table 3.3. Model results from a second modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), and year on translocated scaled quail (*Callipepla squamata*) mortality and reproductive parameters. Hens were considered to be in one of five biological states: non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D), thus transitions in the model described mortality in non-breeding (Ψ_{AD}), nesting (Ψ_{ND}), reneating propensity (Ψ_{FN}), and mortality outside release area (Ψ_{BD}). Hens observed not nesting were assigned event 1 which allowed for one of three potential realities: observed not nesting and was truly not nesting ($\delta_{1|A}$) observed not nesting, but did have a nest and was temporarily off the nest ($\delta_{1|N}$), or observed not nesting, but had previously initiated and failed an unobserved nest, thus was truly a failed nester ($\delta_{1|F}$). Hens with known previous nest failures were assigned event 2 which allowed for observations where failed nesters were observed not nesting and were truly not nesting ($\delta_{2|F}$), or observed not nesting, but were truly nesting ($\delta_{2|N}$). Two delta parameters ($\delta_{2|N}$ and $\delta_{1|F}$) were fixed to low (<0.0001) constant probabilities to aid in model convergence. All other transitions ($\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$, Ψ_{FN} , Ψ_{NN}) were held constant (.) while focusing on Ψ_{AN} . The corrected Akaike's information criterion (AIC_c) for the top model was 4420.04.

Model	ΔAIC_c	w_i^1	L^2	k^3	Deviance
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age)	0.00	0.13	1.00	9	4397.95
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + release)	0.71	0.09	0.70	10	4396.65
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + year)	1.21	0.07	0.55	10	4397.14
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (release)	1.45	0.06	0.48	9	4399.40
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + release + year)	1.60	0.06	0.45	11	4395.52
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + ranch)	1.80	0.05	0.41	10	4397.74
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + source)	1.85	0.05	0.40	10	4397.79
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (.)	2.15	0.04	0.34	8	4402.11
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + ranch + release)	2.49	0.04	0.29	11	4396.41
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + source + release)	2.55	0.04	0.28	11	4396.47
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + ranch + year)	2.98	0.03	0.23	11	4396.89
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (source + release)	3.09	0.03	0.21	10	4399.02
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + source + year)	3.10	0.03	0.21	11	4397.02
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (release + year)	3.22	0.03	0.20	10	4399.16
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + ranch + release + year)	3.33	0.02	0.19	12	4395.23
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (ranch + release)	3.35	0.02	0.19	10	4399.29
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{FN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{AN} (age + source + release + year)	3.48	0.02	0.18	12	4395.38

$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{age} + \text{ranch} + \text{source})$	3.64	0.02	0.16	11	4397.56
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{source})$	3.78	0.02	0.15	9	4401.73
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{ranch})$	4.08	0.02	0.13	9	4402.03
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{year})$	4.16	0.02	0.12	9	4402.11
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{age} + \text{ranch} + \text{source} + \text{release})$	4.32	0.02	0.12	12	4396.22
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{age} + \text{ranch} + \text{source} + \text{year})$	4.86	0.01	0.09	12	4396.76
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{source} + \text{release} + \text{year})$	4.88	0.01	0.09	11	4398.79
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{ranch} + \text{source} + \text{release})$	4.98	0.01	0.08	11	4398.90
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{ranch} + \text{release} + \text{year})$	5.12	0.01	0.08	11	4399.04
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{age} + \text{ranch} + \text{source} + \text{release} + \text{year})$	5.21	0.01	0.07	13	4395.09
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{ranch} + \text{source})$	5.69	0.01	0.06	10	4401.63
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{source} + \text{year})$	5.79	0.01	0.06	10	4401.73
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{ranch} + \text{year})$	6.09	0.01	0.05	10	4402.02
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{ranch} + \text{source} + \text{release} + \text{year})$	6.76	0.00	0.03	12	4398.66
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{AN}(\text{ranch} + \text{source} + \text{year})$	7.71	0.00	0.02	11	4401.63

¹ Akaike weights

² Model likelihood

³ Number of parameters

Table 3.4. Model results from a second modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), and year on translocated scaled quail (*Callipepla squamata*) mortality and reproductive parameters. Hens were considered to be in one of five biological states: non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D), thus transitions in the model described mortality in non-breeding (Ψ_{AD}), nesting (Ψ_{ND}), reneating propensity (Ψ_{FN}), and mortality outside release area (Ψ_{BD}). Hens observed not nesting were assigned event 1 which allowed for one of three potential realities: observed not nesting and was truly not nesting ($\delta_{1|A}$) observed not nesting, but did have a nest and was temporarily off the nest ($\delta_{1|N}$), or observed not nesting, but had previously initiated and failed an unobserved nest, thus was truly a failed nester ($\delta_{1|F}$). Hens with known previous nest failures were assigned event 2 which allowed for observations where failed nesters were observed not nesting and were truly not nesting ($\delta_{2|F}$), or observed not nesting, but were truly nesting ($\delta_{2|N}$). Two delta parameters ($\delta_{2|N}$ and $\delta_{1|F}$) were fixed to low (<0.0001) constant probabilities to aid in model convergence. All other transitions ($\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$, Ψ_{AN} , Ψ_{NN}) were held constant (.) while focusing on Ψ_{FN} . The corrected Akaike's information criterion (AIC_c) for the top model was 4408.56.

Model	ΔAIC_c	w_i^1	L^2	k^3	Deviance
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (release + year)	0.00	0.22	1.00	10	4384.46
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (release)	1.63	0.10	0.44	11	4388.10
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (age + release + year)	1.71	0.09	0.43	11	4384.14
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (source + release + year)	1.95	0.08	0.38	11	4384.39
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (ranch + release + year)	1.99	0.08	0.37	11	4384.42
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (ranch + release)	3.51	0.04	0.17	10	4387.97
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (source + release)	3.57	0.04	0.17	10	4388.03
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (age + ranch + release + year)	3.63	0.04	0.16	12	4384.04
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (age + release)	3.64	0.04	0.16	10	4388.10
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (.)	3.66	0.03	0.16	8	4392.15
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{NN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{FN} (age + source + release + year)	3.67	0.03	0.16	12	4384.09

$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{ranch} + \text{source} + \text{release} + \text{year})$	3.96	0.03	0.14	12	4384.38
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{year})$	4.81	0.02	0.09	9	4391.28
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age})$	5.11	0.02	0.08	9	4391.58
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{source})$	5.18	0.02	0.07	9	4391.66
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{ranch} + \text{source} + \text{release})$	5.49	0.01	0.06	11	4387.93
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{ranch} + \text{release})$	5.52	0.01	0.06	11	4387.96
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{ranch})$	5.58	0.01	0.06	9	4392.05
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{source} + \text{release})$	5.59	0.01	0.06	11	4388.03
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{ranch} + \text{source} + \text{release} + \text{year})$	5.63	0.01	0.06	13	4384.02
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{year})$	6.00	0.01	0.05	10	4390.46
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{source} + \text{year})$	6.33	0.01	0.04	10	4390.78
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{ranch} + \text{year})$	6.74	0.01	0.03	10	4391.19
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{source})$	6.79	0.01	0.03	10	4391.25
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{ranch})$	6.94	0.01	0.03	10	4391.39
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{ranch} + \text{source})$	7.15	0.01	0.03	10	4391.61
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{ranch} + \text{source} + \text{release})$	7.51	0.01	0.02	12	4387.93
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{source} + \text{year})$	7.74	0.00	0.02	11	4390.17
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{NN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{FN}(\text{age} + \text{ranch} + \text{year})$	7.80	0.00	0.02	11	4390.23

$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\cdot) \Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{FN}(\text{ranch} + \text{source} + \text{year})$	8.31	0.00	0.02	11	4390.74
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\cdot) \Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{FN}(\text{age} + \text{ranch} + \text{source})$	8.69	0.00	0.01	11	4391.13
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\cdot) \Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot) \Psi_{FN}(\text{age} + \text{ranch} + \text{source} + \text{year})$	9.61	0.00	0.01	12	4390.03

¹ Akaike weights

² Model likelihood

³ Number of parameters

Table 3.5. Model results from a second modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), and year on translocated scaled quail (*Callipepla squamata*) mortality and reproductive parameters. Hens were considered to be in one of five biological states: non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D), thus transitions in the model described mortality in non-breeding (Ψ_{AD}), nesting (Ψ_{ND}), reneating propensity (Ψ_{FN}), and mortality outside release area (Ψ_{BD}). Hens observed not nesting were assigned event 1 which allowed for one of three potential realities: observed not nesting and was truly not nesting ($\delta_{1|A}$) observed not nesting, but did have a nest and was temporarily off the nest ($\delta_{1|N}$), or observed not nesting, but had previously initiated and failed an unobserved nest, thus was truly a failed nester ($\delta_{1|F}$). Hens with known previous nest failures were assigned event 2 which allowed for observations where failed nesters were observed not nesting and were truly not nesting ($\delta_{2|F}$), or observed not nesting, but were truly nesting ($\delta_{2|N}$). Two delta parameters ($\delta_{2|N}$ and $\delta_{1|F}$) were fixed to low (<0.0001) constant probabilities to aid in model convergence. All other transitions ($\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$, Ψ_{AN} , Ψ_{FN}) were held constant (.) while focusing on Ψ_{NN} . The corrected Akaike's information criterion (AIC_c) for the top model was 4422.74.

Model	ΔAIC_c	w_i^1	L^2	k^3	Deviance
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (age)	0.00	0.09	1.00	9	4404.68
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (.)	0.41	0.07	0.82	8	4407.10
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (source)	0.58	0.07	0.75	9	4405.27
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (year)	0.65	0.07	0.72	9	4405.33
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (age + source)	0.69	0.06	0.71	10	4403.36
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (source + year)	1.12	0.05	0.57	10	4403.79
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (release)	1.44	0.04	0.49	9	4406.12
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (age + year)	1.47	0.04	0.48	10	4404.13
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (source + release)	1.49	0.04	0.48	10	4404.15
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (age + ranch)	1.85	0.04	0.40	10	4404.52
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (age + release)	1.86	0.04	0.39	10	4404.53
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (age + source + year)	2.23	0.03	0.33	11	4402.89
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (ranch)	2.25	0.03	0.33	9	4406.93
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (release + year)	2.27	0.03	0.32	10	4404.94
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$ (.) Ψ_{AN} (.) Ψ_{FN} (.) Ψ_{NB} (.) $\delta_{1 A}$ (.) $\delta_{1 N}$ (.) $\delta_{2 F}$ (.) Ψ_{NN} (age + source + release)	2.43	0.03	0.30	11	4403.08

$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{ranch} + \text{source})$	2.48	0.03	0.29	10	4405.15
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{ranch} + \text{year})$	2.54	0.03	0.28	10	4405.21
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{ranch} + \text{source})$	2.60	0.02	0.27	11	4403.25
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{source} + \text{release} + \text{year})$	2.61	0.02	0.27	11	4403.27
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{ranch} + \text{source} + \text{year})$	3.05	0.02	0.22	11	4403.71
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{ranch} + \text{release})$	3.23	0.02	0.20	10	4405.90
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{ranch} + \text{source} + \text{release})$	3.34	0.02	0.19	11	4403.99
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{ranch} + \text{year})$	3.34	0.02	0.19	11	4404.00
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{release} + \text{year})$	3.39	0.02	0.18	11	4404.04
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{ranch} + \text{release})$	3.69	0.01	0.16	11	4404.34
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{source} + \text{release} + \text{year})$	4.05	0.01	0.13	12	4402.69
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{ranch} + \text{release} + \text{year})$	4.12	0.01	0.13	11	4404.77
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{ranch} + \text{source} + \text{year})$	4.16	0.01	0.13	12	4402.79
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{ranch} + \text{source} + \text{release})$	4.31	0.01	0.12	12	4402.95
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{ranch} + \text{source} + \text{release} + \text{year})$	4.51	0.01	0.11	12	4403.14
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{ranch} + \text{release} + \text{year})$	5.24	0.01	0.07	12	4403.88
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (.) \Psi_{AN} (.) \Psi_{FN} (.) \Psi_{NB} (.) \delta_{1 A} (.) \delta_{1 N} (.) \delta_{2 F} (.) \Psi_{NN}(\text{age} + \text{ranch} + \text{source} + \text{release} + \text{year})$	9.99	0.00	0.01	13	4402.57

- ¹ Akaike weights
- ² Model likelihood
- ³ Number of parameters

Table 3.6 AICc cumulative variable weights from the second modeling step in a multistate mark-recapture model with state uncertainty to describe reproduction of translocated scaled quail (*Callipepla squamata*). Weights in boldface type indicate variables with cumulative weight >0.5 and that were retained to the final round of modeling. Hens were considered to be in one of five biological states: non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D), thus transitions in the model described mortality ($\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$), nesting propensity (Ψ_{AN}), renesting propensity (Ψ_{FN}), and nest survival (Ψ_{NN}) using a multistate mark-recapture model with state uncertainty.

Parameters	Variables				
	source	release	age	ranch	year
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$	0.28	0.65	0.30	0.75	0.99
Ψ_{AN}	0.29	0.47	0.70	0.28	0.34
Ψ_{FN}	0.28	0.83	0.30	0.27	0.65
Ψ_{NN}	0.44	0.32	0.44	0.29	0.38

Table 3.7. Model results from a third modeling step evaluating the effect of source population (source), release treatment (release), age, release ranch (ranch), and year on translocated scaled quail (*Callipepla squamata*) mortality and reproductive parameters. Hens were considered to be in one of five biological states: non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D), thus transitions in the model described mortality in non-breeding (Ψ_{AD}), nesting (Ψ_{ND}), reneating propensity (Ψ_{FN}), and mortality outside release area (Ψ_{BD}). Hens observed not nesting were assigned event 1 which allowed for one of three potential realities: observed not nesting and was truly not nesting ($\delta_{1|A}$) observed not nesting, but did have a nest and was temporarily off the nest ($\delta_{1|N}$), or observed not nesting, but had previously initiated and failed an unobserved nest, thus was truly a failed nester ($\delta_{1|F}$). Hens with known previous nest failures were assigned event 2 which allowed for observations where failed nesters were observed not nesting and were truly not nesting ($\delta_{2|F}$), or observed not nesting, but were truly nesting ($\delta_{2|N}$). Two delta parameters ($\delta_{2|N}$ and $\delta_{1|F}$) were fixed to low (<0.0001) constant probabilities to aid in model convergence. The corrected Akaike's information criterion (AIC_c) for the top model was 4396.39.

Model	ΔAIC_c	w_i^1	L^2	k^3	Deviance
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{release} + \text{year}) \Psi_{FN}(\text{release} + \text{year}) \delta_{1 A}(\cdot)$ $\delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	0.00	0.23	1.00	16	4364.20
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{year}) \Psi_{FN}(\text{release} + \text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot)$ $\delta_{2 F}(\cdot)$	1.48	0.11	0.48	13	4367.70
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{release} + \text{year}) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot)$ $\delta_{2 F}(\cdot)$	1.62	0.10	0.44	13	4367.85
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{release} + \text{year}) \Psi_{FN}(\text{release} + \text{year}) \delta_{1 A}(\cdot)$ $\delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	2.09	0.08	0.35	13	4368.31
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{release} + \text{year}) \Psi_{FN}(\text{release} + \text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot)$ $\delta_{2 F}(\cdot)$	2.24	0.07	0.33	13	4368.47
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{year}) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	3.11	0.05	0.21	12	4371.35
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{year}) \Psi_{FN}(\text{release} + \text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot)$ $\delta_{2 F}(\cdot)$	3.53	0.04	0.17	12	4371.78
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{release} + \text{year}) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot)$ $\delta_{2 F}(\cdot)$	3.71	0.04	0.16	12	4371.96
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{year}) \Psi_{FN}(\text{release} + \text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	3.73	0.03	0.15	12	4371.98
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{release} + \text{year}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	3.83	0.03	0.15	12	4372.07
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{release} + \text{year}) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	3.87	0.03	0.14	12	4372.11
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{release} + \text{year}) \Psi_{FN}(\text{release} + \text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot)$ $\delta_{2 F}(\cdot)$	4.33	0.03	0.11	12	4372.58
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{release} + \text{year}) \Psi_{FN}(\text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot)$ $\delta_{2 F}(\cdot)$	5.01	0.02	0.08	13	4371.24
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}(\text{ranch} + \text{year}) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	5.16	0.02	0.08	11	4375.43

$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{ranch}) \Psi_{FN}(\text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	27.07	0.00	0.00	11	4397.34
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{ranch} + \text{release}) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	27.37	0.00	0.00	11	4397.63
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{ranch} + \text{release}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	27.44	0.00	0.00	11	4397.70
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{release}) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	27.84	0.00	0.00	11	4398.10
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{ranch}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	28.07	0.00	0.00	9	4402.37
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{release}) \Psi_{FN}(\text{release} + \text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	28.26	0.00	0.00	11	4398.52
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	28.56	0.00	0.00	9	4402.86
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{ranch} + \text{release} + \text{year}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	28.57	0.00	0.00	12	4396.82
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	28.64	0.00	0.00	9	4402.94
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{ranch}) \Psi_{FN}(\text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	29.21	0.00	0.00	10	4401.50
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{ranch} + \text{release}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	29.58	0.00	0.00	10	4401.86
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	29.78	0.00	0.00	10	4402.06
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{release}) \Psi_{FN}(\text{release}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	29.98	0.00	0.00	10	4402.26
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{release}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	30.03	0.00	0.00	10	4402.31
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{ranch} + \text{release} + \text{year}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	30.72	0.00	0.00	11	4400.99
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	30.79	0.00	0.00	10	4407.10
$\Psi_{AN}(\text{age}) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{release} + \text{year}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	31.17	0.00	0.00	11	4401.43
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\cdot) \Psi_{FN}(\text{year}) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	31.93	0.00	0.00	9	4406.23
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{release}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	32.19	0.00	0.00	9	4406.49
$\Psi_{AN}(\cdot) \Psi_{NN}(\cdot) \Psi_{NB}(\cdot) \Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD} (\text{release} + \text{year}) \Psi_{FN}(\cdot) \delta_{1 A}(\cdot) \delta_{1 N}(\cdot) \delta_{2 F}(\cdot)$	33.33	0.00	0.00	10	4405.61

¹ Akaike weights

² Model likelihood

³ Number of parameters

Table 3.8. Akaike’s corrected information criterion cumulative variable weights from the final modeling step in a multistate mark-recapture model with state uncertainty to describe reproduction of translocated scaled quail (*Callipepla squamata*). Weights in boldface type indicate variables with cumulative weight >0.5 and that were retained to the final round of modeling. Hens were considered to be in one of five biological states at time t : non-breeding (A), nesting (N), failed nester (F), brooding (B), or dead (D), thus transitions in the model described mortality ($\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$), nesting propensity (Ψ_{AN}), renesting propensity (Ψ_{FN}), and nest survival (Ψ_{NN}) using a multistate mark-recapture model with state uncertainty. NA indicates variable was not used to model parameter.

Parameters	Variables			
	release	age	ranch	year
$\Psi_{AD}=\Psi_{ND}=\Psi_{FD}=\Psi_{BD}$	0.68	NA	0.76	1.00
Ψ_{AN}	NA	0.73	NA	NA
Ψ_{FN}	0.86	NA	NA	0.65
Ψ_{NN}	NA	NA	NA	NA

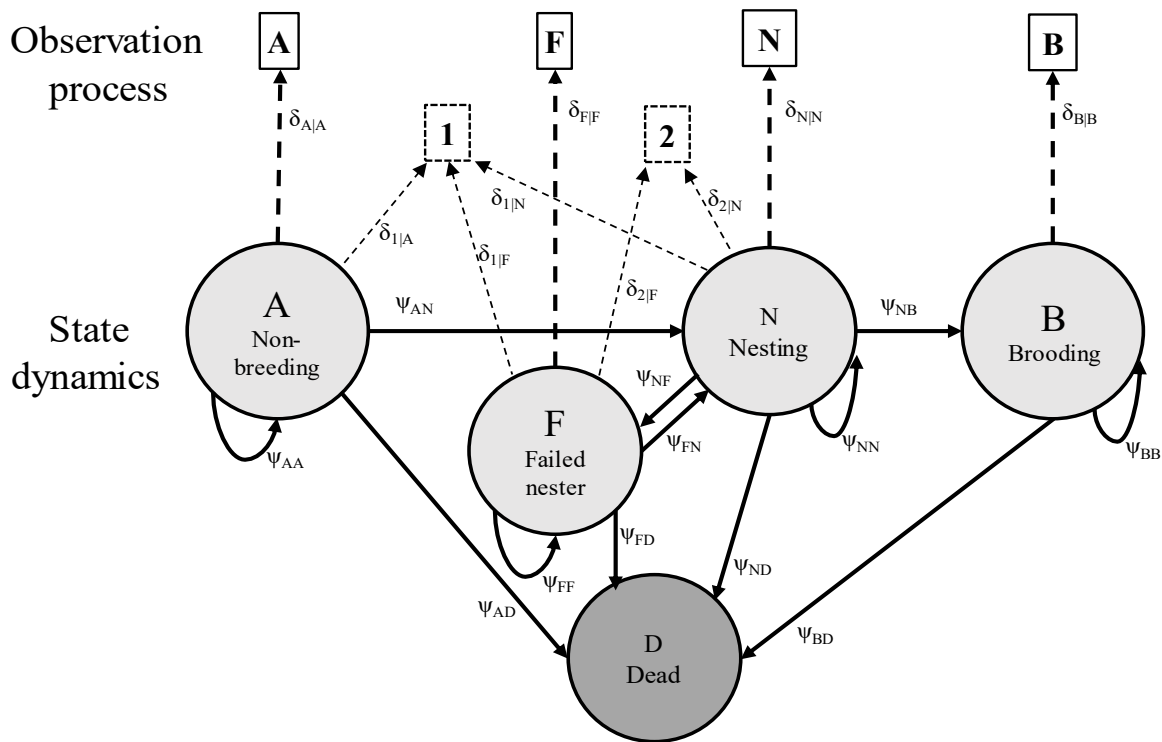


Figure 3.1. Multistate mark-recapture model with state uncertainty used to model scaled quail (*Callipepla squamata*) nesting propensity (Ψ_{AN}), renesting propensity (Ψ_{FN}), and nest success (Ψ_{NN}). Hens could be in one of five true states: alive and non-breeding (A), alive and nesting (N), alive and previously having failed a nest attempt (F), alive and brooding or successfully hatching a nest (B), or dead (D). Allowable transitions between these states are given by the solid arrows. True states and transitions describe the state dynamics. The observation process was also modeled (given by dashed arrows and events 1 and 2) to account for observer uncertainty in assigning true state to the hen. Hens could be: 1) observed not nesting and truly were not nesting ($\delta_{1|A}$), 2) observed not nesting, but did have a nest and were temporarily not on nest ($\delta_{1|N}$), or 3) observed not nesting, but had previously initiated and failed an unobserved nest, thus were truly a failed nester ($\delta_{1|F}$). Hens that were known to have previously failed a nest could be 1) observed not nesting and were truly not nesting ($\delta_{1|F}$), or 2) observed not nesting, but were truly nesting ($\delta_{2|N}$).

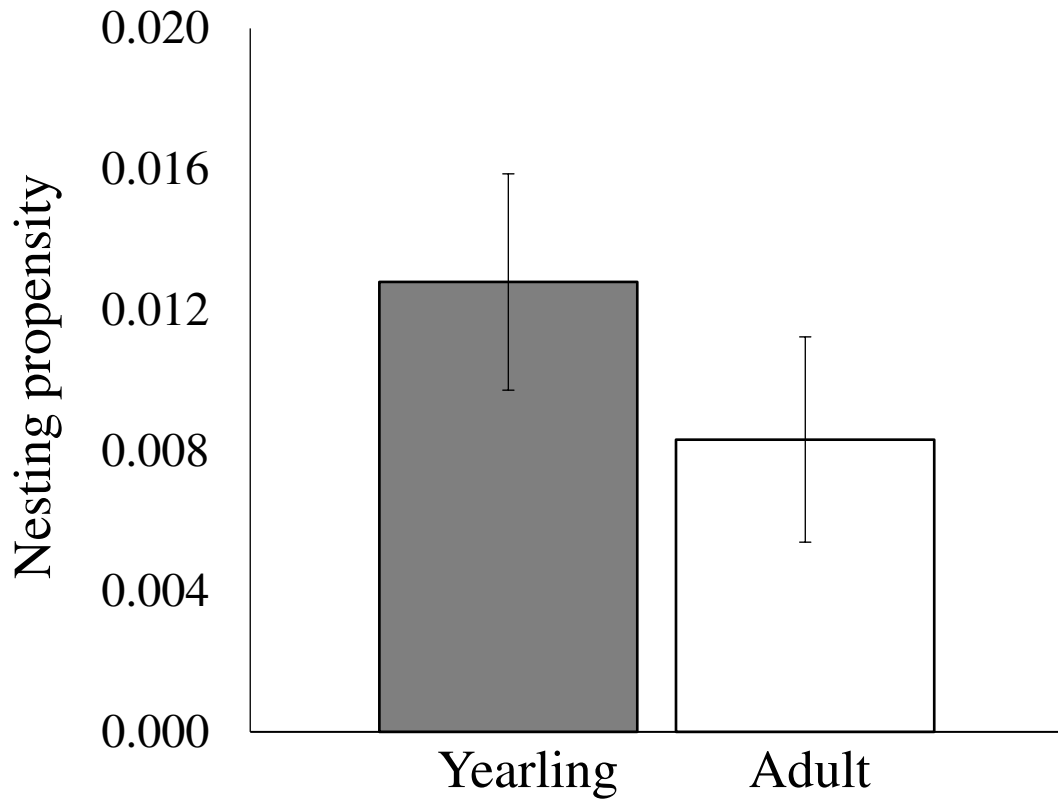


Figure 3.2. Estimated daily probability of nesting and 95% confidence intervals for yearling and adult translocated scaled quail (*Callipepla squamata*) in Knox County, Texas, USA, 2016–2017.

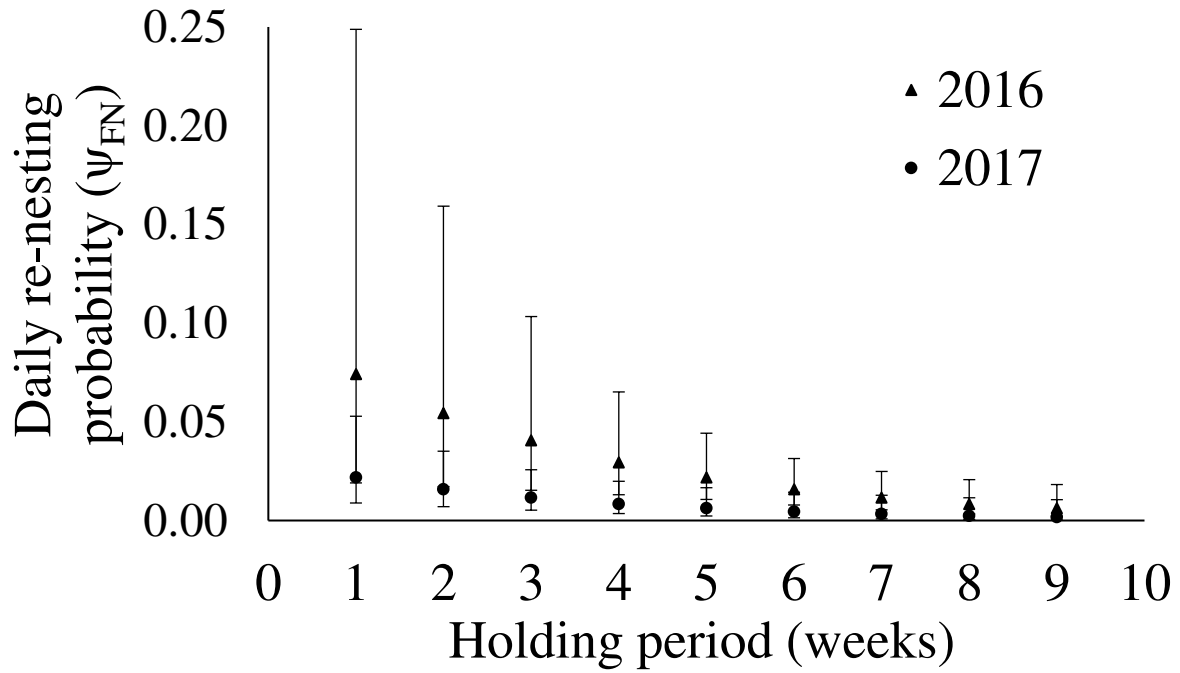


Figure 3.3. Estimated daily probability of re-nesting of translocated scaled quail (*Callipepla squamata*) as a function of year and the duration of a delayed release holding period in Knox County, Texas, USA, 2016–2017.

CHAPTER 4. TRANSIENT DYNAMICS ARE IMPORTANT FOR TRANSLOCATED, SHORT-LIVED SPECIES: SCALED QUAIL AS A CASE STUDY

Matrix population models (MPMs) are vital in ecology for understanding population growth and managing species, especially amidst increasing global threats. While traditional MPM analyses focus on asymptotic dynamics, transient dynamics are more relevant for short-term population responses. I compared asymptotic and transient dynamics under wet and dry conditions in a translocated population of Arizona scaled quail (*Callipepla squamata pallida*), a short-lived bird species with a two stage (i.e., adult and yearling) life cycle. Population projections incorporating transient dynamics revealed that asymptotic projections could potentially overestimate population growth by 14%. Additionally, asymptotic growth rates were most sensitive to changes in reneating rate, while transient growth rates were sensitive to changes in hatchability and reneating rates. Selectively translocating yearlings, the stage class with the highest reproductive value, would be expected to result in a population 16% higher after one year than if only adults were translocated. Managers should consider transient dynamics when modeling populations where short-term outcomes are relevant such as translocation. Species with more complex life cycles and greater variation in vital rates will exhibit greater divergence from asymptotic dynamics.

INTRODUCTION

Understanding population growth and contributions of vital rates is key in population ecology for informing species management, especially as threats to species rise globally (Gaston 2005, Caswell 2019). Matrix population/projection models (MPMs) are commonly used to evaluate discrete life stage (e.g., yearling, adult) dynamics and sensitivities because of their biological relevance and analytical simplicity (Caswell 2001, Stott et al. 2011). MPMs predict over time that the proportion of individuals in each life stage (i.e., stage distribution) will converge on a stable stage distribution (SSD) regardless of initial numbers (Caswell 2001). The interval over which stage distribution differs from its stable, asymptotic structure is defined as the transient period (Koons et al. 2005, Caswell 2007).

Transient period dynamics caused by vital rate disparities across life stages can diverge from the asymptotic state and have long lasting implications for population size (Ezard et al. 2010, Stott 2016, Koons et al. 2021). Initial stage distributions favoring high-reproductive-value stages lead to amplified growth rates compared to asymptotic conditions, while distributions skewed toward low-reproductive-value stages result in attenuated growth (Stott et al. 2010, Koons et al. 2021). Consequently, populations with amplifying initial stage distributions achieve higher densities than those at SSD or with attenuated growth (Stott et al. 2010, Koons et al. 2021). Population inertia quantifies the long-term impact of initial stage distributions relative to the size that would have been achieved if the population had always been at the SSD (Koons et al. 2007).

The traditional MPM analyses focused on asymptotic dynamics (e.g., λ_∞ or dominant eigenvalue) largely avoid the uncertainty of transient dynamics, however assessing transient dynamics is

important for assessing population responses to management actions in the short-term (Hastings 2004, Ezard et al. 2010, Hastings et al. 2018). Disturbances to stage structure or perturbations of vital rates produce discrepancies between current stage distribution and SSD inducing a new transient period (Koons et al. 2005, Koons et al. 2021). In wild populations, disturbances to stage structure occur frequently when, for example, subadults engage in natal dispersal (Howard 1960), differential harvest of age-classes occurs (Priadka et al. 2020), or managers focus on a particular age class for reintroduction (Todd and Lintermans 2015). Perturbations to vital rates produce a new SSD (Koons et al. 2005) and can occur when populations respond to, e.g., habitat restoration (Homyack 2010), annual variation in weather conditions (Frederiksen et al. 2014), or changes in predator abundance (Armstrong et al. 2006).

Translocation (i.e., the movement of wild-caught animals for reintroduction or supplementation) is a common conservation strategy (Armstrong et al. 2015). Despite widespread application, many programs experience low success rates (Fischer and Lindenmayer 2000). The goal is a self-sustaining population, but short-term success hinges on vital rates and population growth of founding individuals (Griffith 1989, Terhune et al. 2007). Reintroduced populations have inherently dynamic vital rates and are unlikely to be at a stable age structure (Iles et al. 2016). Even if the stage structure of the source population is stable, capture rates may vary by stage and/or vital rates may differ on the release site compared to the source site. Founding individuals often have lower vital rates relative to subsequent generations due to stress of the translocation process and unfamiliarity with the release site (Lunsford et al. 2019, Mathews et al. 2019). When populations are regulated by density dependence, early generations may experience a period of high growth rates followed by a decline in fecundity and/or survival as the population nears carrying capacity (Armstrong et al. 2002). Therefore, even if vital rates in the population

stabilize over time, reintroduced populations are likely to experience an extended period of transient dynamics due to uncertainty in stage structure and vital rates.

Transient dynamics studies often focused on long-lived species due to their extended transient periods (e.g., >10 years) that result from longer generation lengths and larger differences in vital rates among stages (Koons et al. 2005, Buhnerkempe et al. 2011, Gerber and Kendall 2016). In contrast, short-lived species experience shorter transient periods (e.g., 1–3 years) following a perturbation, but more frequent perturbations due to higher annual variability in vital rates (Koons et al. 2005, Montero-Serra et al. 2018). Consequently, short-lived species whose vital rates differ among stages and exhibit high annual variability are often in a transient state.

Here, I present a comparison of transient and asymptotic dynamics in a population of Arizona scaled quail (*Callipepla squamata pallida*) reintroduced via translocation. Scaled quail are a short-lived, gallinaceous bird species native to the southwestern U.S. that have experienced range-wide declines and been the focus of recent translocation efforts (Rho et al. 2015, Ruzicka et al. 2017, Sauer et al. 2017, Yancey 2019). Scaled quail populations exhibit large annual variation in survival and fecundity which result in approximately 5-yr boom and bust cycles of abundance (Lusk et al. 2007, Silvy et al. 2007). These cyclic changes in abundance are highly correlated with regional drought indices (Bridges et al. 2001). The population I studied was translocated over two years that captured variation in drought conditions on the release site. The first year of the study was characterized by cool, wet weather with no drought conditions, while the second year experienced 33 weeks of moderate to severe drought beginning just prior to breeding season (Chapter 2).

My objectives were to 1) compare transient versus asymptotic growth rates, 2) evaluate implications of the founding populations' stage structure on growth rates and population size, and 3) compare sensitivity of asymptotic and transient population growth rates to lower-level vital rates. I addressed all three objectives comparing vital rates observed in wet and dry years. Additionally, I present a species-specific population model for scaled quail that is applicable for future conservation modeling questions. An understanding of population growth rates and sensitivity to vital rates will aid managers in the conservation of this species by providing guidance on which life stage to focus efforts especially in the context of wet and dry conditions.

METHODS

Population Vital Rates

I modeled a population of scaled quail translocated to a release site with >40,000 ha of contiguous rangeland owned by five private landowners in Knox County, Texas, USA. This site was located in the eastern Rolling Plains ecoregion (Gould 1975). Quail were sourced from 8 private ranches and released in April just prior to breeding season in 2016 and 2017. Breeding season vital rates, including yearling nest initiation (I_Y), adult nest initiation (I_A), reneating (R), first clutch size (C_1), second clutch size (C_2), nest survival (S_n), and breeding season survival (S_B) were estimated from data collected on 212 radio-marked hens that were tracked from April-September each year (Table 4.1). I did not find evidence that R , C_1 , C_2 , or S_n varied by hen age, and I also did not include age variation in those parameters here (Chapter 3). For more information on the study area, protocols, and parameter estimation see (Chapters 2 and 3).

I used a nearby (>125 km) reference population of radio-marked Arizona scaled quail hens in the Rolling Plains ecoregion in Fisher County, Texas, USA that were monitored year-round 2016–2017 to obtain estimates of juvenile survival (S_J) and non-breeding season survival (S_{NB}) (Chapter 1). The Fisher County population was self-sustaining but reintroduced via translocation in 2013–2014. Radio-marking and monitoring protocols were like the methods used in Knox County. Fisher County also experienced wet conditions in 2016 and drought conditions in 2017 (Figure 4.1). For more information on the study area, protocols, and parameter estimation see Chapters 1 and 2.

Few estimates of brood survival (S_b , i.e., proportion of brood surviving from hatch to end of breeding season) in quails exist outside of estimates derived from flush counts which are known to be biased by uncorrected imperfect detection and brood amalgamations (Tanner et al. 2019, Kubečka et al. 2021). Therefore, I selected estimates of chick survival from the only study to estimate survival from radio-marked scaled quail chicks (Orange et al. 2016, but also see Tanner et al. 2019). Orange et al. (2016) marked individual chicks in 2013–2014 at 8–12 days old and monitored broods for the remainder of breeding season. Although not reported, the quail subspecies is likely *C. s. hargravei* based on the study location at the Beaver River Wildlife Management Area in the Rolling Plains ecoregion of western Oklahoma, USA (Williford et al. 2014). The authors pooled data on broods for both years of the study. I extrapolated estimates of brood survival from Orange et al. (2016) to obtain a breeding season estimate based on the average day of observed hatch (1 Jul) in Knox County. I approximated standard errors for breeding season estimates using the Delta method in the *msm* package in R (Jackson 2011, www.r-project.org). The Orange et al. (2016) study site experienced drought conditions from January–June in both years.

I used an estimate of hatchability (H, i.e., proportion of eggs in clutch surviving to hatch and hatching) from a 1999–2000 study on scaled quail in the southern High Plains ecoregion in Cochran County, Texas, USA (Pleasant et al. 2006). The subspecies, is likely *C. s. pallida* based on location (Williford et al. 2014). Though other estimates of hatchability for scaled quail exist (Schemnitz 1961, Gonzalez Gonzalez et al. 2017), I chose to use estimates from Pleasant et al. (2006) because the study area experienced one wet and one dry year similar to the Knox and Fisher County studies, the study site was closest to Knox County, and the estimate was based on a large sample size of nests (N = 106). I used a constant value of hatchability because Pleasant et al. (2006) did not find a difference in hatchability between years or by age of hen.

Matrix Population Model

I constructed a female only, discrete-time, pre-breeding MPM with 2 stages: yearlings and adults (Figure 4.2). The MPM was defined as such:

$$\begin{bmatrix} N_Y \\ N_A \end{bmatrix}_{t+1} = \begin{bmatrix} F_Y & F_A \\ S_B^Y & S_B^A \end{bmatrix} \begin{bmatrix} N_Y \\ N_A \end{bmatrix}_t$$

Where $F_Y = I_Y \times (S_n \times 0.5 \times C_1 \times H) + (I_Y \times (1-S_n)) \times (R \times S_n \times 0.5 \times C_2 \times H) \times S_b \times S_j$ and $F_A = I_A \times (S_n \times 0.5 \times C_1 \times H) + (I_A \times (1-S_n)) \times (R \times S_n \times 0.5 \times C_2 \times H) \times S_b \times S_j$. I did not observe hens reneesting after successfully hatching a first nest, so I did not include that possibility (Chapter 3).

Yearlings were defined as hens hatched in the previous year, entering their first breeding season. Adult hens were entering at least their second breeding season. Scaled quail can be reliably aged using primary covert coloration up to the first post-nuptial molt (Wallmo 1956). I defined the

interval between time steps as one year from 1 April in time t to 1 April in time $t+1$. I further decomposed the annual interval into breeding season (1 April– 30 September) and non-breeding season (1 October– 31 March) to evaluate sensitivity of population growth to seasonal survival and define seasonal reproductive probabilities (Figure 4.3). In a pre-breeding model, sampling is assumed to occur instantaneously just prior to breeding season. Thus, I assumed that translocated hens entered breeding season immediately post-release in April. This assumption was supported by field observations of pairs forming in just 1 week post-release (Ruzicka Pers. Obs.). The seasonal probabilities I used to inform yearling and adult nest initiation and renesting rate were estimated over the period April–August (Chapter 3). I did not extrapolate these seasonal estimates to include the probability of initiation or renesting in September because no hens were observed nesting past August (Chapter 3).

I calculated asymptotic growth, SSD, and reproductive values of the MPM with vital rates observed in 2016 (wet year) and 2017 (dry year) using the popbio package in R (Stubben and Milligan 2007). I calculated inertia of the population, or the effect of transient dynamics on long-term population size (Koons et al. 2007), using package popdemo in R (Stott et al. 2012) under wet and dry conditions and under maximum amplification (i.e., weighted to stage class with highest reproductive value) and maximum attenuation (i.e., weighted to stage class with lowest reproductive value). I reported the range of responses in population size possible under maximum amplification and attenuation compared to what the population would have achieved under SSD, i.e., the transient envelope (Koons et al. 2021). I also calculated transient population growth rate from founding through tenth year for wet and dry conditions and with maximum amplification and attenuation to determine the expected length of transient dynamics given stationary vital rates.

Sensitivity Analyses

I evaluated asymptotic sensitivities to all lower-level vital rates (excluding clutch size in first and second nests) with a prospective, deterministic analysis using the `vitalsens` function in the `popbio` package in R (Stubben and Milligan 2007). The `vitalsens` function calculates lower-level sensitivities using the partial derivative. I evaluated transient sensitivity of population growth rates in the first year to lower level vital rates using methods from Caswell (2007) in MATLAB (version 23.2.0.2485118, R2023b, Update 6) because transient population growth rate is directly comparable to asymptotic growth. I evaluated the growth rate in the first year only because I modeled a population of founding individuals. The growth rate of the reintroduced population in subsequent years would be a function of the founding individuals that survived and the offspring, to whose vital rates I did not have inference. I would also expect vital rates to change as the population became weighted more heavily to offspring versus founders and because of annual weather variation. Performance of founding individuals in the first year of reintroduction is critical for success in short-lived species (Ducatez and Shine 2019). Thus, an evaluation of sensitivities in the first-year post-release is most relevant for management in the context of translocation of short-lived, such as this species.

For both asymptotic and transient analyses, I compared sensitivities between wet and dry years. I also compared 3 age ratio scenarios in the transient analyses to evaluate the effect that manipulating stage structure during the translocation process would have on sensitivities. I simulated populations dominated by yearlings (10:1 yearlings:adults), dominated by adults (1:10), and even age ratios (1:1) to encapsulate the full range of potential age ratios. I considered sensitivities to indicate a meaningful change in growth rate if the sensitivities were > 1 (Caswell

2001). Clutch size is on a different scale compared to the other vital rates, which are proportions. Comparing sensitivities of parameters with different scales is potentially problematic (Link and Doherty Jr 2002). Although elasticity is commonly used to alleviate this problem of scale, elasticities are not robust to changes in model parameterization (Link and Doherty Jr 2002). Thus, I elected to exclude clutch size and focus solely on sensitivities.

I was interested in comparing population dynamics between wet and dry years for translocated quail. I chose a deterministic model instead of a stochastic model because of the limited vital rate estimates available. Yancey (2019) reported vital rates for chestnut-bellied scaled quail (*C. S. castanogastris*) translocated to release sites where the Arizona subspecies is native. Ruzicka et al. (2017) reported apparent breeding season survival only for translocated, radio-marked scaled quail because they experienced high dispersal and low detectability. I could not separate process from sampling variance nor do I have estimates of annual variation of vital rates in populations influenced by similar weather conditions (Wisdom et al. 2000). In the absence of more complete data on temporal variation in vital rates, I opted for a simple method to predict the influence of changes to each vital rate on population growth (Caswell 2000). Comparing wet and dry conditions in separate MPMs preserved the observed pattern of covariation in the data (Clark et al. 2008).

RESULTS

Asymptotic and transient MPM metrics differed in both scenarios (Table 4.2). Asymptotic growth was 0.86 in wet and 0.48 in dry conditions. I found that transient growth rates in the first year could vary by as much as 0.1 depending on founding population structure and weather

scenarios. Translocating only yearlings would result in a 16% larger population size after 1 year in dry conditions and 12% in wet conditions compared to translocating only adults in those scenarios (Figure 4.4). In total, projected population size because of transient dynamics differed from asymptotic dynamics by 2–14%. For example, using asymptotic growth rate to project size in a population with all adult founders under dry conditions would overshoot abundance by 14%. All scenarios indicated declining populations, but dry conditions scenarios declined by ~ 50% in a single year. The stable stage structure was 3:2 in wet and 4:1 in dry conditions. The reproductive value of yearlings in wet (1.05) and dry (1.03) conditions was greater than adults in wet (0.93) and dry (0.86) conditions. For all scenarios, population growth rates converged on the asymptotic values in the third year. Most variation in growth rates was observed in the first year. Growth rates in years 2 and 3 differed from asymptotic values by <0.002 .

Sensitivities differed between asymptotic and transient analyses. Asymptotic sensitivities indicated that population growth would be most sensitive to reneesting rate and that reneesting rate was influential on the population growth (Figure 4.5). No transient sensitivities indicated a meaningful change in population growth rate (Figure 4.6). Breeding season survival, non-breeding season survival, and yearling nest initiation were relatively more important in a wet year compared to a dry year. The least important vital rates were adult nest initiation in a dry year and hatchability. Population growth in a dry year was most sensitive to changes in hatchability, followed by brood survival and yearling nest initiation. In wet years, transient growth was equally sensitive to hatchability and reneesting rate. In scenarios where the population was composed primarily of yearlings, yearling nest initiation was more important compared to scenarios with fewer yearlings. Sensitivities to adult nest initiation responded similarly to age ratios, although adult initiation was less important overall. In general, transient sensitivities were

similar across age ratio scenarios. For both wet and dry conditions, transient growth was relatively insensitive to changes in nest survival.

DISCUSSION

I found that transient dynamics diverged from asymptotic dynamics in all aspects I evaluated in a translocated population of scaled quail, a short-lived species with a simple life cycle. Yearling hens had higher reproductive value in both wet and dry conditions compared to adults. This variation stemmed from differences in a single vital rate: nest initiation. Transient dynamics only occur in species whose reproductive values differ among stages (Koons et al. 2005). Therefore, all transient dynamics I describe here result from the difference in yearling and adult nest initiation observed in the Knox County translocated population (Chapter 3). Populations with greater disparity of fecundity vital rates between or among stages would be expected to experience even larger transient effects (Koons et al. 2005). Based on the Knox County translocation, I recommend weighting future founding populations of scaled quail toward the yearling stage.

In a dry year, the founding population was projected to decline by approximately 50% in the first year post translocation. The decreased population growth associated with dry conditions observed in this study is corroborated by negative correlations between regional abundance and drought indices (Bridges et al. 2001, Lusk et al. 2007), as well as decreasing adult survival with increasing drought severity (Chapter 1). I modeled founding individuals only rather than successive generations. Founding populations of gallinaceous birds often exhibit poorer performance than subsequent generations or resident populations (Gruber-Hadden et al. 2016,

Duvuvuei et al. 2017, Mathews et al. 2021). However, the population can overcome initially poor performance of founders if those individuals can reproduce (Musil et al. 1993, Mathews et al. 2019). My findings highlight the importance of timing translocations to coincide with favorable regional weather conditions to maximize production of the translocated population and mitigate impacts to source populations (Hardouin et al. 2014, Verdon et al. 2021). Additionally, population growth under wet conditions was likely underestimated by this model as the estimate for brood survival used was from a study area experiencing drought conditions (Orange et al. 2016). Estimates of brood survival obtained using modern techniques (e.g., radio-tagged chicks) across various ecoregions and weather conditions are a conspicuous need for scaled quail demography.

Both asymptotic and transient growth rates were most sensitive to changes in reproductive parameters as would be predicted by the fast life history of scaled quail (Saether and Bakke 2000). Although, transient sensitivities indicated that no one parameter was overly influential on growth rate (i.e., sensitivities <1). Relative to other parameters in the model, transient growth rates in both scenarios were most sensitive to changes in hatchability. The estimate of hatchability for scaled quail (95%) used here is near the upper limit (Pleasant et al. 2006). Other studies report scaled quail hatchability estimates of 91.25% from the Trans Pecos ecoregion of Texas (N = 47; Gonzalez Gonzalez et al. 2017) and 90% from the High Plains ecoregion of Oklahoma (N = 6; Schemnitz 1961). Northern bobwhite (*Colinus virginianus*) hatchability estimates range from 80–95% (Sandercock et al. 2008). Estimates of egg hatchability incorporate failure attributable to fertilization, development, and partial nest depredations (Sandercock et al. 2008, Hemmings et al. 2012, Assersohn et al. 2021). Mechanistically, inbreeding depression is the most common cause of reduced egg hatchability in avian species (Hemmings et al. 2012,

Assersohn et al. 2021) and translocated populations often suffer from low genetic diversity (Jamieson et al. 2006). Managers maintain genetic diversity by translocating a large number of individuals from multiple sources (Tracy et al. 2011). Additional research is needed to quantify the minimum number of scaled quail needed to maintain genetic diversity. However, the Knox County founding population was likely well above the threshold with 888 founding individuals sourced from 8 sources (Chapters 2 and 3). Partial nest depredations occur when a predator (most commonly attributable to snakes and rodents) consumes only part of the clutch either due to satiation, capability, or because the clutch is defended (Staller et al. 2005, Ellis-Felege et al. 2012). Scientific inference is lacking for crucial questions regarding partial nest depredations in western quails including causal predator species, population level impacts, mitigating influence of habitat, and annual variation. Research on northern bobwhites in the southeastern United States revealed a larger assemblage of nest predators than previously thought and many depredations by snakes resulting in partial nest losses (Staller et al. 2005).

Asymptotic growth rate was meaningfully influenced by changes in reneesting rate. Transient growth rate was equally as sensitive to reneesting rate as it was to hatchability. Both reneesting rate and hatchability sensitivities in wet years were relatively higher than the sensitivities for other parameters in the model. Annual reneesting rates were most influenced by weather conditions (Chapter 3). When conditions are cool and wet, females remain in breeding condition for longer, allowing ample time to reneest (Guthery et al. 1988). Although managers cannot influence climate conditions, translocation protocols can be crafted to increase reneesting rates. I found that increased holding times reduced reneesting, likely due to increased chronic stress levels. Managers seeking to maximize reneesting should therefore limit holding time, however reducing holding time comes at a cost of higher dispersal. Additionally, releasing just prior to the start of

breeding season is critical for maximizing the nesting window. Hens that nest and fail early in the breeding season can reneest readily (Arnold et al. 2010). However, releasing quail earlier in the spring may also result in a tradeoff with adult or yearling mortality due to high abundance of raptors during spring migration (Turner et al. 2014, Downey et al. 2017).

I suggest managers to consider transient dynamics when modeling populations where short-term outcomes are relevant such as translocation. In this study, I observed differences in population size and sensitivities that resulted from transient dynamics induced by differences in a single vital rate, nest initiation (I_Y). Additionally, an exploration of transient dynamics prior to translocation is warranted because translocating individuals with the highest reproductive rate will result in greater population size. Selectively translocating individuals with the highest reproductive output (e.g., yearling) could lead to a potential 16% increase in population size after 1 year. Overall, very few quantitative estimates of scaled quail vital rates exist in the literature even for non-translocated populations with exception of breeding season survival. In regard to translocation, more information is needed on offspring of founding individuals to understand which vital rates are most influential for population growth.

Table 4.1. Vital rates used to model asymptotic and transient population dynamics of Arizona scaled quail (*Callipepla squamata pallida*).

Description	Symbol	Wet Year		Dry Year		Biological Definition	Source
		Estimate	SE	Estimate	SE		
Yearling Nest Initiation	I_Y	0.81	0.04	0.81	0.04	Probability of 1 st nest in 1 st breeding season	Chapter 3
Adult Nest Initiation	I_A	0.66	0.07	0.66	0.07	Probability of 1 st nest in 2 nd + breeding season	Chapter 3
Renesting Rate	R	0.91	0.08	0.50	0.19	Probability of initiating 2 nd nest	Chapter 3
First Clutch Size	C_1	11.00	0.33	11.00	0.33	# eggs in first clutch	Chapter 3
Second Clutch Size	C_2	8.00	0.68	8.00	0.68	# eggs in second clutch	Chapter 3
Nest Survival	S_n	0.24	0.03	0.24	0.03	Probability of nest surviving to hatch	Chapter 3
Hatchability	H	0.95	0.01	0.95	0.01	Probability of egg hatching	Pleasant et al. 2006
Brood Survival	S_b	0.69	0.07	0.69	0.07	Probability of chick surviving breeding season	Orange et al. 2016
Juvenile Survival	S_j	0.53	0.05	0.49	0.05	Probability of surviving first non-breeding season	Chapter 1
Breeding Season Survival	S_B	0.71	0.06	0.30	0.06	Probability of surviving 1 st + breeding season	Chapter 2
Non-Breeding Season Survival	S_{NB}	0.33	0.05	0.28	0.04	Probability of surviving 2 nd + non-breeding season	Chapter 1

Table 4.2. Comparison of matrix population model metrics in wet and dry years describing population dynamics metrics of a translocated Arizona scaled quail (*Callipepla squamata pallida*) population. All ratios are yearling:adult.

Metric	Wet	Dry
Inertia with All Yearlings (10:0)	1.05	1.02
Inertia with All Adults (0:10)	0.93	0.87
Amplified Transient Growth	0.90	0.50
Attenuated Transient Growth	0.80	0.42
Stable Stage Structure	3:2	4:1
Asymptotic Lambda	0.86	0.48
Yearling Reproductive Value	1.05	1.03
Adult Reproductive Value	0.93	0.86

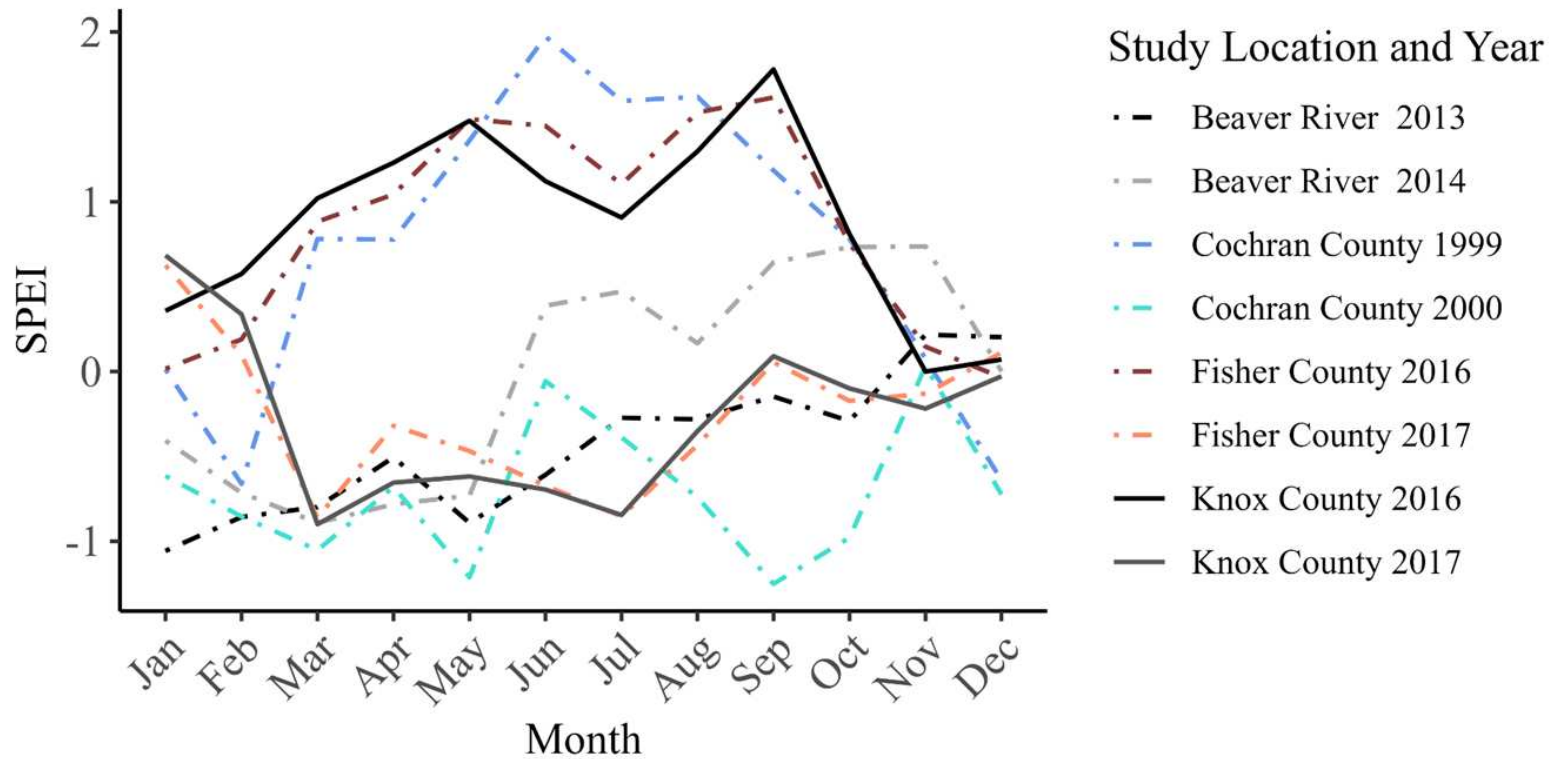


Figure 4.1. Monthly standardized precipitation evapotranspiration index (SPEI) for study sites and years where data were collected to inform parameters in a matrix population model of translocated scaled quail (*Callipepla squamata*). All study locations were in Texas, USA except Beaver River which was in Oklahoma.

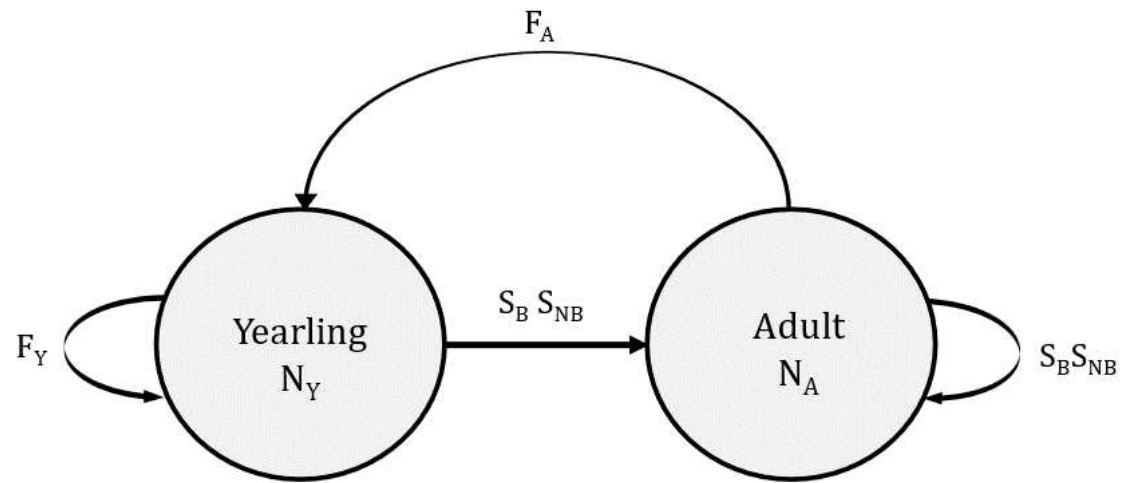


Figure 4.2. Life cycle diagram for a pre-breeding matrix population model of Arizona scaled quail (*Callipepla squamata pallida*).

Fecundity: Offspring Survival	Juvenile Survival		Brood Survival	Juvenile Survival								
Fecundity: Nesting		Yearling and Adult Nest Initiation and Re-nesting										
Yearling and Adult Survival	Non-breeding Season Survival	Breeding Season Survival			Non-breeding Season Survival							
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec

Figure 4.3. Annual timeline for probabilities in a pre-breeding matrix population model of translocated Arizona scaled quail (*Callipepla squamata pallida*) hens where census occurred 1 April each year.

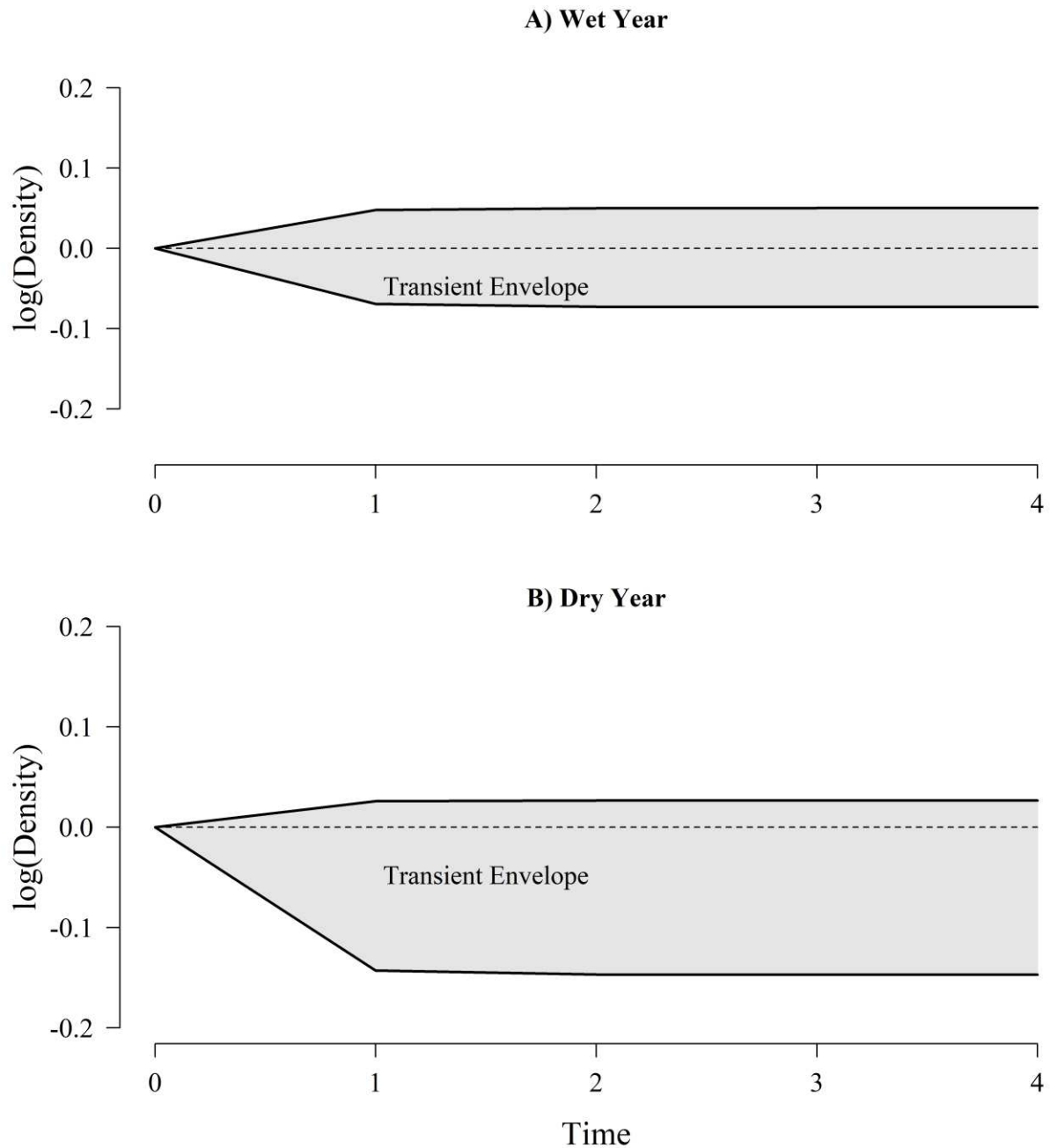


Figure 4.4. Comparison of transient population dynamics between a wet (A) and dry (B) year for translocated Arizona scaled quail (*Callipepla squamata pallida*). Bold lines indicate a scenario with all yearlings or amplification (upper) and all adults or attenuation (lower) compared to a projection of using stable stage distribution (i.e., asymptotic projection, dotted line). Population density is standardized to remove population trends for comparison.

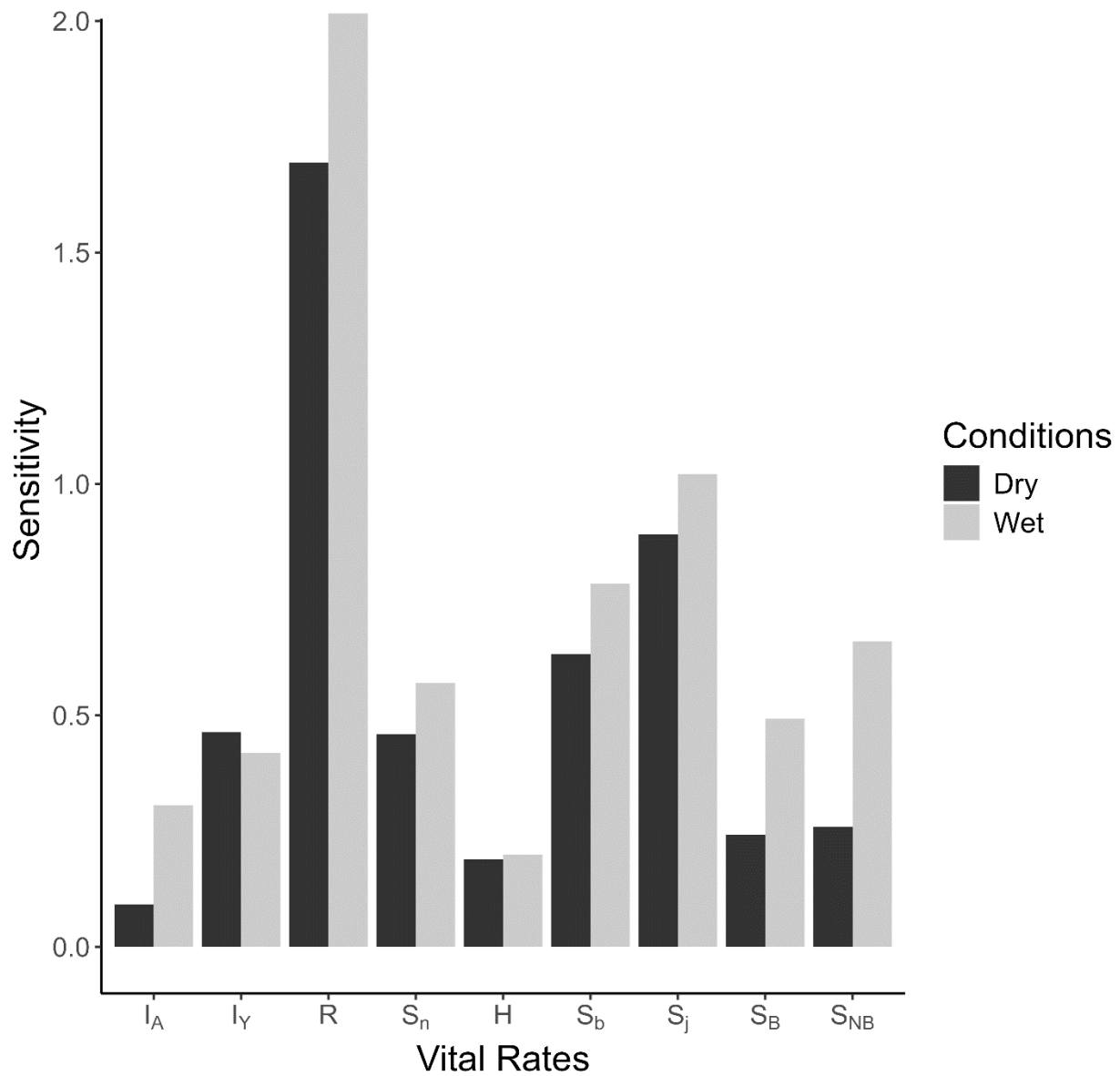


Figure 4.5. Comparison of asymptotic sensitivities under wet and dry conditions for translocated Arizona scaled quail (*Callipepla squamata pallida*). Vital rates are defined as yearling nest initiation (I_Y), adult nest initiation (I_A), renesting rate (R), nest survival (S_n), hatchability (H), brood survival (S_b), juvenile survival (S_j), breeding season survival (S_B), and non-breeding season survival (S_{NB}).

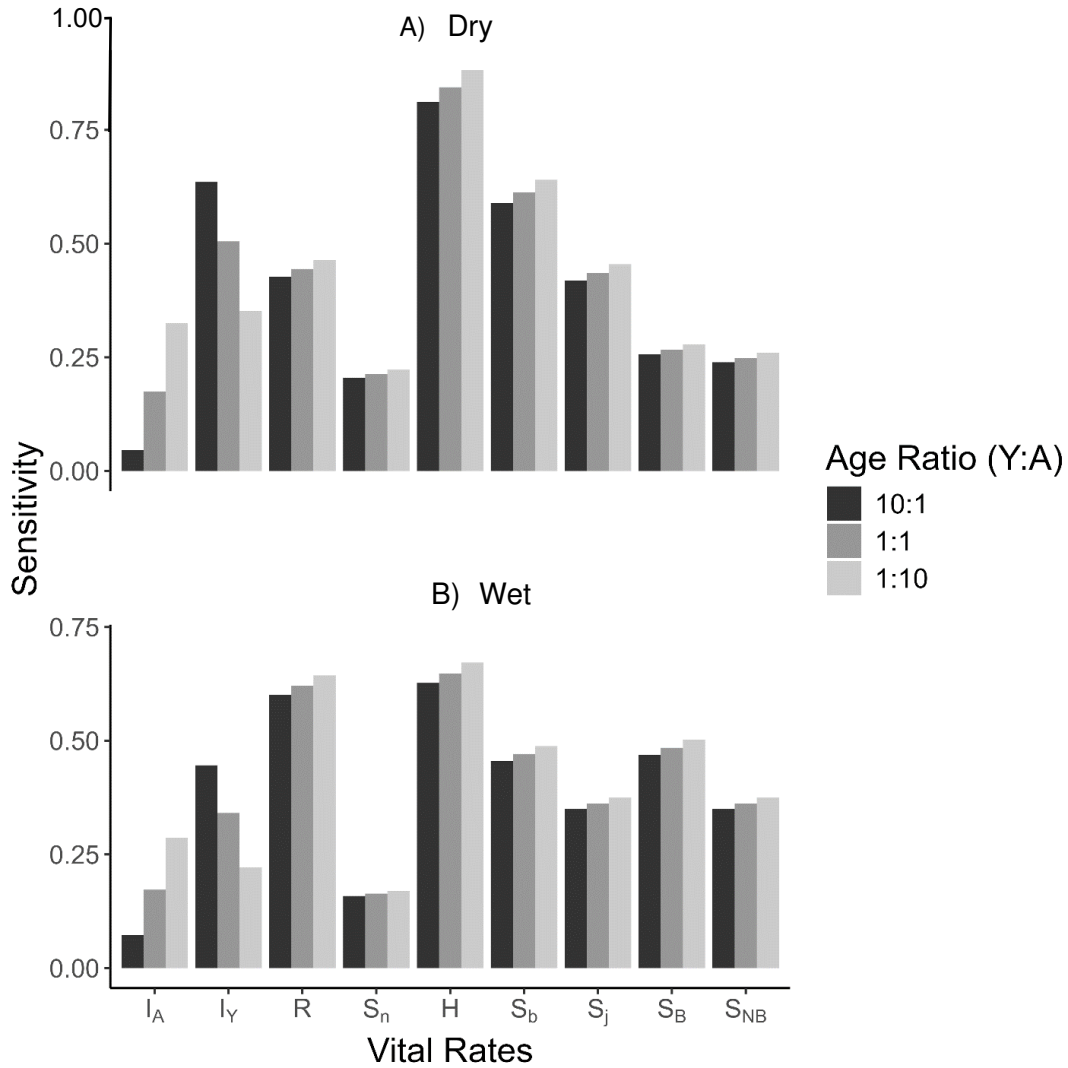


Figure 4.6. Comparison of transient sensitivities under wet (A) and dry (B) conditions for translocated Arizona scaled quail (*Callipepla squamata pallida*) using three scenarios of yearling (Y) to adult (A) age ratios for the founding population. Vital rates are defined as yearling nest initiation (I_Y), adult nest initiation (I_A), renesting rate (R), nest survival (S_n), hatchability (H), brood survival (S_b), juvenile survival (S_j), breeding season survival (S_B), and non-breeding season survival (S_{NB}).

CHAPTER 5. OPTIMUM DELAYED RELEASE HOLDING TIME FOR TRANSLOCATED SCALED QUAIL

Scaled quail are declining range wide and interest in refining translocation protocols is growing. A delayed release translocation strategy is frequently employed to reduce immediate post-release dispersal by the founding individuals, but increased mortality and decreased reproduction can result. Conflicting information exists on the optimum holding time for scaled quail when weighing the benefit of reduced dispersal with mortality and reproduction costs. My goal was to identify an optimum delayed release holding time for scaled quail by accounting for the effect of delayed release on mortality, dispersal, and re-nesting probability in a single omnibus metric, individual fitness. I found that the optimum holding period is 2–3 weeks in a year with above average precipitation and <1 week in a year with below average precipitation.

INTRODUCTION

Scaled quail (*Callipepla squamata*), an arid grassland species native to the southwestern U.S., declined range wide 0.7% per year from 1966–2019 (Downey et al. 2023). Declines have been most severe in the periphery of their range where populations with the lowest abundances have lost the cyclical “boom and bust” behavior indicative of healthy quail populations in arid environments (Lusk et al. 2007). Population declines are the consequence of habitat fragmentation and degradation primarily due to the conversion of grass-dominated rangelands to shrublands and row crops (Rho et al. 2015). As a result, interest in translocating scaled quail to reestablish populations is growing.

Translocation is the physical process of moving wild-caught individuals from source to release sites for the purpose of introducing, reintroducing, or augmenting a population (Griffith 1989). Northern bobwhites (*Colinus virginianus*) have been translocated successfully in the mesic southeastern U.S. to reestablish populations (Terhune et al. 2006). Outcomes of scaled quail translocations in the xeric western U.S. have been more varied. Translocation successfully augmented a population of scaled quail on the Rolling Plains Quail Research Ranch in Fisher County, Texas (Chapter 1). However, an introduction of chestnut-bellied scaled quail from South Texas to Collingsworth County, Texas failed (Yancey 2019) and several prior undocumented translocations failed due to high dispersal post release (Pers. Comm. Dale Rollins).

A delayed release strategy is frequently employed in translocations to reduce immediate post-release hyperdispersal by the founding individuals when the species being translocated is social, such as quails (Moseby et al. 2014). Hyperdispersal is movement that carries an individual far enough away from the release site that it no longer contributes to population establishment and should be distinguished from exploratory dispersal within a release site (Bilby and Moseby 2024). Hyperdispersal poses several challenges for translocation success including: reducing the founding population size which increases risks of inbreeding depression or Allee effects, increasing animal stress, and increasing costs either due to monitoring over larger areas or the need to translocate more individuals to overcome demographic depression (Bilby and Moseby 2024). Due to high dispersal in previous translocations, Ruzicka et al. (2017) tested a delayed release strategy compared to immediate release on the Matador Wildlife Management Area in Cottle County, Texas. The authors found that a 4-week delayed release strategy was effective at increasing apparent survival (i.e., the probability that an individual survives and stays

on site) of translocated scaled quail compared to an immediately released group. However, breeding season apparent survival of both groups was low (0.00–0.33; Ruzicka et al. 2017).

Subsequently, another translocation study was initiated in Knox County, Texas to refine delayed release holding period (Chapters 2 and 3). I found that optimum holding period was 8-9 weeks due to a tradeoff between increased mortality and decreased dispersal as holding period increased (Chapter 2). However, the optimum holding time was <1 week when evaluating only reproductive parameters within the same population due to a negative effect of longer holding periods on re-nesting probability (Chapter 3). Delayed release was effective at reducing dispersal post-release but incurred a cost of increased mortality and decreased re-nesting.

My objective was to find an optimum delayed release holding time for scaled quail by accounting for the effect of delayed release on mortality, dispersal, and re-nesting probability in a single omnibus metric, individual fitness (Caswell 2001). I used estimates of demographic rates from the founding population of scaled quail reintroduced to Knox County, a reference population, and the literature to evaluate theoretical individual fitness for female quail held 1–9 weeks (Chapter 2 and 3).

METHODS

Data Collection and Parameter Estimates

For in-depth description of the data collection and analysis see Chapters 2 and 3. Briefly, Arizona scaled quail (*C. s. pallida*) were trapped on private ranches in West Texas and transported to the release site in Knox County where they were transferred to holding pens on site. A subset (~

50%) of hens were radio-marked. Quail were held for their assigned delayed release treatment which varied by one-week intervals from 1–9 weeks. All quail were released over a 10-day period in April of each year. Radio-marked hens were monitored daily throughout breeding season (10 Apr–15 Aug; 131 days) to collect information on mortality, location, and nesting status. In 2016 the release site received average precipitation, however, 2017 was a dry year. The data were analyzed using two multi-state mark-recapture models with state uncertainty to evaluate mortality and dispersal in one model and reproduction in the second model. Dispersal was defined as moving >2 km away from the release point. All relevant transition parameters in both models were evaluated for an effect of release treatment, year, age, and other individual covariates. Breeding season vital rates, including yearling nest initiation (I_Y), adult nest initiation (I_A), renesting rate (R), first clutch size (C_1), second clutch size (C_2), nest survival (S_n), and breeding season apparent survival (S_B) were estimated from data collected on the Knox County founding population in 2016–2017 (Chapters 2 and 3).

Estimates of juvenile survival (S_j) and non-breeding season survival (S_{NB}) in 2016–2017 were obtained from an augmented population of scaled quail in Fisher County (Chapter 1). I used brood survival (S_b , i.e., proportion of brood surviving from hatch to end of breeding season) estimates from Orange et al. (2016). I used an estimate of hatchability (H , i.e., proportion of eggs in clutch surviving to hatch and hatching) from a 1999–2000 study (Pleasant et al. 2006). For more information on demographic rates see Chapter 4. To simulate holding period scenarios, I calculated apparent breeding season survival and renesting rate for specific intervals from 1–9 weeks in 2016–2017. I calculated apparent breeding season survival as the joint probability that a quail would survive breeding season and would not disperse.

Theoretical Modeling Approach

I calculated an integrated measure of individual fitness (λ) as the dominant eigenvalue of a matrix population model (MPM; McGraw and Caswell 1996). For more information on the MPM see Chapter 4. I constructed a female only, discrete-time, pre-breeding matrix MPM with 2 stages: yearlings and adults (Figure 4.2). The MPM was defined as such:

$$\begin{bmatrix} N_Y \\ N_A \end{bmatrix}_{t+1} = \begin{bmatrix} F_Y & F_A \\ S_B^Y & S_B^A \end{bmatrix} \begin{bmatrix} N_Y \\ N_A \end{bmatrix}_t$$

Where $F_Y = I_Y \times (S_n \times 0.5 \times C_1 \times H) + (I_Y \times (1 - S_n)) \times (R_Y \times S_n \times 0.5 \times C_2 \times H) \times S_b \times S_j$ and $F_A = I_A \times (S_n \times 0.5 \times C_1 \times H) + (I_A \times (1 - S_n)) \times (R_Y \times S_n \times 0.5 \times C_2 \times H) \times S_b \times S_j$. I applied parameter estimates to the MPM to obtain holding period specific values of λ .

RESULTS

I found that λ was maximized in 2016 at 2- and 3-week holding periods ($\lambda = 0.67$; Figure 5.1) using a 2 km dispersal threshold. In 2017, λ was maximized at week 1 ($\lambda = 0.53$). Overall fitness was lower in 2017, the drought year, compared to 2016.

DISCUSSION

Optimal holding time balanced out at 2–3 weeks when considering the combined effects of delayed release on mortality, dispersal, and reproduction in a year with above average precipitation. A holding time of 2–3 weeks reduced dispersal without incurring negative impacts to fitness. The range of holding period also gives managers flexibility in planning for the often-

challenging logistics of translocation, such as obtaining access to private land for capturing or staffing release sites for monitoring. However, the effect of delayed release was mediated by year. In 2017, a dry year, the optimal holding time was <1 week. The shift of optimum holding period is due to a relatively greater increase in mortality and reduced reneating compared to dispersal that was observed in 2017 (Chapters 2 and 3). The difference in these parameters between years was the largest effect observed in the study and was attributed to weather due to 2017 being much drier than 2016. Weather is known to be highly influential for scaled quail populations (Campbell et al. 1973, Bridges et al. 2001, Lusk et al. 2007). Overall, I recommend against initiating a translocation in years that are expected to be dry, however if conducting a translocation in a dry year managers should hold scaled quail for <1 week.

In this study, individual fitness was low (< 1). However, I used apparent survival which combines survival and dispersal into a single term. I used a dispersal threshold of 2 km. This threshold was based on previous literature on northern bobwhites (*Colinus virginianus*) (Townsend et al. 2003, Downey et al. 2017) and the minimum area required by Texas Parks and Wildlife Department to initiate a quail translocation (Connolly et al. 2008). The threshold is important because increasing the threshold would increase apparent survival and fewer individuals would be classified as dispersers. The population studied here was released into a large (>40,000 ha), contiguous rangeland, thus it is likely that individuals that dispersed >2 km could still contribute to the reintroduced population. However, on a smaller property in a fragmented landscape dispersers would be less likely to contribute. Thus, reducing distance dispersed may be relatively more important on smaller release sites and in more fragmented landscapes. Evaluating dispersal distance and dispersal thresholds within the metapopulation

concept (Hanski 1998) would be fruitful, especially in the context of quail management in fragmented landscapes.

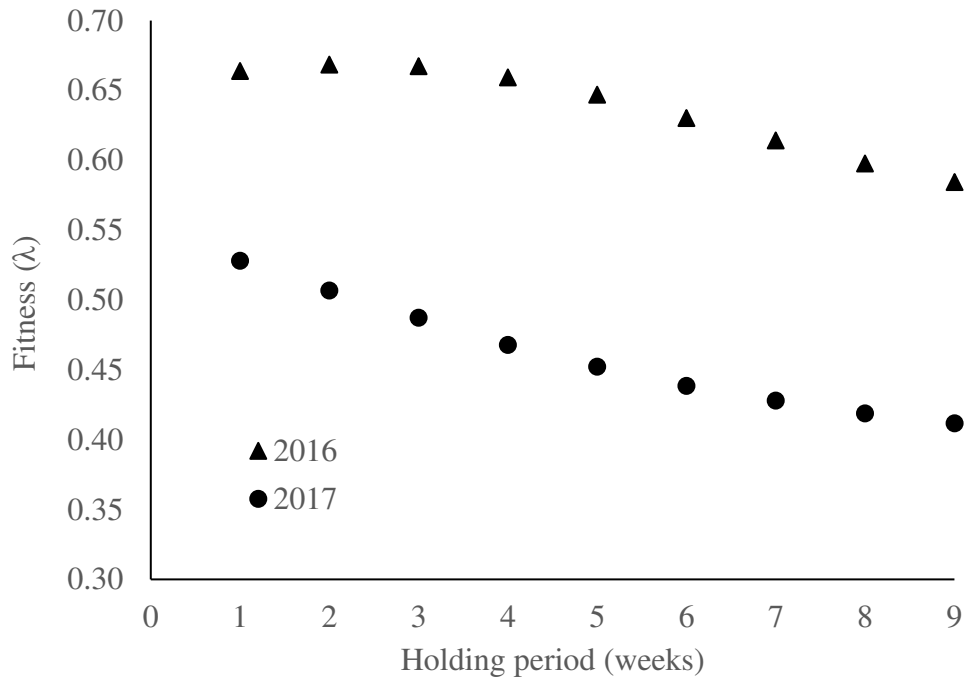


Figure 5.1. Theoretical fitness (λ) at different delayed release holding periods of a founding population of scaled quail (*Callipepla squamata*) translocated to Knox County, Texas, USA 2016–2017.

APPENDIX 1. NESTING SUBSTRATES

Table A1.1. Nesting substrates and nests fates of scaled quail (*Callipepla squamata*) translocated to Knox County, Texas, USA 2016–2017.

Year	Fate	Nesting Substrate 1	Nesting Substrate 2	Nesting Substrate 3
2016	Fail	Bare Ground	<i>Berberis trifoliolata</i>	
2016	Fail	Bare Ground	<i>Juniperus pinchotii</i>	<i>Berberis trifoliolata</i>
2016	Fail	Bare Ground	Bunch Grass	
2016	Fail	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Fail	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Fail	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Fail	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Fail	Bunch Grass		
2016	Fail	<i>Cylindropuntia leptocaulis</i>		
2016	Fail	<i>Dalea frutescens</i>		
2016	Fail	<i>Juniperus pinchotii</i>	Bare Ground	
2016	Fail	<i>Juniperus pinchotii</i>		
2016	Fail	<i>Juniperus pinchotii</i>		
2016	Fail	<i>Opuntia</i> sp.	Bunch Grass	
2016	Fail	<i>Opuntia</i> sp.	Bunch Grass	
2016	Fail	<i>Yucca</i> sp.		
2016	Fail	<i>Yucca</i> sp.		
2016	Hatch	Bare Ground	<i>Juniperus pinchotii</i>	
2016	Hatch	Bare Ground	Rock	<i>Juniperus pinchotii</i>
2016	Hatch	Bunch Grass	Dead Wood	
2016	Hatch	Bunch Grass	Unknown Forb	<i>Prosopis glandulosa</i>
2016	Hatch	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Hatch	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Hatch	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Hatch	Bunch Grass	<i>Juniperus pinchotii</i>	<i>Prosopis glandulosa</i>
2016	Hatch	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Hatch	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Hatch	Bunch Grass	<i>Juniperus pinchotii</i>	
2016	Hatch	Bunch Grass	<i>Prosopis glandulosa</i>	
2016	Hatch	Bunch Grass	<i>Opuntia</i> sp.	
2016	Hatch	Bunch Grass	<i>Opuntia</i> sp.	
2016	Hatch	Bunch Grass	<i>Cylindropuntia leptocaulis</i>	
2016	Hatch	Bunch Grass	<i>Cylindropuntia leptocaulis</i>	<i>Prosopis glandulosa</i>
2016	Hatch	Bunch Grass	<i>Yucca</i> sp.	
2016	Hatch	Dead Wood		
2016	Hatch	<i>Ephedra</i> sp.	<i>Prosopis glandulosa</i>	
2016	Hatch	<i>Juniperus pinchotii</i>		

2016	Hatch	<i>Opuntia</i> sp.		
2016	Hatch	<i>Yucca</i> sp.	<i>Opuntia</i> sp.	
2017	Fail	Annual Grass	<i>Acacia greggii</i>	
2017	Fail	Annual Grass	Dead Wood	
2017	Fail	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Fail	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Fail	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Fail	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Fail	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Fail	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Fail	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Fail	Annual Grass	<i>Prosopis glandulosa</i>	
2017	Fail	Annual Grass	<i>Prosopis glandulosa</i>	
2017	Fail	Annual Grass	<i>Prosopis glandulosa</i>	
2017	Fail	Annual Grass	<i>Opuntia</i> sp.	
2017	Fail	Annual Grass	<i>Yucca</i> sp.	
2017	Fail	Annual Grass	<i>Yucca</i> sp.	
2017	Fail	Bunch Grass	<i>Dalea frutescens</i>	<i>Juniperus pinchotii</i>
2017	Fail	Bunch Grass	<i>Juniperus pinchotii</i>	
2017	Fail	Bunch Grass	<i>Juniperus pinchotii</i>	
2017	Fail	<i>Cucurbita foetidissima</i>	Bunch Grass	
2017	Fail	<i>Juniperus pinchotii</i>	Annual Grass	
2017	Fail	<i>Juniperus pinchotii</i>	Bunch Grass	
2017	Fail	<i>Juniperus pinchotii</i>	Bunch Grass	
2017	Fail	<i>Juniperus pinchotii</i>	Bunch Grass	
2017	Fail	<i>Juniperus pinchotii</i>	Bunch Grass	
2017	Fail	<i>Juniperus pinchotii</i>	Bunch Grass	
2017	Fail	<i>Juniperus pinchotii</i>	Bunch Grass	
2017	Fail	<i>Juniperus pinchotii</i>	Bunch Grass	
2017	Fail	<i>Opuntia</i> sp.	Annual Grass	
2017	Fail	<i>Opuntia</i> sp.		
2017	Fail	<i>Prosopis glandulosa</i>	Bunch Grass	
2017	Fail	<i>Prosopis glandulosa</i>		
2017	Fail	Rock		
2017	Fail	<i>Yucca</i> sp.	Annual Grass	
2017	Hatch	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Hatch	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Hatch	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Hatch	Annual Grass	<i>Juniperus pinchotii</i>	
2017	Hatch	Annual Grass	<i>Prosopis glandulosa</i>	
2017	Hatch	Annual Grass		
2017	Hatch	Annual Grass		
2017	Hatch	Bunch Grass	<i>Yucca</i> sp.	
2017	Hatch	<i>Juniperus pinchotii</i>	Bunch Grass	
2017	Hatch	<i>Juniperus pinchotii</i>		
2017	Hatch	<i>Juniperus pinchotii</i>		

2017	Hatch	<i>Juniperus pinchotii</i>	
2017	Hatch	<i>Juniperus pinchotii</i>	
2017	Hatch	<i>Juniperus pinchotii</i>	
2017	Hatch	<i>Opuntia</i> sp.	Bunch Grass
2017	Hatch	<i>Prosopis glandulosa</i>	Dead Wood

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