

THESIS

CINNAMON TEAL BREEDING ECOLOGY IN THE SAN LUIS VALLEY OF COLORADO

Submitted by

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In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2018

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ABSTRACT

CINNAMON TEAL BREEDING ECOLOGY IN THE SAN LUIS VALLEY OF COLORADO

The foundation of effective waterfowl management is an abundant and resilient waterfowl population, which begins with an understanding of what drives population size and growth. Population growth rate is the product of a number of vital rates, all of which remain relatively unknown for the cinnamon teal (*Spatula cyanoptera*). I investigated the interactions between biotic and abiotic factors influencing the basic demographic rates of cinnamon teal during the breeding season in the San Luis Valley of Colorado. Specifically, I assessed the relationship between the habitat around a selected nest site and cinnamon teal nesting success. Additionally, I evaluated whether a relatively novel approach to surveying social groupings of waterfowl can act as an effective index of breeding effort and success for cinnamon teal, the intraspecific variation in nest attendance patterns during incubation and how it affects nest survival, and the rates at which breeding females and ducklings survive the breeding season. This research has the potential to enhance the understanding of the basic population ecology of this overlooked species and provide information about vital rates that can be used in future analyses and management of the population on a larger scale.

I found that cinnamon teal select nest sites with habitat characteristics that are also associated with a higher probability of nest survival (Chapter 2, this thesis). Specifically, I observed cinnamon teal selecting nest sites characterized by a lower proportion of forbs relative to what was available, which were also associated with higher nest survival among the nests I observed. I established that weekly transect surveys assessing the social groupings of cinnamon

teal throughout the breeding season have the potential to act as an index of reproductive success if done on a larger scale (both temporally and geographically; Chapter 3, this thesis). I also found differences in the nest attendance patterns during early incubation compared to late incubation, which were also impacted by time of day and temperature (Chapter 4, this thesis). Finally, I estimated breeding season duckling and hen survival rates that were comparable to other waterfowl species and provided suggestions for future cinnamon teal researchers (Chapter 5, this thesis).

ACKNOWLEDGMENTS

I would first and foremost like to thank my advisor, Dr. Bill Kendall, for providing me with the opportunity to conduct this research. It was an honor to work with him, and his compassion and unique perspective have pushed me to become a better ecologist, scientist, and person. I would also like to thank my committee members, Dr. Paul Doherty, Dr. Cameron Aldridge, and Dave Olson. All three have been extremely generous with their time and commitment to this project, and their guidance was invaluable as I wove my way through this portion of my career. I owe a special debt of gratitude to Dave Olson, without whose initiative and passion for conservation this project would not exist and the field of waterfowl ecology would be worse off.

I appreciate all of the time and thought that have gone into this project on the part of US Fish and Wildlife Service employees, both within the Division of Migratory Birds and the National Wildlife Refuge system. Special thanks go to Casey Stemler, Jim Dubovsky, Kammie Kruse, and Dave Sharp for getting this project off the ground and supporting me throughout this process. The staff of the San Luis Valley National Wildlife Refuge Complex could not have been a more wonderful group of people to spend the summers with. Suzanne Beauchaine, Sharon Vaughn, Scott Miller, Dean Lee, Pete Striffler, Dewane Mosher, and David Dean were all invaluable in helping with the logistics of field work, providing me with housing and vehicles during my field seasons, and allowing this research to take place under their watch. I would also like to thank all of the folks living in the San Luis Valley who made me feel at home and who have a special tie to the wildlife and the land in that region. It's a special place and I feel very lucky to have lived there for three summers. Thanks especially to Jenny Nehring and Cary Aloia

for being my SLV role models and constantly highlighting the work being done by women in waterfowl/wetlands research. Stephanie Ferrero and Brent Frankland with Colorado Parks & Wildlife (CPW) also shared their knowledge of the area and provided assistance via telemetry flights to locate some lost birds. Thanks to Dr. Jim Gammonley of CPW for not only providing financial support for nest monitoring cameras, but also for paving the way for this research to take place with his past work on cinnamon teal and in the San Luis Valley.

None of this work would have been possible without the technicians and volunteers that helped out along the way. Meghan Keating, Brandon Nooner, Liz Smith, Katherine Scott, Kelsey Persyn, Josh Houghtaling, Christina Meuhlbauer, Hailey Glasko, Michelle Moyer, all of my video and photo reviewers, and all of the Student Conservation Association/Pathways interns who helped out (especially Adam Braddock, Cloe Traylor, and Hilary Syvertson), thank you for bearing with me throughout this learning process and for being the workhorses of the project. You made field work and living in the bunkhouses so enjoyable, and I'm glad to call you all friends.

Thank you to everyone in the Fish, Wildlife, and Conservation Biology department and the USGS Cooperative Fish and Wildlife Research Unit who has supported, challenged, and laughed with me over the course of my Master's. Gabriele Engler provided constant logistical support over the course of three remote field seasons and the day-to-day administrative challenges of being a graduate student. Thank you to all of the other graduate students who have shaped my time at Colorado State University. The other members of the Kendall lab, Brian Gerber, Perry Williams, Kristen Pearson, and Maria Dzul, were extremely influential mentors, role models, and friends. The Doherty Lab welcomed me into their group when I was without a

lab group to attend, as did the Bailey/Huyvaert “Superpopulation” Lab. All of these people provided instrumental advice on both professional and personal levels.

Thanks to my mom, for showing me the delightful world of birds at a young age and for always being willing to lend an ear, Michael, Amy, and Pete for showering me with humor and joy throughout a sometimes-difficult degree, and my dad, who is the strongest, hardest working man I know. A special thanks goes to Adam Behney for not only geeking out about ducks with me on a regular basis, but for being a constant source of support and being generally wonderful. Finally, thanks to my cat, Aloo, for falling asleep on my keyboard every time I tried to write this thesis.

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Chapter 1 - INTRODUCTION

Cinnamon Teal Population Dynamics and Life History Traits

The cinnamon teal is a relatively understudied dabbling duck species breeding in high densities in the intermountain west. It is the least abundant and least widely distributed of all three teal species native to North America, with breeding population estimates ranging from 260,000-300,000 during the breeding season to 500,000-600,000 in the fall (Bellrose 1980, Baldassarre 2014). Small banding samples and difficulty distinguishing between female cinnamon teal and female blue-winged teal (*Spatula discors*) have made population analyses difficult to carry out and have led to relatively few studies historically. Current management for this species is based on estimates from the Waterfowl Breeding Population and Habitat Survey (WBPHS) in the traditional survey area, which encompasses the northern US, central Canada, and parts of Alaska, in addition to independent breeding waterfowl surveys, but data on cinnamon teal are often combined with those of blue-winged teal due to the uncertainty of identification (USFWS 2013). In addition, a large majority of cinnamon teal breed outside the traditional survey area and researchers have conducted few breeding studies (Spencer 1953, Vest, unpublished data). The 2012 North American Waterfowl Management Plan proposes an acceptable threshold of cinnamon teal abundance of 300,000 birds continent-wide, but thresholds within the traditional survey area are combined with blue-winged teal and are based upon abundance estimates from the 1970s (Baldassarre 2014).

The North American subspecies of cinnamon teal (*S. c. septentrionalium*) breeds throughout western North America, with four other subspecies breeding and wintering solely in various regions of South America. They generally exhibit a fast life-history strategy relative to other ducks; hens will typically breed as yearlings and will reneest following the failure of an

initial nesting attempt. They are elusive nesters, utilizing very thick perennial vegetation near or over water in seasonal and semi-permanent wetlands and tunneling through the vegetation to get to and from their nests (Gammonley 2012). Females with broods are extremely secretive, typically foraging in areas of dense submergent vegetation with abundant emergent cover. Nest initiation typically occurs by mid-May in Colorado and hatch is usually at its peak by late July (Laubhan and Gammonley 2000). Hens choose the nest site while males guard foraging sites nearby, and distance to water at the time of selection seems to be vital in the selection process (Gammonley 2012). In Colorado, 83% of nests found in an unpublished study by Laubhan and Gammonley and 87% of the active nests I located in this study were <10 meters from water. Cinnamon teal are known to use highly alkaline wetlands, perhaps one of the few preferences of theirs that differs from the closely related blue-winged teal (Gammonley 2012). Connelly and Ball (1984) found that cinnamon teal preferred more emergent vegetation than blue-winged teal, but that their remaining habitat and food preferences were nearly identical. In their study, Connelly and Ball (1984) found cinnamon teal were subordinate to most other species, including blue-winged teal, giving blue-winged teal a competitive advantage in areas where the two species have begun to overlap in recent decades. Research remains limited regarding whether cinnamon teal can remain robust to changes in land use and climate patterns across North America, especially as the western United States becomes increasingly arid and blue-winged teal continue to encroach upon their historic range. Without proper estimates of population size, vital rates, and trends, proper management regimes cannot be enacted to ensure the longevity of this species, such as identifying key areas of habitat to be protected.

Historic Cinnamon Teal Studies

Few published studies thus far have focused specifically on identifying vital rates of cinnamon teal, although an abundance of information regarding their natural history is available (Gammonley 2012). Spencer (1953) conducted one of the early descriptive studies of cinnamon teal ecology and life history, and since then, most of the research has focused on foraging patterns and morphological differences between cinnamon teal subspecies and blue-winged teal (Stark 1979, Connelly and Ball 1984, Gammonley 1995a, Gammonley 2012, Wilson et al. 2011). Laubhan and Gammonley (2000) conducted a study on foraging habitat selection of waterbirds in the San Luis Valley of Colorado, determining that selection patterns differed throughout the breeding season for cinnamon teal. Hohman and Ankney (1994) conducted a study on pre-nesting male cinnamon teal body condition in relation to pair status, finding limited evidence to support the predictions that paired males are older and physically superior to unpaired males and that superior males pair earlier.

Studies of breeding cinnamon teal have provided estimates of nest survival ranging from 32% for 1707 nests monitored across the western US (Bellrose 1980) to 62.2% at the Bear River marshes in Utah (Williams and Marshall 1938). These estimates, however, likely contain samples of blue-winged teal nests and are exclusively estimates of apparent nest survival, which is typically biased high (Mayfield 1961, Dinsmore et al. 2002). Gilbert et al. (1996) conducted a study of the effects of habitat management on duck species at Monte Vista National Wildlife Refuge, but all three teal species were lumped together due to the uncertainty of identification. This seminal work also provided initial evidence indicating the San Luis Valley in Colorado was the best location for a breeding study. In it, Gilbert et al. (1996) estimated that Monte Vista National Wildlife Refuge in the San Luis Valley had the highest breeding density of waterfowl

on the continent. Although diminished water supply has altered the hydrological regimes in the region, and thus the breeding density of waterfowl, it still plays a significant role in the production of Colorado's waterfowl, especially cinnamon teal (Szymczak 1986, USFWS 2015).

Project Impetus

Under a directive from the U.S. Fish and Wildlife Service in 2009, representatives from all North American flyways came together to create an assessment of the population dynamics of all three North American teal species (i.e., blue-winged, green-winged, and cinnamon teal). This report provided survival and recovery estimates for all species, but concluded that very little published information existed on cinnamon teal and that precision for the survival and recovery estimates remained poor (USFWS 2013). To increase the precision of these estimates, The Division of Migratory Birds in Region 6 of the U.S. Fish and Wildlife Service initiated a banding project focused specifically on cinnamon teal across the Intermountain West. The primary objective for this project was to band enough cinnamon teal to decrease the current coefficient of variation for survival and recovery rates ($CV = 48\%$) by 50% ($CV = 24\%$; Olson, unpublished report). In conjunction with this broad scale project, a breeding ecology project was funded in Colorado to estimate cinnamon teal nest and duckling survival, characterize nest site selection, and determine whether social index surveys have the potential to provide a time-efficient measure of reproductive success. Cinnamon teal are thought to breed in high densities in Colorado and the preliminary banding data showed the largest numbers of cinnamon teal being captured there, rendering it the most appropriate location to initiate a breeding study. Updated estimates of reproductive rates were meant to provide managers with the ability to improve nesting habitat as well as efficiently monitor cinnamon teal productivity in their respective areas.

Thesis Objectives and Format

The primary goal of this project was to estimate breeding vital rates of nesting cinnamon teal that would help characterize demographic trends, population status, and responses to habitat and water management. The secondary goals were to evaluate cinnamon teal behavior during the breeding season, to better understand the evolutionary processes that have scaled up to characterize their demography, and to determine whether these behavioral patterns can be used to estimate reproductive success over a large scale. This thesis is divided into an introduction and four main chapters, and all chapters are formatted as manuscripts.

The introduction provides a background for the completed project as well as an introduction to the available literature on cinnamon teal biology. Chapters one through four correspond to the objectives outlined above. Specifically, Chapter one is an evaluation of cinnamon teal nest site selection and nest survival on Monte Vista National Wildlife Refuge, with an emphasis on the nest site and individual hen characteristics that influence survival rates to determine whether teal are selecting for those specific characteristics when choosing a nest site. Chapter two is an evaluation of social indices and whether they are an appropriate metric of reproductive effort for cinnamon teal. In it, I calculate indices of several measures of reproductive success derived from surveys of waterfowl social groupings and evaluate whether they are correlated with independently collected estimates of reproductive success (e.g., nest survival and duckling:pair ratios). Chapter three evaluates nest attendance during incubation with respect to the factors driving the duration and frequency with which hens leave their nests. I investigate patterns of incubation attendance among cinnamon teal, evaluating whether certain attendance strategies are associated with nest survival and whether environmental characteristics

impact the attendance strategies they employed. Finally, chapter four details my estimates of hen survival and duckling survival during the breeding season.

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Chapter 2 - NEST SITE SELECTION INFLUENCES CINNAMON TEAL NEST SURVIVAL IN COLORADO

SUMMARY

Nest survival of ducks is partially a function of the spatiotemporal characteristics of the site at which a bird chooses to nest. Nest survival is also a fundamental component of population growth in waterfowl, but remains almost entirely unstudied for cinnamon teal (*Spatula cyanoptera*). I investigated cinnamon teal nest survival in an intensively managed wetland complex in southern Colorado and assessed nest site selection to investigate whether certain nest site characteristics were adaptive. I monitored 85 nests from 2015-2017 on Monte Vista National Wildlife Refuge and did not detect a difference in nest survival across years (Probability of nest survival from 2015-2017 = 0.194, SE = 0.076). Teal selected nest sites characterized by a lower proportion of forbs ($\hat{\beta}_{\text{PForbs}} = -0.799$, SE = 0.250) than available sites. The relationships between habitat characteristics and nest survival varied both in direction and by nest stage (i.e., laying or incubation). Microhabitat characteristics exhibited only a weak effect on laying survival, but incubation survival was influenced by the proportion of forbs at the nest site and to a lesser extent the proportion of grasses ($\hat{\beta}_{\text{Pforbs for Inc.}} = -0.432$, SE = 0.172, $\hat{\beta}_{\text{PGrass}} = 0.315$, SE = 0.219). Nest site selection was predictive of future nest survival for some nest site characteristics but not others, suggesting teal might be selecting nest locations to benefit reproductive success.

INTRODUCTION

Nest survival, the probability that a nesting attempt results in at least one egg hatching, has been identified as one of the most influential components of recruitment, and ultimately the rate of population change, for many duck species (Jehle et al. 2004, Rotella et al. 2003, Shaffer 2004). A large body of research exists focusing solely on ascertaining nest survival in a variety of waterfowl species and determining explanatory factors that account for the spatial and

temporal variation in success rates (Emery et al. 2005, Stephens et al. 2005, Pieron and Rohwer 2009, Grant and Shaffer 2012, Thompson et al. 2012, Ringelman et al. 2014). Cinnamon teal are relatively absent from this body of literature due to their range being outside traditional survey areas and the difficulty differentiating them from blue-winged teal. Nest survival and hen success (i.e., the product of the probabilities that a hen will nest, reneest should her initial attempt fail, and that the nest is successful) are the most influential parameters in models of the reproductive success of mallards (Johnson et al. 1992, Hoekman et al. 2002). In addition, Greenwood et al. (1995) determined that nest success was the most influential vital rate determining mallard production, and that the percentage of cropland in Prairie Canada influenced the nest success rates of five duck species. Understanding patterns of variation in nest survival and the mechanisms that give rise to these patterns is therefore highly useful to managers of duck populations.

Nest success depends on a variety of factors including, but not limited to, the local assemblage of predators (Pieron and Rohwer 2009, Amundson et al. 2012), perceptibility of the nest to predators (Devries and Armstrong 2011, Doherty et al. 2014), nest age (Smith and Wilson 2010), distance and access to high quality foraging sites (Greenwood et al. 1995, Holopainen et al. 2015), nesting density of concurrent species (Ringelman et al. 2014, Grant and Shaffer 2015), nest initiation date (Greenwood et al. 1995, Drever and Clark 2007, Ringelman et al. 2018), and annual variation in weather patterns (Skagen and Yackel Adams 2012, Webb et al. 2012). If management techniques can be identified that address any or all of the factors resulting in higher cinnamon teal nest survival, then these tactics can be implemented to increase cinnamon teal productivity.

The selection of a nest site has immense fitness implications for waterfowl. In the arid west, where nesting habitat can be limited, ducks must find and secure a nest site that enables them to avoid predators, access foraging areas, and provides the necessary conditions for incubation. The relationship between breeding habitat selection and fitness is rarely studied for birds (but see Gunnarsson et al. 2005, Arlt and Pärt 2007, Gibson et al. 2016, Pärt et al. 2017), and not at all for waterfowl. The relationship between nest site characteristics and nest survival implies that hens that have access to and choose higher quality nest sites should have a higher probability of breeding successfully. The term “adaptive” has been used to characterize these decisions in previous literature, pertaining to the benefits conferred on a bird’s reproductive success based on where they choose to breed (Gibson et al. 2016). My primary objectives were to determine the influence of nest site habitat characteristics, temporal characteristics, and individual hen characteristics on daily survival rate (DSR) of cinnamon teal nests in an intensively managed wetland complex, and to establish whether teal selected those characteristics disproportionately to their availability in an adaptive manner.

I was interested in the ecological and behavioral processes driving cinnamon teal reproductive success and the modifiable habitat characteristics associated with these processes. As vegetation structure is frequently considered a predominant driver of nest site selection and survival in birds, I centered my hypotheses around these structural traits. I predicted that, of the covariates corresponding to the microhabitat around the nest, visual obstruction rating, a higher proportion of graminoids surrounding the nest, and a higher proportion of water surrounding the nest would be associated with higher nest survival and a higher probability of nest site selection (Table 1). Dense nesting cover, typically consisting of live stems and matted dead graminoids in the case of cinnamon teal, affords birds protection from visual identification by predators

(Ringelman et al. 2017), while nearby water provides easily accessible foraging opportunities close to the nest (Jungers et al. 2015). Conversely, I predicted higher proportions of bare ground, forbs, and shrubs around the nest would be associated with lower nest survival and nest site selection probability. These characteristics are associated with a less dense vegetation community, precluding the opportunity for teal to create tunnels through the vegetation to their nests (Grant et al. 2017). In addition, higher proportions of shrubs surrounding the nest could provide perching opportunities for avian predators (Grant et al. 2017). I also evaluated covariates relating to a hen's access to foraging areas (e.g., distance to water) and predators' access to the nest (e.g., distance to shrubland), which I predicted would be negatively and positively related to nest survival, respectively. I predicted these relationships would also hold for nest site selection, given the need for hens to balance their energetic requirements and safety throughout nesting (Gibson et al. 2016). In addition to habitat characteristics, I predicted that several traits associated with an individual hen might influence nest survival. For example, increased clutch size has been shown to have mixed effects on the probability that a nest will be successful (Rohwer 1985, Dillon and Conway 2018). In addition, the date at which the hen initiates a nest relative to other nests and the weight of the hen during nesting are commonly associated with intraspecific variability in nest survival among waterfowl species (Ringelman et al. 2014, Dugger et al. 2016). I therefore predicted these hen traits would be unrelated, negatively related, and positively related to nest survival, respectively.

STUDY AREA

Monte Vista National Wildlife Refuge (NWR) is part of the San Luis Valley NWR Complex, situated 6 miles south of the town of Monte Vista, Colorado. The 2015 San Luis Valley Comprehensive Conservation Plan fully characterizes this 6,003-hectare study area,

which sits at approximately 2,255 meters of elevation and receives less than 20 centimeters of precipitation annually. Most of the water in this region comes from snowmelt, a shallow unconfined aquifer, and a deep artesian aquifer (Huntley 1979). The primary vegetation throughout the study area consists of bulrush (*Schoenoplectus sp.*), cattails (*Typha latifolia*), Baltic rush (*Juncus arcticus*), and sedges (*Carex sp.*) in the semi-permanent and permanent wetlands, as well as rabbitbrush (*Ericameria nauseosa*), greasewood (*Sarcobatus vermiculatus*), saltgrass (*Distichlis spicata*), and alkali sacaton (*Sporobolus airoides*) in the upland areas. Rotational cattle and sheep grazing is used as a management tool for invasive plant species, and some center pivot irrigation produces barley and alfalfa (USFWS 2015). Historically, Monte Vista NWR had the highest waterfowl nesting density on the continent (Gilbert et al. 1996), but drawdown of the aquifers and prolonged drought have resulted in increasingly arid conditions. Under their 2015 Comprehensive Conservation Plan, the San Luis Valley NWR Complex included cinnamon teal as a focal species for their chosen plan alternative, linking their life history and population dynamics directly to their habitat-based objectives (USFWS 2015).

METHODS

Data Collection

I searched for nests from 2015-2017 using a combination of systematic searches and rope-dragging (Wiens 1969) on foot through all areas of the refuge containing appropriate teal nesting habitat. These included flooded or potentially flooded meadows of Baltic rush, bulrush, and grasses. I also specifically searched areas near cinnamon teal drakes on waiting sites (Bellrose 1980). Additionally, I systematically searched 18 randomly selected 8.5-hectare plots in 2017 every one to two weeks in addition to opportunistically searching other wetland habitats. I selected these plots from the aforementioned appropriate habitat and did so to ensure a

representative sample of teal nests. I trapped cinnamon teal hens using decoy traps from 20 April 2016 to 10 May 2016 and 4 April 2017 to 17 May 2017 and attached a prong-and-suture VHF radio transmitter (Model A4350 or A4420 weighing 12g [3.6% of the bird's body weight] and 8g [2.4% of the bird's body weight], respectively; Advanced Telemetry Systems, Isanti, MN, USA) and a metal leg band (U.S. Geological Survey [USGS]), in order to search for nests via telemetry. All trapping and handling of cinnamon teal followed protocols approved by the Colorado State University Animal Care and Use Committee (Protocol #15-5756A). I attempted to locate nests of radiomarked birds by homing in on their approximate location until I could conclude that they had likely entered the incubation stage to reduce investigator-caused nest abandonment. I also included in this analysis 19 teal nests found by refuge staff during their independent nest monitoring project.

I recorded a GPS location and candled eggs to backdate nest initiation date and estimate a hatch date for all nests found (Weller 1956). I checked nests every five to seven days, which typically required flushing the hen each time. To reduce investigator disturbance, I monitored some nests via trail camera (Covert MP8 Trail Camera, Mossy Oak Break-Up Country or Stealth Cam G42 No-Glo Trail Game Camera STC-G42NG) or video surveillance cameras (Advance Security Model SSC-24940-36) in 2016 and 2017, allowing me to visit the nest less frequently.

At each identified nest site, I visually characterized habitat information I predicted might be predictive of selection and subsequent survival of the nest. These included visual obstruction rating (Robel et al. 1970), nest substrate, the most prevalent live and dead plant genera, distance of the nest to water, distance to shrubland, and the percent cover of grasses, forbs, shrubs, water, and bare ground (see Table 1 for citations). I recorded this information within a four-meter radius centered on the nest using the radius created by the Robel pole cord as a convenient method of

characterizing the habitat in the immediate vicinity of the nest. In 2017, I measured the same vegetation information at five randomly generated points within a 30-meter radius of the nest (Messmer et al. 2015, Guerena et al. 2016). I recorded these measurements within a week of finding a nest to evaluate a hen's environment as close to the time that it selected its nest site as possible (Gibson et al. 2016). Measuring vegetation at that scale allowed me to examine the factors driving a hen's selection of a nest site within its home range. Cinnamon teal hens have been shown to maintain relatively small home ranges, remaining close to their nests during incubation recesses, and centering home ranges on a high-quality body of water used for foraging (Gates 1962, Derrickson 1978). Spencer (1953) rarely found the average cinnamon teal home range around a nest to exceed 0.075 ha and Evans and Black (1956) reported that the blue-winged teal mean activity radius was 29 ha. I was interested in whether habitat selected at the nest site scale was chosen for its adaptive impacts on nest survival and therefore wanted to avoid variability between home ranges incurred by sampling at a larger scale.

Statistical Analyses - Nest Site Selection

I developed a resource selection function (RSF) to evaluate nest site selection of cinnamon teal. I used discrete choice models (*clogit* function from *survival* package in Program R; Cooper and Millsbaugh 1999, R Core Team 2013, Therneau 2015) to fit models with a binary response variable (1 = used and 0 = available sites) using data sampled in a matched case-control framework (Hosmer and Lemeshow 2000), and I standardized covariates to compare coefficient estimates across scales and units. I built an *a priori* model set including various combinations of 10 covariates corresponding to biologically feasible hypotheses (Table 2.1, Table 2.2). Most models included only a single covariate given my limited sample size, but I did include several models incorporating more than one covariate if I thought the interaction between these

covariates was biologically important to nest site selection. I compared each model to an intercept-only null model to evaluate which habitat characteristics influenced nest site selection.

Statistical Analyses - Nest Survival

I used a hidden Markov framework (*sensu* Pradel 2005, Kendall et al. 2012, Johnson et al. 2016) that extends Devineau et al. (2014) and Miller et al. (2017), to estimate stage-specific survival rates for both the laying and the incubation periods, allowing for uncertainty in the stage at which a nest failed. I included five states in these models (Figure 1): Laying (1), Incubation (2), Failed During Laying (3), Failed During Incubation (4), and Hatched (5). This model structure includes five parameter types: S_t^i , the probability of survival for individuals in state i from time t to $t+1$, ψ_t^{ij} , the probability of transitioning from state i to state j between times t and $t+1$ given that it survives, p_t^i , the probability of being detected at time t given that it is in state i at time t , π_t^i , the probability, given it is released in an unknown state at time t , that it is actually in state i at time t , and δ_t^{ii} , the probability that, given it is encountered, the state is assigned correctly given it is actually in state i . Given that nest survival is expressed through the transitions ψ_t^{13} and ψ_t^{24} , which are the daily failure probabilities for each nesting stage (i.e., laying and incubation), I set $S_t^i \equiv 1$ (Devineau et al. 2014). I also fixed $p_t^i \equiv 1$ since the modeling only began after my initial location of the nest and its relocation was guaranteed once I had already detected it. All δ_t^i were fixed to 1 for each living state (i.e., $i = 1$ and $i = 3$) since I had the ability to candle eggs to determine the nest's age and thus the state, in addition to the fact that I was mainly interested in my ability to assign the correct state at which a nest failed (i.e., δ_t^i for $i = 2$ and $i = 4$). I considered the daily transition probability from incubation to hatch (ψ_t^{25}) a nuisance parameter (Miller et al. 2017) and each occasion within the encounter history

corresponded to an additional day of nest age, which typically average 10 days for laying and 23 days for incubation. I constrained all models to preclude biologically infeasible transitions and constrained ψ_t^{12} , the probability of transitioning from laying to incubation, to occur within a biologically reasonable timeframe. Since there was some variability in how many eggs hens laid and when they began incubation, ψ_t^{12} was allowed to vary over several days when the transition was most likely to happen. I constrained ψ_t^{12} to 0 before those days and 1.00 afterwards to preclude unrealistic scenarios and help with estimation. I excluded nests that I judged to have failed due to investigator activity (n = 32), nests that I found after they had already hatched or failed (n = 30), and nests inappropriate for other reasons (e.g., could not identify fate, etc.; n = 3) from the nest survival analysis. I used the number of eggs on my most recent nest visit as a cue for whether or not the nest failed due to investigator activity. For example, if a nest had 3 eggs on a given visit, and several days later the nest still had 3 eggs and all eggs were cold, I assumed that my interruption of the laying period caused that nest to fail.

I included covariates in the models in a two-step approach. I added temporal covariates first to assess whether daily survival rate varied by nest age or by timing of nest initiation, as it has been shown to do for many other bird species (Daan et al. 1990). I therefore included linear and quadratic trends on nest age as well as nest initiation date. To the most parsimonious of those models I added individual covariates from the Microhabitat, Access, and Intrinsic covariate groups in biologically meaningful combinations (Table 1). I standardized habitat covariates in order to compare them across scales and to compare them to the coefficients estimated from the nest site selection analysis (see below). I implemented these models in Program MARK (White and Burnham 1999), using the Hidden Markov model (see Pradel 2005, Kendall et al. 2012).

RESULTS

I found a total of 152 nests from 2015-2017 (N = 40 in 2015, N = 52 in 2016, and N = 60 in 2017). After excluding unusable nests as defined in the methods section, 85 nests remained (N = 30 in 2015, N = 23 in 2016, and N = 32 in 2017) with which to evaluate nest survival. I used 57 nests found in 2017 to evaluate nest site selection, excluding only those for which I failed to obtain random vegetation points for logistical reasons. Of the 85 nests included in the nest survival analysis, 31 were depredated, 6 were abandoned, and 4 failed due to other causes (e.g., flooding, inviable eggs, hen killed, etc.).

Nest Site Selection

Baltic rush was the primary substrate for cinnamon teal nests (98.2%), followed by other graminoids (grasses and sedges; 1.75%). Most nests (70.2%) were in flooded meadows, followed by upland areas (9.27%). Consistent with my predictions (Table 2.1), hens were more likely to select sites with high proportions of grasses ($\hat{\beta}_{\text{PGrass}} = 0.535$, SE = 0.204; Table 2.2, Figure 2.2) and low proportions of forbs ($\hat{\beta}_{\text{PForbs}} = -0.799$, SE = 0.250; Table 2.2, Figure 2.2) in the immediate vicinity around the nest. Adding the proportion of grass to the model including the proportion of forbs did not improve the fit, but the apparent effect for PGrass still exhibited the predicted positive relationship with nest site selection (Table 2.2; Arnold 2010) and percent forbs was therefore considered the most important variable. The model including distance to shrubland was the third ranked model, predicting that hens would select sites closer to shrubland relative to available sites ($\hat{\beta}_{\text{DShrub}} = -0.934$, SE = 0.351, $\Delta AICc = 5.91$, Table 2.3). Percent water exhibited a positive but weak relationship with nest site selection consistent with my predictions ($\hat{\beta}_{\text{PWater}} = 0.243$, SE = 0.168, $\Delta AICc = 11.7$). The model including percent bare ground exhibited a negative relationship with nest site selection, consistent with my predictions ($\hat{\beta}_{\text{PBG}} =$

-0.343, SE = 0.231), but received weak support ($\Delta AICc = 6.76$, $w_i = 0.007$). Contrary to my predictions, neither distance to water nor visual obstruction rating affected nest site selection at the scale I measured ($\hat{\beta}_{D_{Water}} = -0.432$, SE = 0.383; $\hat{\beta}_{VOR} = 0.063$, SE = 0.198; Tables 2.2 & 2.3, Figure 2.2). Percent shrubs also failed to exhibit the negative relationship with nest site selection I predicted ($\hat{\beta}_{P_{Shrubs}} = -0.032$, SE = 0.165).

Nest Survival

My top model indicated that nest survival was 0.194 (SE = 0.076) across the full 33-day nesting period and did not vary by year (Tables 2.4 & 2.5, Appendix A). Daily survival rate during the laying period (\overline{DSR}_{lay}) was 0.887 (SE = 0.033; Overall survival for 10-day laying period = 0.301, SE = 0.073) compared to 0.981 (SE = 0.006) for daily survival rate during incubation (\overline{DSR}_{inc} ; Overall survival for 23-day incubation period = 0.643, SE = 0.027). A quadratic effect of nest initiation date (NID²) was consistently included in the top models, and the most parsimonious models in the first model-building step included a linear age trend on ψ^{12} , ψ^{25} , δ_{Lay} , and δ_{Inc} . Percent forbs (PForbs) was the only microhabitat covariate consistently included in the top models ($\hat{\beta}_{P_{forbs}} \text{ for Inc.} = -0.432$, SE = 0.172; Tables 2.2 & 2.5). Distance to water, distance to shrubland, and percent water all exhibited weakly negative relationships with incubation survival, all of which were consistent with my predictions except percent water ($\hat{\beta}_{D_{Water}} = -0.182$, SE = 0.157, $\hat{\beta}_{D_{Shrub}} = -0.121$, SE = 0.272, $\hat{\beta}_{P_{Water}} = -0.160$, SE = 0.305). The relationship between percent of living vegetation and incubation survival was also consistent with my predictions, exhibiting a positive relationship ($\hat{\beta}_{P_{Live}} = 0.556$, SE = 0.256). However, the positive direction of relationships between percent bare ground and incubation survival and percent of shrubs and incubation survival opposed my predictions ($\hat{\beta}_{P_{BG}} = 0.278$, SE = 0.226, $\hat{\beta}_{P_{Shrub}} = 0.456$, SE = 0.563). The relationship between vegetation density and incubation survival

approached zero, contrary to my predictions ($\hat{\beta}_{\text{VOR}} = 0.020$, SE = 0.237). Clutch size and hen weight were also very weakly associated with incubation survival ($\hat{\beta}_{\text{Clutch}} = -0.105$, SE = 0.267, $\hat{\beta}_{\text{Weight}} = 0.003$, SE = 0.012). The relationship between daily survival rate and NID varied between the two nest stages (Figure 2.3 and Figure 2.4). Laying DSR exhibited a weakly positive relationship with NID, whereas incubation DSR exhibited a negative relationship ($\hat{\beta}_{\text{NID,Lay}} = 0.011$, SE = 0.045, $\hat{\beta}_{\text{NID,Inc}} = -0.145$, SE = 0.065).

Relationships between Nest Site Selection and Nest Survival

Relationships between characteristics influencing nest site selection and nest survival varied by both nest stage and covariate. All of the microhabitat and access covariates exhibited weak, statistically insignificant relationships with nest survival during the laying period, with visual obstruction rating showing the most substantial trend ($\hat{\beta}_{\text{VOR for Lay}} = 0.497$, SE = 0.288; Appendix A). During incubation, however, PForbs was negatively associated with nest survival ($\hat{\beta}_{\text{PForbs for Inc.}} = -0.432$, SE = 0.172), and was disproportionately selected less frequently than other plant taxa at the nest site scale ($\hat{\beta}_{\text{PForbs}} = -0.799$, SE = 0.250; Figure 2.2). PGrass exhibited a complementary relationship with PForbs, with higher proportions of grass exhibiting a positive apparent effect on incubation survival ($\hat{\beta}_{\text{PGrass}} = 0.315$, SE = 0.219) and teal selecting higher proportions of grass more frequently ($\hat{\beta}_{\text{PGrass}} = 0.535$, SE = 0.204; Figure 2.2).

DISCUSSION

Adaptive Nest Site Selection

I found variable relationships between nest site selection and nest survival during different cinnamon teal nesting stages. Although my study provides some evidence that cinnamon teal selected nest sites adaptively for some characteristics and not for others, I caution

the reader that this study was observational (i.e., without manipulation to the system) and sample size was limited, and it should therefore be interpreted accordingly. Birds selected sites with lower proportions of forbs and higher proportions of grasses, which subsequently led to higher incubation survival. Although I did not identify forbs or grasses down to species, a majority of the forb species consisted of invasive plants, most commonly perennial pepperweed (*Lepidium latifolium*). This species can drastically change the productivity and composition of herbaceous wetland plant communities (Young et al. 1995, USFWS 2015) and spreads rapidly throughout wetland areas. It is a tall plant that grows densely and may break up the structure of the vegetation enough to prevent teal from tunneling to and from their nests (Gammonley 2012). If invasive forb species are, in fact, a culprit of reduced cinnamon teal nest survival, it appears as if they are attempting to mitigate this effect by selecting nest sites in areas less affected by invasive species. Although the cinnamon teal has a relatively fast life history strategy, it is likely able to adjust its selection criteria annually to reflect past experiences and local conditions, as seen in a variety of other bird species (Forstmeier and Weiss 2004, Lawrence et al. 2016, Devries et al. 2018, Porzig et al. 2018). To truly test whether natural selection is driving the directionality of cinnamon teal nest site selection, however, a long-term study of the temporal variability in nest site selection would be necessary (Clark and Shutler 1999, Devries et al. 2018).

Nest Survival

This study represents the only attempt of which I am aware to estimate nest survival for cinnamon teal using modern, unbiased methodology. Although inference can only be made at the scale of the study area, nest survival estimates are comparable to those of other fast-lived waterfowl species (Johnson 1979, Lokemoen et al. 1990). Using a hidden Markov approach to estimate nest survival not only allowed me to incorporate uncertainty in the state at which a nest

failed, but also to view patterns that would otherwise have been inestimable. Daily survival rate of nests was lower during the laying stage than the incubation stage for cinnamon teal. Hens lay one egg a day, and typically do not attend the nest regularly during the laying period (Gammonley 2012). Their eggs are therefore more exposed and less protected from nest predators. Consequently, nesting studies that fail to incorporate nests found during the laying stage or include few nests in the analysis that were found during laying might be biasing nest survival estimates high. Using the stage-based framework to analyze nest survival also allowed me to elucidate differing relationships between nest initiation date and nest survival during the two nesting stages. Waterfowl typically exhibit a negative relationship between nest survival and initiation date, although evidence is frequently mixed (Drever and Clark 2007). I found a negative relationship between nest survival and initiation date during only the incubation period for cinnamon teal. Trade-offs in nest initiation date and the amount of available resources on the landscape likely shape this relationship, since nesting earlier allows hens to occupy high-quality nesting sites with easily accessible foraging areas during an energetically expensive time (Emery et al. 2005). This might not be as important during the laying stage, when hens spend considerably more time off the nest and therefore have the ability to spend more time foraging. This relationship, therefore, might only present itself during the incubation stage of nesting. Therefore, studies that do not partition nest survival into the different nesting stages might be overlooking the nuanced ways in which nesting behavior can be both adaptive and maladaptive (Blums et al. 2005, Ringelman et al. 2018). Studies that find mixed effects of nest initiation date on nest survival might actually find the expected negative effect were they to examine only the incubation period. I did, however, monitor nests less frequently during the laying stage than

during incubation to prevent investigator-caused abandonment, and my power to detect an effect during the laying stage was therefore lower.

Conclusions

This study offers novel insights into an enigmatic duck species whose breeding habits are rarely studied. Estimating differences in its nest survival across the nesting stages and preferences for nest site selection provides a first step in describing the productivity of this species and managing for a stable, if not increasing, population. More research is necessary to ascertain the underlying mechanisms producing differences among laying and incubation survival, and nest attendance patterns might provide a starting point for such research. In addition, sample size was limited and repeating this study at Monte Vista NWR as well as other sites could greatly enhance the evidence for the processes exemplified here. Fitness consequences of the choices made during reproduction can scale up to subsequently affect overall population dynamics. Therefore, understanding the mechanisms guiding choices that affect reproductive output have the potential to not only guide management actions, but to broaden our understanding of the evolution of differing life history strategies and species population dynamics.

MANAGEMENT IMPLICATIONS

Cinnamon teal management is not frequently at the forefront of discussion among waterfowl managers given its relative population stability and the lack of information pertaining to many of its vital rates (USFWS 2013). This study represents an advancement of the baseline information necessary to determine whether large-scale management interventions are necessary to maintain a stable cinnamon teal population throughout the Intermountain West. An estimated nest survival rate that is similar to other species of teal across North America and breeding

habitat selection trends consistent with management already carried out for a majority of waterfowl species indicate few management actions are likely required beyond the status quo. Although generalizations outside of my study area are limited and the observational nature of this study limits causal inference, I did find evidence to suggest that cinnamon teal are adaptively avoiding high densities of forbs when choosing a nest site. Some of these forbs may consist of late-successional wetland plants like cattails, but many of the forbs influencing teal nest site selection and survival are likely invasive species such as perennial pepperweed and Canada thistle. Late-successional species can be minimized and food-producing emergent vegetation maximized through the use of moist-soil management regimes and prescribed burns (Kantrud 1986; Ringelman 1990; Haukos and Smith 1993; de Szalay and Rush 1997). Monte Vista National Wildlife Refuge already takes extensive measures to combat the spread of invasive plant species using pesticides, burning, and hydrological management. My results represent substantial support for continuing those practices as they indicate some of the forb species on the refuge may be negatively influencing both habitat use and nest survival of one of their focal species, the cinnamon teal. Current management of cinnamon teal does not differ drastically from management of other waterfowl species in the Intermountain West, and other species might also benefit from management regimes favoring breeding cinnamon teal.

Table 2.1: Descriptions of covariates used in analyses of cinnamon teal nest survival and nest site selection on Monte Vista NWR from 2015-2017 and the predicted direction of the effect of each covariate on the response.

Covariate Group	Covariate	Covariate Abbreviation	Description	Nest Survival Prediction	Nest Site Selection Prediction	Citations
Microhabitat	Visual Obstruction Rating	Robel	The height of vegetation (in cm) that visually obstructed the nest bowl. Measurements were taken from each cardinal direction at a distance of 4 m and then averaged.	+	+	Crabtree et al. 1989, Lokemoen et al. 1990, Fondell and Ball 2003, Thompson et al. 2012, Ness and Klaver 2016
	% Grass	PGrass	The percent of the total area within a 4 m radius plot around the nest that consisted of graminoids (grasses, sedges, and rushes).	+	+	Greenwood et al. 1995, Phillips et al. 2003, Stephens et al. 2005, Gammonley 2012
	% Water	PWater	The percent of the total area within a 4 m radius plot around the nest that was taken up by water.	+	+	Laubhan and Gammonley, unpublished study, Wheeler and Harris 1970, Myers 1982

	% Bare Ground	PBG	The percent of the total area within a 4 m radius plot around the nest that was taken up by bare ground.	-	-	Lokemoen and Woodward 1992
	% Forbs	PForbs	The percent of the total area within a 4 m radius plot around the nest that consisted of forbs (any non-graminoid herbaceous wetland plant).	-	-	Dion et al. 2000; Hines and Mitchell 1983
	% Shrubs	PShrub	The percent of the total area within a 4 m radius plot around the nest that consisted of shrubs (most frequently greasewood or rabbitbrush).	-	-	Thompson et al. 2012
	% Live	PLive	The percent of the total area within a 4 m radius plot around the nest that consisted of living vegetation rather than dead, matted stems from the previous year.	+	+	
Access	Distance to Shrubland	DShrub	Distance in m to the closest patch of shrubs ≥ 1 ha in size.	+	+	Paton 1994, Stephens et al. 2005

	Distance to Water	DWater	Distance (m) to any water body, including ponds or flooded meadows.	-	-	Laubhan and Gammonley, unpublished study, Wheeler and Harris 1970, Myers 1982, Crabtree et al. 1989, Jungers et al. 2015
Intrinsic/Other	Clutch Size	Clutch	Number of cinnamon teal eggs in the nest.	0	NA	Rohwer 1985
	Hen Weight	Weight	Weight (g) of the hen.	+	NA	Reviewed by Johnson et al. 1992, Pace and Afton 1999
	Nest Initiation Date	NID	The number of days past my arbitrary start date (10 May) the nest was initiated. Can be negative if the nest was initiated before 10 May.	-	NA	Crabtree et al. 1989, Daan et al. 1990, Drever and Clark 2007, Ringelman et al. 2014

Table 2.2 Coefficient estimates for each covariate corresponding to analyses of cinnamon teal nest site selection and nest survival on Monte Vista NWR, 2015-2017. Nest survival was analyzed in a multistate framework to assess the effects of covariates on both the laying and incubation stages of nesting.

Covariate	Nest Site Selection β	SE	Laying Survival	SE	Incubation Survival	SE
	Estimate		β Estimate		β Estimate	
DShrub	-0.934	0.351	0.248	0.370	-0.182	0.157
DWater	-0.432	0.383	-0.038	0.047	-0.121	0.272
PBG	-0.521	0.295	0.322	0.607	0.556	0.256
PForbs	-0.799	0.250	0.290	0.325	0.278	0.226
PGrass	0.535	0.204	0.149	0.270	-0.160	0.305
PLive	-0.315	0.198	0.321	0.291	0.456	0.563
PShrub	-0.036	0.178	-0.471	0.313	0.315	0.219
PWater	0.243	0.168	-0.146	0.265	-0.432	0.172
VOR	0.063	0.198	0.497	0.288	0.020	0.237

Table 2.3: AICc table for nest site selection analysis using discrete choice models of cinnamon teal nesting on Monte Vista NWR in 2017. **PForbs** = % of the area within a four-meter radius plot around the nest consisting of forbs, **PGrass** = % of the area within a four-meter radius plot around the nest consisting of grass, **PBG** = % of the area within a four-meter radius plot around the nest consisting of bare ground, **PWater** = % of the area within a four-meter radius plot around the nest consisting of water, **PLive** = % of the area within a four-meter radius plot around the nest in which the vegetation is living (i.e., the current year's growth), **PShrub** = % of the area within a four-meter radius plot around the nest consisting of shrubs, **DShrub** = distance (in m) from the nest to the closest area of shrubs \geq one ha in size, **DWater** = distance (in m) from the nest to the closest water body or flooded meadow, and **Robel** = the height of vegetation (in cm) that visually obstructed the nest bowl. Measurements were taken from each cardinal direction at a distance of 4 m and then averaged.

Model Structure	Df	LogLik	AICc	Delta AICc	Model Weight
$\beta_1^*(PForbs)$	1	-95.3	192.6	0.0	0.7
$\beta_1^*(PForbs) + \beta_2^*(PGrass)$	2	-95.3	194.6	2.0	0.2
$\beta_1^*(DShrub)$	1	-98.2	198.5	5.9	0.0
$\beta_1^*(PGrass)$	1	-98.3	198.6	6.1	0.0
$\beta_1^*(DShrub) + \beta_2^*(DWater)$	2	-98.0	200.1	7.6	0.0
$\beta_1^*(PBG)$	1	-99.9	201.7	9.2	0.0
$\beta_1^*(PLive)$	1	-101	203.8	11.2	0.0
$\beta_1^*(PWater)$	1	-101	204.2	11.7	0.0
$\beta_1^*(DWater)$	1	-101	204.9	12.3	0.0
$\beta_1^*(VOR)$	1	-102	206.2	13.6	0.0
$\beta_1^*(PShrub)$	1	-102	206.2	13.7	0.0

Table 2.4: Summary of cinnamon teal nest fates for nests found on Monte Vista National Wildlife Refuge from 2015-2017.

Year	Number of Nests Found	Number of Successful Nests	Number of Depredated Nests	Number of Abandoned Nests*	Number of Nests Failed Due to Other Causes	Nest Survival
2015	40	9	19	10	2	0.194
2016	52	17	13	20	2	0.194
2017	60	23	26	10	1	0.194

*Includes nests whose hens abandoned due to investigator activity as well as those that abandoned due to other causes.

Table 2.5: 90% confidence set (based on Akaike weights) indicating support for models explaining cinnamon teal nest survival on Monte Vista NWR from 2015-2017. ψ^{12} = The probability that a nest will transition from the laying stage to the incubation stage, δ_{Lay} = The probability of being able to detect that a nest failed during the laying state given that it did fail during the laying state, ψ^{13} = The probability that a nest will fail during the laying stage, ψ^{24} = The probability that a nest will fail during the incubation stage, ψ^{25} = The probability that a nest will transition from the incubation stage to the hatched stage, at which point modeling stops, δ_{Inc} = The probability of being able to detect that a nest failed during the incubation state given that it did fail during the incubation state, **NID**² indicates a quadratic effect on nest initiation date, + indicates an additive effect, **Age** = Linear time trend, **Pforbs** = % of the area within a four-meter radius plot around the nest consisting of forbs, **Pgrass** = % of the area within a four-meter radius plot around the nest consisting of grass, **Pshrub** = % of the area within a four-meter radius plot around the nest consisting of shrubs, **Robel** = visual obstruction rating as measured using a Robel pole (Robel et al. 1970), **Dshrub** = distance (in m) from nearest patch of shrubs ≥ 1 ha in size, and **Clutch** = the number of eggs laid by a hen once she enters incubation (i.e., the full clutch size).

Model Structure	Number of Parameters	Model Likelihood	AICc	Delta AICc	Model Weight	Deviance
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Pforbs}) \psi^{25}(\text{Age}) \delta_{Lay}(\text{Age}) \delta_{Inc}(\text{Age})$	13	1.0	351.3	0.0	0.3	324.8
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{Pforbs}) \psi^{24}(\text{NID}^2 + \text{Pforbs}) \psi^{25}(\text{Age}) \delta_{Lay}(\text{Age}) \delta_{Inc}(\text{Age})$	14	0.6	352.5	1.2	0.1	323.9
$\psi^{12}(\text{Age}) \psi^{13}(\text{Age} + \text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Pforbs}) \psi^{25}(\text{Age}) \delta_{Lay}(\text{Age}) \delta_{Inc}(\text{Age})$	14	0.5	352.5	1.2	0.1	323.9
$\psi^{12}(\text{Age}) \psi^{13}(\text{Age} + \text{NID}^2) \psi^{24}(\text{Age} + \text{NID}^2 + \text{Pforbs}) \psi^{25}(\text{Age}) \delta_{Lay}(\text{Age}) \delta_{Inc}(\text{Age})$	15	0.4	353.4	2.1	0.1	322.7
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2) \psi^{25}(\text{Age}) \delta_{Lay}(\text{Age}) \delta_{Inc}(\text{Age})$	12	0.2	354.9	3.5	0.0	330.4
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Pgrass}) \psi^{25}(\text{Age}) \delta_{Lay}(\text{Age}) \delta_{Inc}(\text{Age})$	13	0.2	355.0	3.6	0.0	328.4
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{Clutch}) \psi^{24}(\text{NID}^2 + \text{Clutch}) \psi^{25}(\text{Age}) \delta_{Lay}(\text{Age}) \delta_{Inc}(\text{Age})$	14	0.1	355.2	3.9	0.0	326.6
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{robel}) \psi^{24}(\text{NID}^2 + \text{robel}) \psi^{25}(\text{Age}) \delta_{Lay}(\text{Age}) \delta_{Inc}(\text{Age})$	14	0.1	355.8	4.4	0.0	327.1

$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{Pshrub}) \psi^{24}(\text{NID}^2 + \text{Pshrub}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	14	0.1	355.9	4.6	0.0	327.3
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Age}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	13	0.1	356.2	4.9	0.0	329.7
$\psi^{12}(\text{Age}) \psi^{13}(\text{Pforbs}) \psi^{24}(\text{Age} + \text{Pforbs}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	11	0.1	356.6	5.3	0.0	334.2
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{Pgrass}) \psi^{24}(\text{NID}^2 + \text{Pgrass}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	14	0.1	356.7	5.4	0.0	328.1
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Dshrub}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	13	0.1	356.8	5.4	0.0	330.2
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Clutch}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	13	0.1	356.8	5.5	0.0	330.3
$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{robel}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	13	0.1	356.9	5.6	0.0	330.4

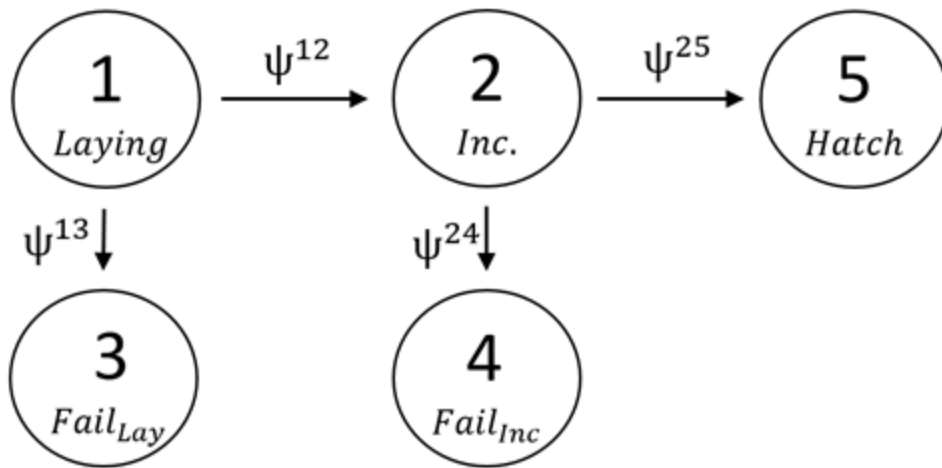


Figure 2.1: Diagram of nesting stages for cinnamon teal nest survival analysis in a multistate framework. For nest failures, the stage at failure is allowed to be uncertain.

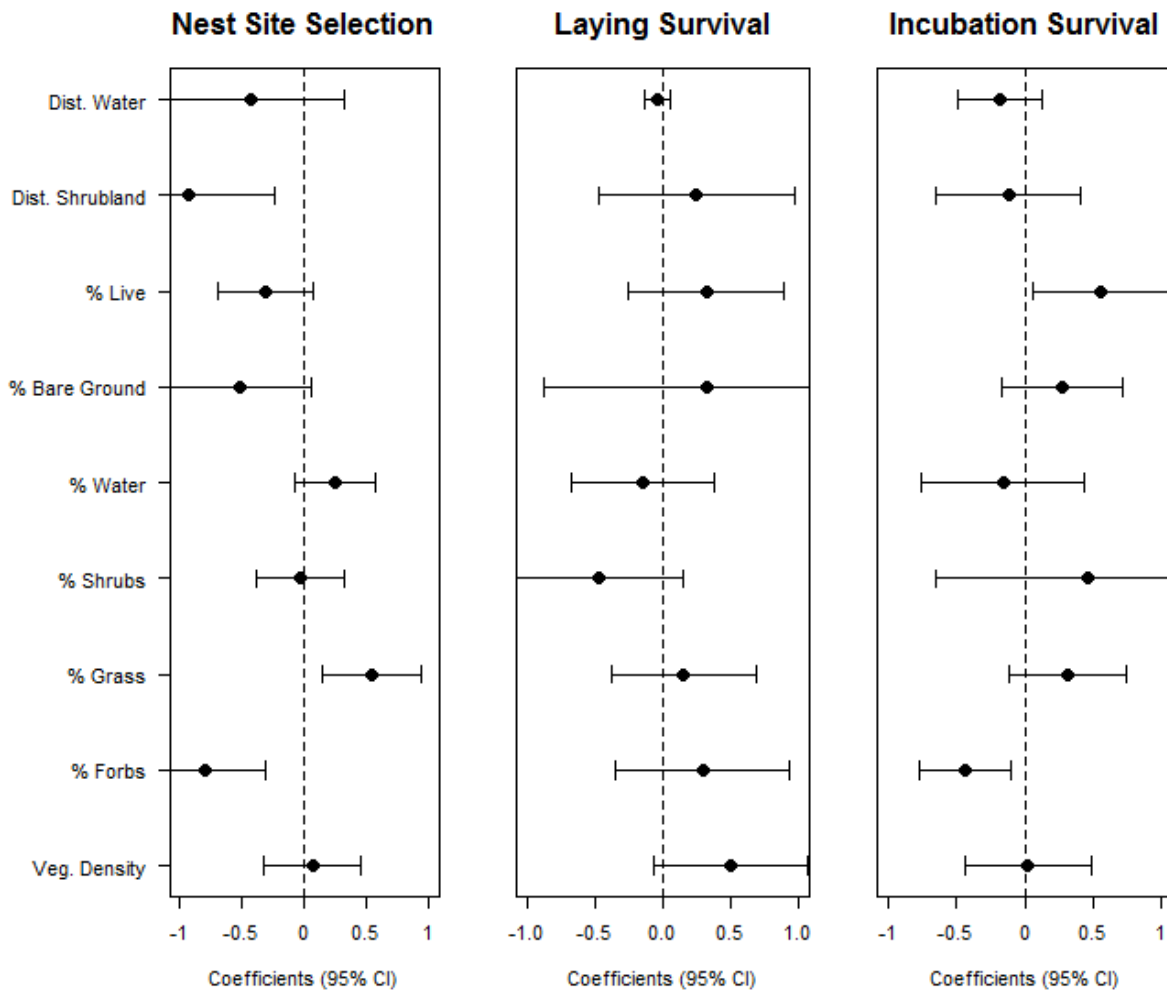


Figure 2.2: β parameter estimates corresponding to nest site selection (from univariate discrete choice models) and nest survival (from hidden Markov model) during cinnamon teal laying and incubation on Monte Vista NWR from 2015-2017. Nest site selection results are based on 57 cinnamon teal nests from 2017, while nest survival results are based on 85 nests pooled across 2015-2017. Points indicate apparent effect and error bars indicate 95% confidence intervals.

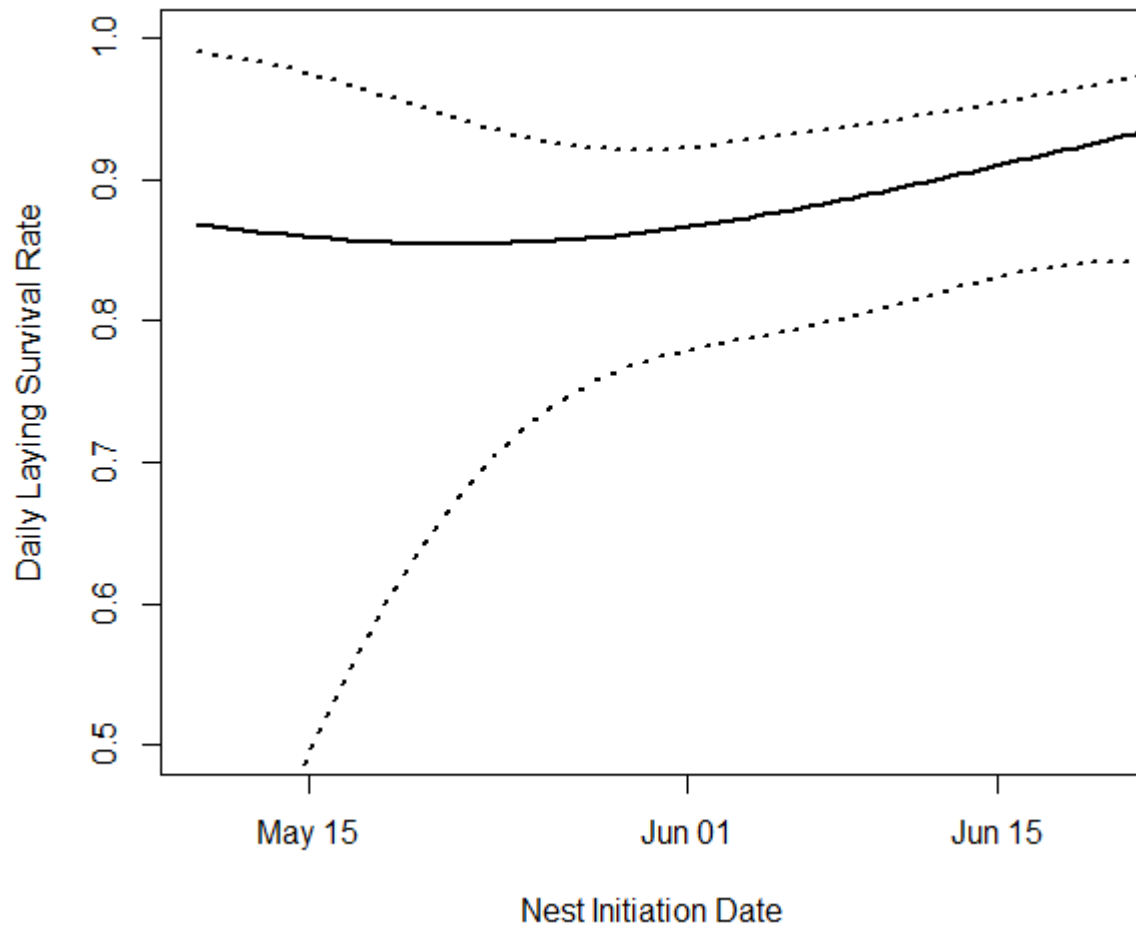


Figure 2.3: Relationship between nest initiation date and daily survival rate of cinnamon teal nests on Monte Vista NWR from 2015-2017 during the laying stage of nesting.

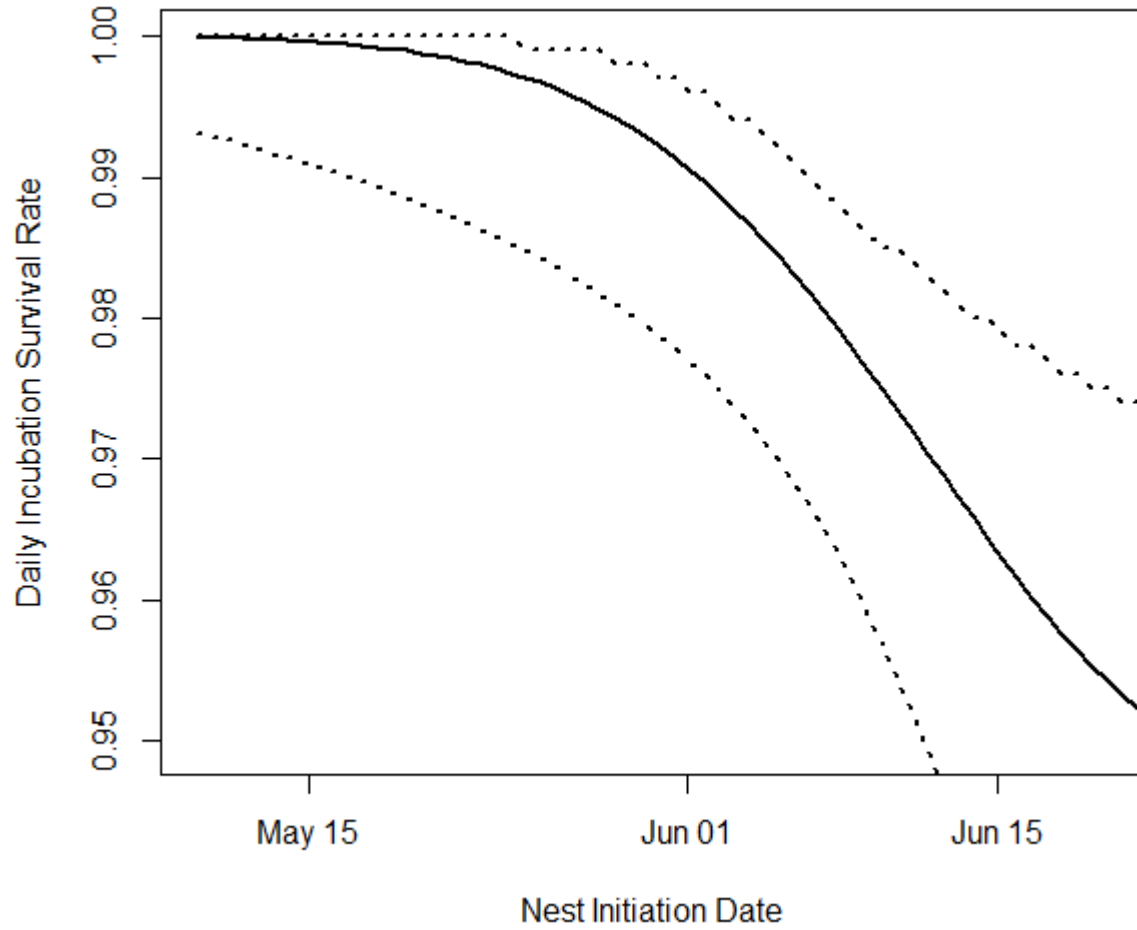


Figure 2.4: Relationship between nest initiation date and daily survival rate of cinnamon teal nests on Monte Vista NWR from 2015-2017 during the incubation stage of nesting.

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Chapter 3 - SOCIAL INDICES OF CINNAMON TEAL REPRODUCTIVE SUCCESS IN COLORADO

SUMMARY

The cinnamon teal (*Spatula cyanoptera*) is a difficult duck species to study using traditional techniques due to its secretive habits and limited range during the breeding season. I evaluated whether previously established social indices, which were developed to assess reproductive success in waterfowl through consecutive roadside transect surveys of social groupings (i.e., pairs, lone males, flocked males), were an appropriate indicator of success for breeding cinnamon teal in Colorado. I conducted social index surveys from 2015 to 2017 on Monte Vista National Wildlife Refuge while concurrently evaluating nest survival using traditional nest monitoring methods. I also used dependent double observer methodology to adjust for observer-specific detection rates for each social grouping observed on surveys in 2017. Only one of the seven calculated indices (Area 4) was significantly correlated ($r = -0.999$, p -value = 0.007) with nest survival, while none of the indices were correlated with duckling:pair ratio, an additional measure of productivity calculated from the transect surveys. The estimate of overall detection was high ($\hat{P} = 0.998$, $SD = 0.004$) but differed by observer ($\hat{P}_1 = 0.980$, $SD = 0.027$ and $\hat{P}_2 = 0.895$, $SD = 0.085$) across social groupings. Estimates of detection were similar between observers for lone drakes ($\hat{P}_1 = 0.912$, $SD = 0.098$, $\hat{P}_2 = 0.891$, $SD = 0.157$, $t = -0.123$, p -value = 0.667) and between social groupings (Pair detection: $\hat{P}_1 = 0.975$, $SD = 0.044$ $\hat{P}_2 = 0.899$, $SD = 0.101$), but varied significantly between observers for pairs ($t = -2.40$, p -value = 0.030). Social indices have the potential to act as a useful tool for difficult-to-study duck species if they are carried out consistently over long timespans and across geographic areas.

INTRODUCTION

While effective, typical nest monitoring methods used to determine vital rates of waterfowl species are extremely time- and effort-intensive. Previous studies have shown that roadside transect counts of social groupings of waterfowl conducted throughout the breeding season can indicate breeding effort and timing information regarding when significant events are occurring (i.e., peak hatch date, peak nest initiation date, peak incubation initiation date, etc.; Dzubin 1969, Hochbaum et al. 1987, Serie and Cowardin 1990, Arnold et al. 2008). Dzubin (1969) determined that the ratio of pairs to lone males in a breeding area decreases as more hens begin nesting, at which point transect surveys start to reveal increasing numbers of lone drakes. At some point, if hens are successful in their nesting attempts, males will start to flock up into small groups of 2-5 individuals, whereas nest failures will result in increasing pair numbers as hens prepare for reneeding. When plotted against Julian date throughout the breeding season, the curves created by the number of lone males, pairs, and flocked males can provide an index of the number of breeding pairs in an area and their level of success (Dzubin 1969, Hochbaum et al. 1987, Serie and Cowardin 1990, Arnold et al. 2008). The areas beneath different sections of these lone male and pair curves have been used as indices of nesting effort and success as shown by correlations with independent nest monitoring studies in the same geographic regions (Hochbaum et al. 1987, Serie and Cowardin 1990, Arnold et al. 2008). The use of social indices has been relatively scarce since its inception, however, and even more so in regions outside the Prairie Potholes. Some indices calculated from curves of pairs and lone drakes have been shown to be useful for predicting brood production of commonly breeding duck species in Prairie Canada, while others were more appropriate for predicting nest survival (Hochbaum et al. 1987). Other social indices calculated using the pair, lone drake, and flocked drake curves of canvasbacks (*Aythya valisineria*) in Manitoba were strongly correlated with hen success, which

accounts for both nesting success and reneating success (Serie and Cowardin 1990). More recently, the efficacy of these indices was tested on a long-term mallard (*Anas platyrhynchos*) dataset, resulting in mixed findings regarding the reliability of social indices as reproductive predictors (Arnold et al. 2008).

The seven original indices these authors calculated from the social grouping curves were quite similar, but differed slightly in their execution. Serie and Cowardin (1990) used pair, lone drake, and flocked drake curves to calculate indices A-C where Social Index A computed the area between the pair and lone drake curves from peak pair numbers to the intersection of pair and lone male curves (Figure 1). This area should be large in years of high early nesting success, but it does not capture reneating effort later in the season. Social Index B calculated the area from the peak in pair numbers to the peak in flocked males, indicating few actively nesting females when the area is large as pairs would theoretically decline quickly and remain low in years of high nesting effort. This index may also capture reneating effort better than index A. Similar to Area B, Social Index C calculated the area from the initial peak in pair numbers to the time when pairs reach zero, which should also be small if reproductive success is high. Hochbaum et al. (1987) used only the pair and lone drake curves to calculate indices 1-4 where Area 1 measured the entire area under the pair curve (equivalent to Area C), Area 2 was the entire area under the lone drake curve, Area 3 was the area between the pair and lone drake curves early in the season when pairs exceeded drakes (equivalent to Area A), and Area 4 was the area between the lone drake and the pair curves later in the season when drakes exceeded pairs (Figure 2).

Different indices may be more beneficial for different species and measures of reproductive success based on the timing of a given species' breeding season and its social

behavior (Hochbaum et al. 1987, Serie and Cowardin 1990). Given the correlations between social indices and the reproductive success of breeding waterfowl in Prairie Canada, my goal was to apply these same indices to cinnamon teal (*Spatula cyanoptera*) breeding in Colorado and begin to evaluate whether this is a viable option for indexing cinnamon teal vital rates. Vital rate estimates for cinnamon teal are frequently combined with those for the closely related blue-winged teal (*Spatula discors*) because the hens and drakes in basic plumage are nearly impossible to differentiate. A visual survey conducted during the breeding season when teal are in their easily identifiable breeding plumage, however, has the potential to provide accurate species-specific estimates of reproductive success. The cinnamon teal is an early to mid-season nester that forms pairs on the wintering grounds and begins nesting as soon as it finds suitable habitat on its northward migration (Gammonley 2012). There is typically a steep drop-off of pair numbers as females initiate nesting. Thus, I predicted that social indices A (analogous to Area 3) and B would most effectively capture their reproductive success (as measured by nest survival) while indices C and 4 might be more indicative of productivity (i.e., the number of ducklings produced; Arnold et al. 2008).

STUDY AREA

Monte Vista National Wildlife Refuge (NWR) is part of the San Luis Valley NWR Complex, situated 6 miles south of the town of Monte Vista, Colorado. The 2015 San Luis Valley Comprehensive Conservation Plan fully characterizes this 6,003 hectare study area, which sits at approximately 2,255 meters of elevation and receives less than 20 centimeters of precipitation annually. Most of the water in this region comes from snowmelt, a shallow unconfined aquifer, and a deep artesian aquifer (Huntley 1979). The primary vegetation throughout the study area consists of bulrush (*Schoenoplectus sp.*), cattails (*Typha latifolia*),

Baltic rush (*Juncus arcticus*), and sedges (*Carex sp.*) in the semi-permanent and permanent wetlands, as well as rabbitbrush (*Ericameria nauseosa*), greasewood (*Sarcobatus vermiculatus*), saltgrass (*Distichlis spicata*), and alkali sacaton (*Sporobolus airoides*) in the upland areas. Rotational cattle and sheep grazing is used as a management tool for invasive plant species, and some center pivot irrigation produces barley and alfalfa (USFWS 2015). Historically, Monte Vista NWR had the highest waterfowl nesting density on the continent (Gilbert et al. 1996), but drawdown of the aquifers and prolonged drought have resulted in increasingly arid conditions. Under their 2015 Comprehensive Conservation Plan, the San Luis Valley NWR Complex included cinnamon teal as a focal species for their chosen plan alternative, linking their life history and population dynamics directly to their habitat-based objectives (USFWS 2015).

METHODS

I identified a 19.6 km route along drivable levee roads representative of all Monte Vista NWR habitat types and interspersing areas I subsequently searched for cinnamon teal nests. I conducted surveys at 7 day intervals from early April until early August during the 2015-2017 breeding seasons. I began surveys at sunrise and ended no later than 1030h. I conducted counts of social groupings for cinnamon teal, blue-winged teal, mallards, and gadwall because they are the four most commonly nesting species of waterfowl on the refuge (Scott Miller, USFWS-SLVNWR, personal communication). I grouped birds into one of five categories: lone males, pairs, flocked males, females with ducklings, and mixed-species flocks. Flocked males were defined as any five or more males in close association, and aggregate single-species groups were separated out into pairs and lone males (Serie and Cowardin 1990). I differentiated cinnamon teal hens with ducklings from blue-winged teal with ducklings based on visual identification of field marks, association with other individuals of the same species, and a general understanding

of the relative prevalence of blue-winged teal to cinnamon (i.e., I observed fewer blue-winged teal over the course of three field seasons). I conducted surveys from a vehicle with one or two observers using binoculars and a rangefinder to document all social groups within 0.2 km of the road. I stopped at each wetland location for no more than two minutes to ensure I had time to count the species present, but was not counting birds that landed in the wetland during that time (Hammond 1969, Arnold et al. 2008). I remained in the vehicle and did not make the assumption that observers were detecting all individuals (Serie and Cowardin 1990, Arnold et al. 2008). In 2017, I followed dependent double-observer protocols to adjust for imperfect detection of available ducks/groupings by one or both observers (Nichols et al. 2000). Under this method, a primary observer counted all individual birds and reported them to a secondary observer. The secondary observer recorded the birds reported by the primary observer in addition to any birds missed by the primary observer. I split the survey route into two “sites,” and each observer took turns being the primary observer within a survey route. This allowed me to calculate an observer-specific detection probability for each survey throughout the season.

Index Calculation

I plotted normalized counts of pairs, lone males, and flocked males against survey date each year to assess changes in these social groupings throughout the breeding season. I normalized survey totals by dividing both the number of pairs and the number of lone males by the total number of indicated breeding pairs (the sum of pairs and lone males) each week. I left censored counts before 4 April to ensure that I calculated all indices from the same date. Indices are based on either two or three of these curves, and I calculated each index according to the methodology used by Serie and Cowardin (1990; Figure 1) and Hochbaum et al. (1987; Figure 2). Graph areas used to calculate indices were defined by Serie and Cowardin (1990): "Area A is

the area between the pair and lone male curves starting from date of peak pairs to when these curves intersect, Area B is the area under the pair curve from peak pairs to the point of peak flocked males, and Area C is the area under the pair curve from peak pairs to the point when percent pairs first becomes zero." Areas defined by Hochbaum et al. (1987) were "Area 1, the area under the pair curve, Area 2, the area under the drake curve, Area 3, the area between the pair and drake curves from the date of peak pairs to the date of the crossover of the curves, and Area 4, the area between the pair and drake curves from the first crossover date, prior to and following apparent reneating." I calculated areas using the *auc()* function from the *MESS* package in Program R (Ekstrøm 2011). This function allows users to compute the area under a curve using natural spline interpolation for two vectors.

Independent Measures of Reproductive Success

I calculated Pearson correlation coefficients (r) between each social index value and the estimates of nest survival and duckling:pair ratio from 2015-2017. I estimated nest survival using a multievent framework (see Pradel 2005, Kendall et al. 2012, Setash Chapter 2), which allowed us to estimate laying survival and incubation survival separately and compare the estimates from both nesting stages to the various social indices. Using the multievent framework to estimate nest survival, I did not detect an effect of year on laying survival or incubation survival. I therefore included annual estimates of apparent nest survival in my calculation of correlation coefficients to see whether social indices might act as predictors of yearly nest survival. I calculated duckling:pair ratio according to the methods provided in Arnold et al. (2008). This entailed averaging the number of ducklings seen on all surveys where ducklings were detected and averaging the number of indicated breeding pairs from the three surveys centered on the

crossover point of the pair and lone drake curves. I then compared these averages to calculate the ratio of ducklings to indicated breeding pairs.

Detection Probability

Arnold et al. (2008) encouraged researchers estimating social indices to use methods for evaluating detection probability to reduce bias of duckling:pair ratios. I therefore tabulated observations from surveys conducted in 2017 according to Nichols et al. (2000) to calculate detection using a dependent double observer methodology. For each survey, x_{ij} was the number of birds counted by observer i when observer j was the primary observer. P_i , the detection probability for each observer i , was calculated using equation (3) in Nichols et al. (2000) and I assumed it to be the same whether the observer was serving as primary or secondary observer within a survey. I split observations into social groupings to estimate detection probability of each grouping separately (e.g., pairs, lone males, flocked males, and groups of ducklings) because pairs and groups of ducklings likely fail to meet the assumption that observations of individuals are independent (Nichols et al. 2000). I then decided whether duckling:pair ratios needed to be adjusted or whether counts were biased enough to change the shape of the curve, thus changing a given index, based on these estimates of detection (Arnold et al. 2008).

RESULTS

I conducted an average of 19 surveys each year (range = 17-22). The pair curve decreased and the lone drake curve increased throughout the beginning of the season, intersecting on 22 May 2015, 20 May 2016, and 12 May 2017 (Figure 3.3). These corresponded to the average dates of nest initiation for my independently sampled cinnamon teal nests, which were 3 June in 2015, 22 May in 2016, and 13 May in 2017. I missed the date of peak pairs in both 2015 and 2017, but in 2016 pairs peaked on 26 April, nearly a month later than the other years. Indicated

breeding pairs, however (the sum of pairs and lone drakes), peaked in late April each year, ranging from 13 April to 26 April. The peak numbers of indicated breeding pairs ranged from 148 in 2017 to 224 in 2015.

Yearly apparent nest survival ranged from 0.300 to 0.688 and duckling:pair ratio varied from 0.390 to 0.713 (Table 3.1). Correlation coefficients varied considerably, ranging from 0.053 for the correlation between Area A and duckling:pair ratio to -0.999 for the correlation between Area 4 and apparent nest survival (Table 3.2). Area 4 was the only index significantly correlated with reproductive success, but overall correlation coefficients were quite high (Table 3.2). Duckling:pair ratio was also highly correlated with apparent nest survival although I primarily used it as a measurement of reproductive success to which I compared the indices.

Detection probability varied by observer (Table 3.3, Figure 3.4, $t = 4.11$, $p\text{-value} < 0.001$) throughout the 2017 surveys, but overall it was relatively high ($\hat{P}_1 = 0.980$, $SD = 0.027$ and $\hat{P}_2 = 0.895$, $SD = 0.085$; $\hat{P} = 0.998$, $SE = 0.004$; Table 3.3) across social groupings. Detection probability varied significantly between observers for pairs ($t = -2.40$, $p\text{-value} = 0.030$) but not lone drakes ($t = -0.123$, $p\text{-value} = 0.667$). Although I observed ducklings on four surveys during 2017, I only observed enough groups to estimate detection on two individual surveys. Duckling detection did not vary significantly by observer ($\hat{P}_1 = 1.00$, $SD = 0$, $\hat{P}_2 = 0.726$, $SD = 0.388$, $t = -1.00$, $p\text{-value} = 0.500$) and each observer missed few enough ducklings that the estimate of overall duckling detection was 1.00 ($\hat{P} = 1.00$, $SD = 0$). Overall (i.e., across social grouping) observer-specific detection estimates increased slightly over time and the lower of the two detection rates converged on the higher estimate as the season progressed (Figure 3.4). Abundance estimates incorporating detection rarely differed from the naïve counts of individuals given my high detection probability, and those that did differ (most frequently estimates of pair

numbers) never changed the original number of individuals by more than 1.95. I considered these negligible differences and therefore assumed that my counts and estimates of duckling:pair ratios were unbiased so I did not make further adjustments.

DISCUSSION

Social Indices as a Tool for Estimating Breeding Phenology

Weekly driving surveys were a far more efficient method of detecting important breeding milestones on my study area than monitoring nests using traditional methods such as rope-dragging and subsequent observations. I initially conducted these surveys during a pilot study to determine the timing of reproductive events helpful in planning field season logistics (e.g., peak nest initiation, approximate timing of renesting, etc.; Dzubin 1969) and continued them throughout the study to assess their value in terms of monitoring reproductive success. As a means of estimating breeding phenology, they were an invaluable tool. The date the pair curve and the lone drake curve intersects has been shown to indicate peak nest initiation date on a given study area (Dzubin 1969). The intersection of these curves from my study matched the mean nest initiation dates of nests I monitored separately from 2015-2017, providing evidence for their reliability as a method for monitoring timing.

The pair and lone drake intersection and the mean nest initiation date from monitored nests occurred earliest in 2017 (12 May and 13 May, respectively). This coincided with the lowest number of indicated breeding pairs (IBP) and the highest apparent nest survival and duckling:pair ratio recorded throughout the study period. With fewer breeding birds and therefore less intense competition, hens could potentially obtain high quality breeding sites early in the season, which is often tied to higher reproductive success than nests initiated later in the season (Daan et al. 1990). The reasons for variations in cinnamon teal abundance and subsequent

IBP are unclear, but are likely tied to variation in precipitation and local hydrology across years (Doherty et al. 2015). The San Luis Valley Refuge Complex provides some of the only semi-permanent wetland habitat in the arid region, so variations in their flooding regimes and water availability might directly affect cinnamon teal settling patterns (Finger et al. 2016, Bartzen et al. 2017). Social indices provide an effective and efficient way to estimate cinnamon teal phenology throughout the breeding season and can therefore indicate when to study settling patterns throughout the San Luis Valley and other regions.

Social Indices as a Tool for Monitoring Reproductive Success

The social indices I calculated showed promise as a tool for efficiently monitoring cinnamon teal reproductive success within a limited timeframe. Social indices 2 and 4 were the only areas exhibiting either significant or marginally significant correlations with nest survival, and also displayed two of the strongest correlations with duckling:pair ratio (Table 2). Higher values for indices 2 and 4 result from a higher ratio of lone drakes to pairs throughout the survey period, indicating that breeding effort was consistently high throughout the season since females were theoretically on nests and therefore unavailable for detection (Arnold et al. 2008). Area 4 is thought to specifically reflect information about renesting, with smaller areas indicating high renesting effort (Hochbaum et al. 1987, Arnold et al. 2008). This is consistent with my observations as I located few known re-nests throughout the course of the study period. It is possible, however, that nests found during the later months of the breeding season were renesting attempts, but without individually identifiable markers on birds I could not verify sequential nests. Managers might therefore monitor Areas 2 and 4 of the social index curves in lieu of searching for cinnamon teal nests to evaluate general trends in cinnamon teal nest survival on a large scale. Given the limited timeframe of this study, however, correlations between social

indices and measures of reproductive success should be viewed with caution and interpreted accordingly.

Detection Probability

Using a dependent double observer methodology (Nichols et al. 2000) to estimate detection throughout my 2017 surveys took minimal effort and enabled us to determine whether duckling:pair ratios were biased as well as whether the shape of the plotted social grouping curves should be adjusted (Arnold et al. 2008). Adjusting counts for detection rate would change the ratio of one social grouping to another, therefore modifying the area calculated under the curve (i.e., the social index). Despite the fact that the estimates of detection in this study were high enough to preclude these adjustments, I recommend continuing to use methods for estimating detection in future social index studies. Although my sample sizes were large enough to estimate precise detection probabilities according to social grouping (e.g., pair, lone drake, ducklings), the large number of birds hindered my ability to use an independent double observer approach, since mapping individuals would be difficult as flocks swam and flushed off the water (Pagano and Arnold 2009). In addition, estimates of detection probability resulting from the dependent double observer method are based only on birds that are available for detection. They are therefore potentially biased high when both observers fail to record birds or when there are few instances of the secondary observer recording birds missed by the primary observer. This could be problematic if detection is low enough to warrant adjusting counts, thus changing the shape of the plots and the social indices. However, if the assumption can be made that the individuals being observed are representative of the individuals that are missed (and thus the ratio between social groupings), and this is consistent across the entire season, calculating a detection probability is unnecessary.

Detection probabilities differed between observers and between social groupings of cinnamon teal. However, estimates increased and converged between the experienced and novice observers as surveys progressed (Figure 4), indicating that either both observers were becoming more skilled as the season went on, or that environmental covariates were acting on both observers simultaneously to reduce the number of individuals recorded by one observer but not the other. Contrary to other studies estimating group-specific detection, my estimates of detection probability were similar for lone drakes and for pairs of cinnamon teal (Pagano and Arnold 2009). Larger groups of ducks, especially those including the frequently more colorful males, are expected to be more conspicuous and therefore easier to detect (Marsh and Sinclair 1989, Laake et al. 2008). When I observed groups including both males and females, I split the group up into pairs and “leftover” males, potentially accounting for the similar estimates for the two groups. It would likely be beneficial to keep track of group size as well as social status in future studies to see whether larger groups are easier to detect. My estimates of detection probability may also be a function of an observer learning curve, as pairs are more abundant in the beginning of the season when novice observers are still learning waterfowl identification while lone drakes are more abundant as the season progresses. If this were the case, detection probability would be biased low for pairs and high for lone drakes, potentially explaining the similarity between the two estimates seen in this study.

MANAGEMENT IMPLICATIONS

As a method for monitoring reproductive success in a region, social indices are particularly useful when they are conducted consistently for several years or concurrently in different geographic areas since a sufficient sample size is necessary to calculate a correlation (i.e., ≥ 3 years or study sites; Arnold et al. 2008). If this relatively easy and minimally time-

intensive method were to be utilized for cinnamon teal on a range-wide basis, it could provide baseline estimates of production that are currently lacking for this species. Larger scale surveys might also provide cost-effective estimates of regional population abundance in the absence of more traditional surveys (e.g., BPOP, aerial surveys, etc.). Careful forethought should be given to the selection of a transect route, however, given the bias in density estimates associated with road transects (Austin et al. 2000). Surveying a larger transect width might mitigate this bias, but consideration of the study species, wetland types being surveyed, and waterfowl behavioral effects induced by moving vehicles should be considered before initiating a survey route. Social index surveys are an appropriate tool for managers with limited budgets, questions or concerns about waterfowl reproductive success on their management area, and/or ongoing waterfowl monitoring projects that could be augmented with additional concurrent information.

Table 3.1: Social indices calculated from yearly plots of cinnamon teal numbers surveyed from 2015-2017 on Monte Vista NWR and the corresponding estimates of reproductive success. Areas 1-4 correspond to indices created by Hochbaum et al. (1987) and Areas A-C correspond to indices created by Serie and Cowardin (1990).

Year	Area 1	Area 2	Area 3	Area 4	Area A	Area B	Area C	Apparent Nest Survival	Duckling:Pair Ratio
2015	53.1	81.9	26.6	55.4	26.6	52.9	52.9	0.300	0.390
2016	55.4	67.6	13.3	41.6	13.3	35.2	35.3	0.652	0.476
2017	47.4	63.6	23.7	40.0	23.7	46.2	46.3	0.688	0.713

Table 3.2: Pearson correlation coefficients between social indices calculated from plots of cinnamon teal numbers surveyed from 2015-2017 on Monte Vista NWR and independent measures of reproductive success.

Social Index	Apparent Nest Survival	Duckling:Pair Ratio
Area A	-0.612	0.053
Area B	-0.735	-0.123
Area C	-0.732	-0.118
Area 1	-0.316	-0.854
Area 2	-0.993*	-0.836
Area 3	-0.605	-0.056
Area 4	-0.999**	-0.770
D:P Ratio	0.763	NA

* $0.05 \leq P < 0.08$

*P < 0.05

** P < 0.01

Table 3.3: Observer-specific detection estimates and standard deviations for each social grouping of cinnamon teal averaged across 17 social index surveys conducted on Monte Vista NWR in 2017.

Observer	Pair Detection (SD)	Lone Male Detection (SD)	Flocked Male Detection	Duckling Detection (SD)	Overall Detection (SD)
\hat{P}_1	0.975 (0.044)	0.912 (0.098)	NA ^a	1 (0)	0.980 (0.027)
\hat{P}_2	0.899 (0.101)	0.891 (0.157)	NA ^a	0.726 (0.388)	0.895 (0.085)
\hat{P}	0.997 (0.005)	0.987 (0.027)	NA ^a	1 (0)	0.998 (0.004)

^aToo few groups of flocked males were observed to estimate flocked male detection.

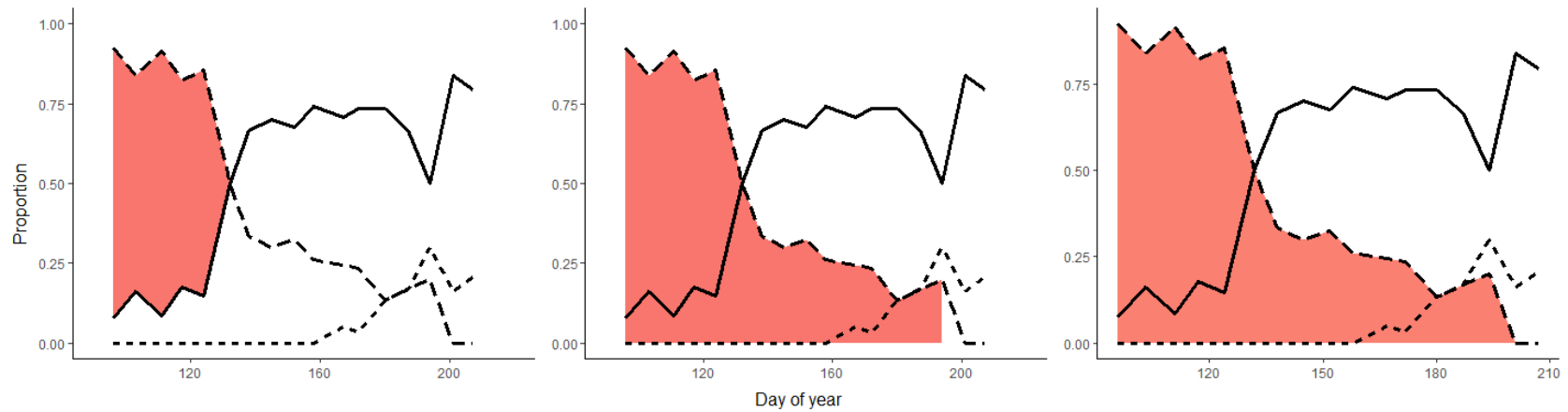


Figure 3.1: Examples of social indices calculated using curves of cinnamon teal pairs (dashed lines), lone drakes (solid lines), and flocked drakes (dotted lines) counted during the breeding seasons of 2015-2017 on Monte Vista NWR. Shaded areas correspond to Area A (left panel), Area B (middle panel), and Area C (right panel) as calculated by Serie and Cowardin (1990).

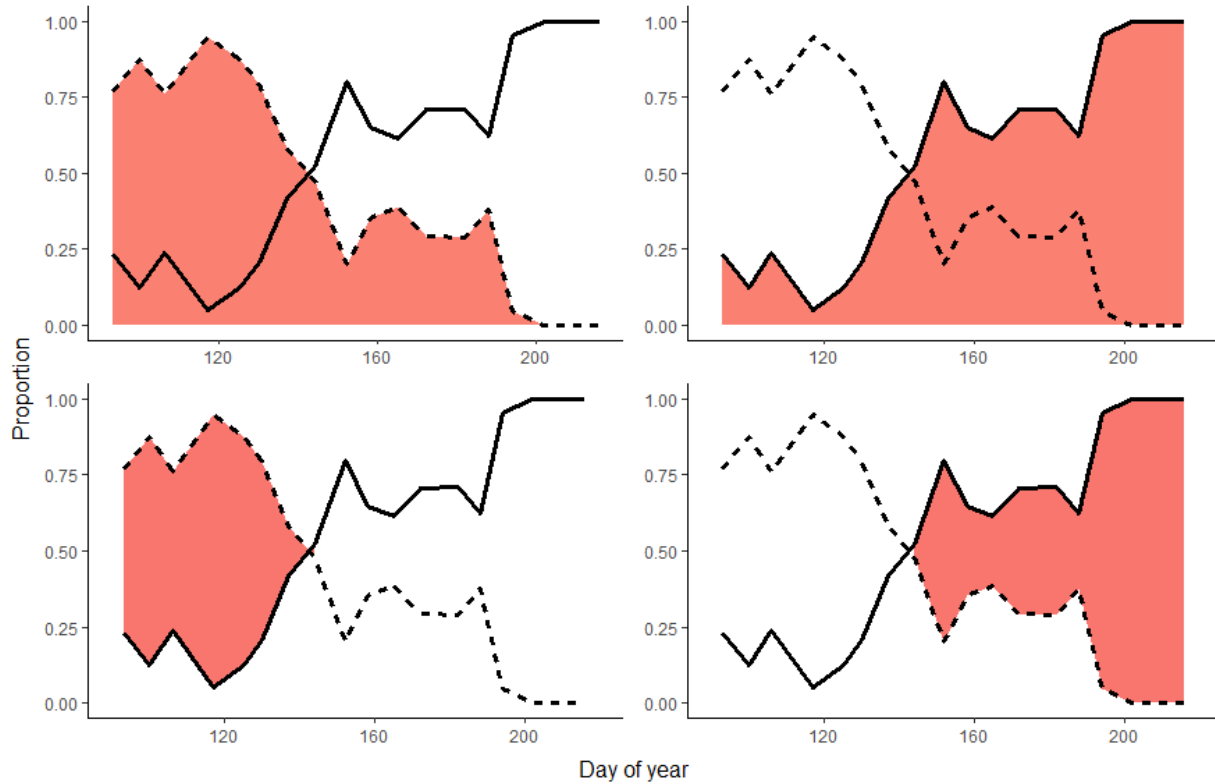


Figure 3.2: Examples of social indices calculated using curves of cinnamon teal pairs (dashed lines) and lone drakes (solid lines) counted during the breeding seasons of 2015-2017 on Monte Vista NWR. Shaded areas correspond to Area 1 (top left panel), Area 2 (top right panel), Area 3 (bottom left panel), and Area 4 (bottom right panel) as calculated by Hochbaum et al. (1987).

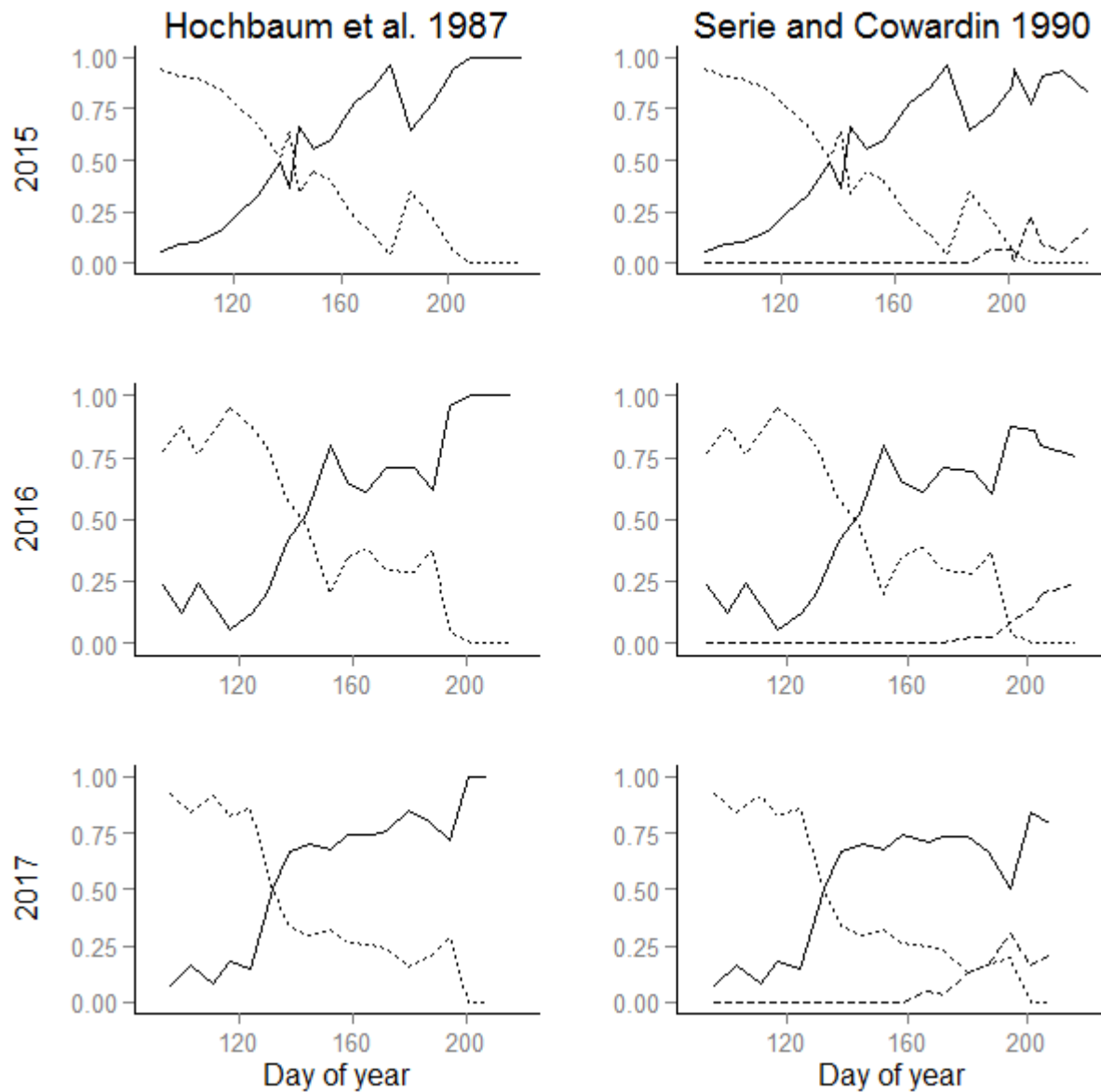


Figure 3.3: Social index plots using counts of cinnamon teal from 2015-2017. Left column represents indices calculated using Hochbaum et al. (1987) methods and right column represents indices calculated using Serie and Cowardin (1990) methods. Dotted line = pairs, solid line = lone drakes, dashed line = flocked males. Each row corresponds to one year of the study period, from 2015-2017.

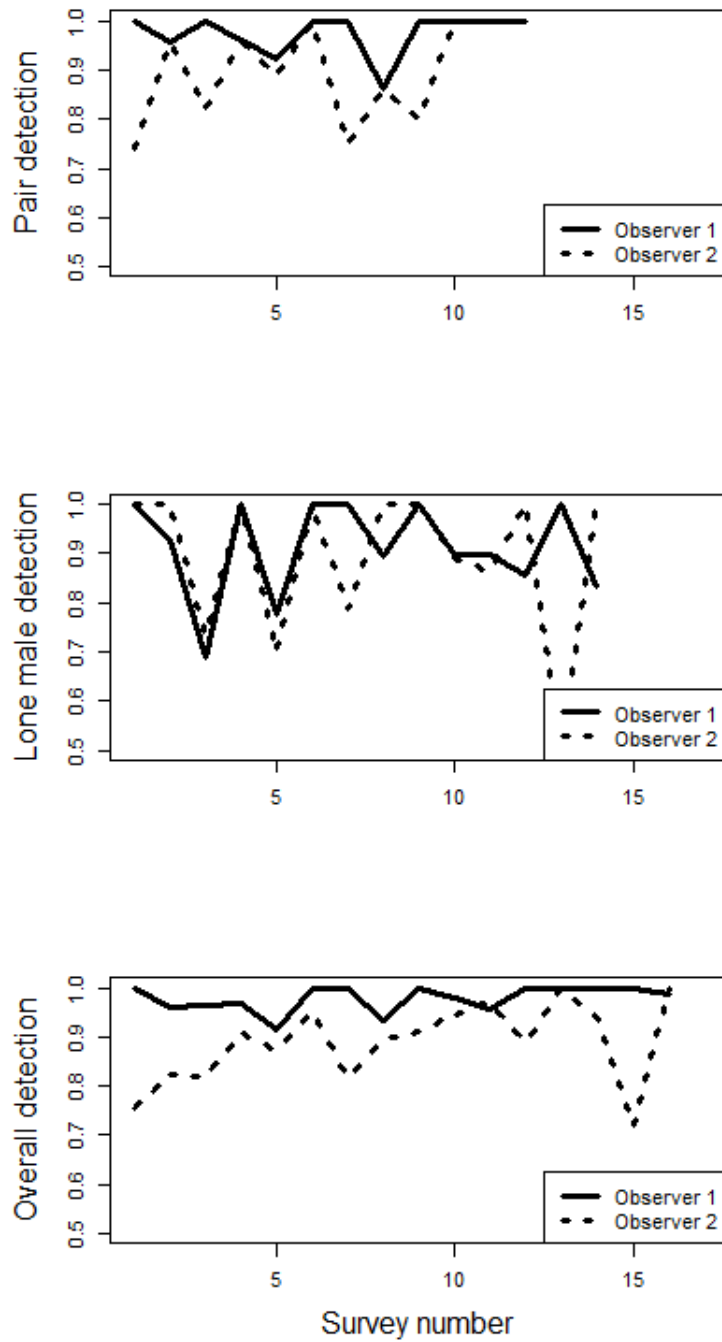


Figure 3.4: Observer-specific detection probabilities for cinnamon teal pairs (top panel), lone males (middle panel), and all social groupings (bottom panel) over the course of 17 surveys in 2017 on Monte Vista NWR.

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Chapter 4 - NEST ATTENDANCE PATTERNS OF CINNAMON TEAL DURING INCUBATION

SUMMARY

Patterns of nest attendance in birds influence whether or not an individual's reproductive attempt is successful and have the potential to impact the future success of its offspring. Parental behaviors during incubation vary based on an individual's body condition, energy requirements, and environmental factors in its breeding habitat. I assessed nest attendance patterns in the cinnamon teal (*Spatula cyanoptera*) breeding in the San Luis Valley of Colorado from 2016-2017. I evaluated the effect of temporal and environmental covariates on the duration and frequency of incubation recesses and the constancy with which a hen incubates. I then assessed the effects of nest attendance patterns on nest survival during the incubation stage. I observed weak support for a negative relationship between nest initiation date and recess frequency, and recess duration varied by nest age and time of day, with hens on older nests taking longer recesses in the afternoon and hens on nests earlier in incubation taking longer recesses in the morning and evening. Incubation constancy decreased with higher ambient temperatures and increased for hens with older nests. Nest survival was positively associated with lower recess frequency and longer recess duration. My results suggest cinnamon teal might be modifying their behavior during the breeding season to use variable climatic conditions to their advantage while maintaining the highest probability of a successful reproductive attempt.

INTRODUCTION

The incubation stage of the nesting period is one of the most energetically taxing stages of a bird's annual cycle. Incubating birds face tradeoffs pertaining to the cost of reproduction that form the foundation of life-history theory (Lack 1968, Stearns 1976, Drent and Daan 1980, Partridge 1989). These costs are a result of the fact that birds, typically females, must remain on

the nest for extended periods of time, often losing body mass, foraging opportunities, and exposing themselves to higher risk of predation in the process. Waterfowl, for example, have been shown to have lower survival during the breeding season than other parts of the year due to their vulnerability while on the nest (Sargeant et al. 1984, Greenwood et al. 1995, Devries et al. 2003). Birds use varying strategies relating to the frequency and duration with which they leave the nest during incubation to ensure that they meet their own energetic requirements while minimizing the time eggs are exposed to predators and adverse conditions. Behavioral strategies that have the lowest ratio of energetic costs to reproductive benefits allow the incubating bird to invest more time in the nest and potentially attain higher reproductive output. These behavioral patterns may therefore provide insight into the underlying mechanisms resulting in differential survival rates among bird species with similar life-history strategies. As nest survival and female survival have both been shown to disproportionately influence the population growth rate of many bird species (Hoekman et al. 2002, McNew et al. 2012, Pollentier et al. 2014), understanding nesting behavior has practical implications as well as the potential to provide evidence for the evolutionary significance of specific behaviors and how they relate to a bird's fitness and life-history strategy.

Among uniparentally incubating birds, energetic demands are typically the limiting factor of the duration for which a female will incubate a nest (Afton and Paulus 1992, Bryan and Bryant 1999, Tulp et al. 2009, Reneerkens et al. 2011). Given finite resources, females face tradeoffs between obtaining energetic resources and nest attendance that have implications for their reproductive output, which may even carry over to future years (Sedinger and Alisauskas 2004). Females make these tradeoffs daily, constrained by their own physical condition, capacity to store nutrients, and the environment in which they are nesting (Cresswell et al. 2004, Burnam

et al. 2012). Many factors have the potential to influence their behavioral decisions, including ambient temperature (Boulton et al. 2010, Mougeot et al. 2014), the microhabitat and microclimate around the nest (Holloran 1999, Dobony 2000, Holloran and Anderson 2003), timing of nesting within the breeding season (Burnam et al. 2012), age or experience of the bird, and life history strategy of the species (Flint 2003).

Some large-bodied species with relatively slow life-history strategies (e.g., common eiders and snow geese) store nearly all the necessary energy reserves to maintain their body condition throughout nesting, requiring them to leave the nest very infrequently, if at all (Meixell and Flint 2017). Species with faster life-history strategies, however (e.g., teal, mallards, and gadwall), must take one or more recesses a day to forage during incubation. For example, the average frequency of such recesses ranges from 0.33 breaks per day in common eiders (Swennen et al. 1993) to 4.7 breaks per day in cinnamon teal breeding in California (Hohman 1991). This variability implies that there is some optimum combination of recess parameters that results in the highest probability of reproductive success for a given species and environment. Infrequent, long recesses expose the nest to the elements for longer periods of time, but may reduce behaviors that draw attention to the nest's location (i.e., leaving and returning to the nest multiple times). Conversely, frequent, short recesses may allow the hen to forage more efficiently, leading to higher overall reproductive output and hen survival, but may lead to increased conspicuousness of the nest.

The cinnamon teal (*Spatula cyanoptera*) is an ideal species with which to investigate variation in incubation behaviors, given its fast life-history strategy relative to other large-bodied bird species. It breeds throughout the Intermountain West of North America, where the environment is variable during the breeding season and provides an opportunity to evaluate the

effects of environmental factors on incubation behavior. As the sole incubating parent, the hen faces increased costs of leaving the eggs relative to both parents trading places during incubation (Cresswell et al. 2004). They are small-bodied dabbling ducks that feed primarily during daylight hours, allowing for relatively easy monitoring via surveillance cameras and providing hens with the potential to take advantage of fluctuations in ambient temperature when leaving their nests.

Variation in nest attendance strategies among individual cinnamon teal may help decipher what drives nest survival in this enigmatic species. The objectives of this study were to identify whether the cinnamon teal exhibits variable strategies of incubation attendance, quantify the environmental factors influencing these strategies, and examine whether these differences result in nest survival disparities. I predicted that, like other bird species with fast life-history strategies (Burnam et al. 2012), cinnamon teal recesses would be bimodal, occurring most often in the early morning and just before dusk. I expected to see hens using a continuum of nest attendance strategies based on body condition and access to foraging areas ranging from very infrequent, long recesses to frequent, short recesses during incubation. I predicted that because longer, less frequent recesses reduce the attention of predators around the nest site, hens using this strategy would have a higher probability of nest survival. I predicted that higher ambient temperature would positively influence recess duration and frequency, thus negatively influencing incubation constancy for this species as a means of safeguarding against a reduction in embryo temperature. However, I hypothesized that these factors would likely interact with environmental characteristics such as distance to water, since the hen's accessibility to foraging habitat may influence how long she must spend off the nest searching for food.

METHODS

Study Area and Field Methods

I conducted this study on Monte Vista National Wildlife Refuge in the San Luis Valley of Colorado. I located nests via systematic foot searches and rope dragging (Wiens 1969) during the breeding seasons from 2016-2017. This 6,003 hectare study area sits at approximately 2,255 meters of elevation and receives less than 20 centimeters of precipitation annually (USFWS 2015). The primary vegetation throughout the study area consists of bulrush (*Schoenoplectus sp.*), cattails (*Typha latifolia*), Baltic rush (*Juncus arcticus*), and sedges (*Carex sp.*) in the semi-permanent and permanent wetlands, as well as rabbitbrush (*Ericameria nauseosa*), greasewood (*Sarcobatus vermiculatus*), saltgrass (*Distichlis spicata*), and alkali sacaton (*Sporobolus airoides*) in the upland areas (USFWS 2015). Historically, Monte Vista NWR had the highest density of waterfowl nests on the continent (Gilbert et al. 1996), but drawdown of the aquifers and prolonged drought have resulted in increasingly arid conditions. Under their 2015 Comprehensive Conservation Plan, the San Luis Valley NWR Complex included cinnamon teal as a focal species for their chosen plan alternative, linking their life history and population dynamics directly to their habitat-based objectives (USFWS 2015).

Camera System

Within 24 hours of finding a nest, I placed either a single trail camera (Covert MP8 Trail Camera, Mossy Oak Break-Up Country or Stealth Cam G42 No-Glo Trail Game Camera STC-G42NG) or a video surveillance camera (Advance Security Model SSC-24940-36) approximately 10-30 cm from the nest. I selected nests based on nest age, placing cameras only on nests that were within one day of the start of incubation to prevent investigator-caused abandonment risked when placing cameras on nests still in the laying stage. If possible, I placed cameras with an overhead view of the nest to obtain the best view through dense vegetation.

Each camera was fitted with a 32GB SD card that I changed every four to seven days. Because trail cameras held the batteries and SD card within the camera body, they required us to flush the hen from the nest to change the batteries and SD card on a regular basis. The video camera came equipped with a 100-foot power cable attached to a 12-volt battery and a DVR containing the SD card, which allowed us to check the nest on a portable LCD screen connected to a video output cable, change the battery, and change the SD card without causing any disturbance to the nest.

Photo and Video Viewing Procedures

I viewed photos with Windows Photo Viewer, recording the date and time when the hen left and returned to the nest. I also recorded the time and date when any other species entered the frame, the hen exhibited any nest defense behaviors, a predator depredated the nest, the first time ducklings became visible (i.e., hatch), ducklings left the nest, and any human disturbed the nest (e.g., flushing the hen to check the nest, change the camera battery, etc.). I viewed video recordings (saved in 15-minute intervals) with Windows Media Player on 2x speed, recording the same information listed above. I tabulated the duration of each recess, the number of recesses each hen took every day, the age of the nest on each day of observation, and whether the recess was caused by investigator disturbance. Occasionally I missed hens leaving or returning to the nest, at which time I would search through previously viewed videos or photos to ensure I recorded every possible recess. To ensure each observation of a hen leaving the nest was paired with an observation of the hen returning, I estimated the total number of recesses per day using a Lincoln-Petersen estimator (see Seber 1982). This allowed us to assess whether I needed to adjust the frequency of recesses taken by a given hen each day.

Explanatory Variables

I evaluated the effects of 11 covariates on nest attendance, which I grouped into temporal, intrinsic, and environmental categories (Table 4.1). Because I expected nest attendance patterns to vary as food availability and energy requirements fluctuated temporally, I included time of day, the age of the nest, nest initiation date, the stage of the breeding season, and the stage of incubation as covariates. I divided the stage of the breeding season into three sections corresponding to average peak nest initiation date across the study period. Early season corresponded to dates between 15 April and 15 May, mid-season to dates between 16 May and 10 June, and late season to dates between 11 June and 30 June. I also divided the incubation period into stages corresponding to the number of days the hen had been incubating. Early incubation ranged from age 7-15 days (assuming the hen had stopped laying and had entered incubation), mid incubation ranged from age 16-23 days, and late incubation ranged from age 24-35 days. Clutch size was the only intrinsic covariate I assessed as increasing clutch size may indicate higher reproductive investment and therefore influence recess frequency, duration, and overall incubation length (Hepp et al. 2005, Burnam et al. 2012, Carter et al. 2014). The nest sites selected by cinnamon teal likely incorporate features camouflaging them from predatory detection, but I also evaluated whether environmental conditions at the nest influenced their recess patterns during incubation. I incorporated distance to water, ambient temperature, percent aerial cover, and visual obstruction rating as covariates to assess whether access to foraging areas and perceived protection from predators had an effect on the frequency and duration with which hens left the nest. Finally, I included a covariate indicating whether a hen's recess was caused by investigator disturbance to assess any variation in recess patterns attributable to human interference.

Statistical Analysis

I identified three response variables to encompass the various strategies available to cinnamon teal hens: frequency of recess, duration of recess, and the total percentage of a 24-hour day that a hen spent on the nest (i.e., incubation constancy). I used generalized linear mixed effects models (*lme4* in Program R; Bates et al. 2015) to examine nest attendance strategies during incubation. These models account for a lack of independence between repeated observations of the same hen throughout the incubation period, preventing pseudoreplication (Hurlbert 1984) of recess bouts. I therefore included nest as a random effect in all models for each of the three response variables. I examined variation in recess frequency using Poisson regression due to the discrete count nature of the frequency data. I log-transformed recess duration (Zuur et al. 2009), arcsine-transformed incubation constancy (Sokal and Rohlf 2012), and standardized covariates to account for heteroscedasticity, meet normality assumptions, and compare effect sizes across multiple scales, respectively. I included various combinations of the covariates described above based on *a priori* biologically feasible hypotheses (Table 4.1), using Akaike's Information Criterion (Akaike 1973) with the adjustment for small sample size (AICc) to select which model best explained the variation in each of the three response variables (Burnham and Anderson 2002). I then conducted an analysis of cinnamon teal nest survival, including average incubation recess duration, frequency, and constancy as covariates (Table 4.2). I used a hidden Markov framework to isolate effects of covariates within nesting stages (i.e., laying and incubation; see Pradel 2005, Kendall et al. 2012, Setash Chapter 2).

RESULTS

I recorded a total of 292,035 photos and 2,541 hours of video on 47 nests for 2016 and 2017 (Table 4.3). Due to camera connection malfunctions and visibility issues (e.g., vegetation

obstructed view), only 21 of those 47 nests had usable photos/footage, representing approximately 2,952 hours of incubation and 155 nest-days. Hens initiated the observed nests from 23 April to 28 May, encompassing a broad range of environmental conditions throughout the spring thaw. Clutch sizes also varied among camera-monitored nests, ranging from eight eggs to 13 eggs. Of the 341 total recesses observed, hens took 77% of those recesses during the afternoon and 23% in the morning (Figure 4.1). A large proportion of the observed recesses occurred during late incubation (n = 153 recesses, 44.9%), followed by mid incubation (n = 128 recesses, 37.5%) and early incubation (n = 60, 17.6%).

Recess Frequency

Hens took an average of 2.95 recesses per day (SD = 1.43; Range = 1-6; Figure 4.2). None of my models outcompeted the null in explaining recess frequency (Table 4.5), but there was substantial support for the second and third best models, which incorporated nest initiation date and its quadratic effect, alone ($\Delta AICc = 0.67$ and 1.58 , $w_i = 0.157$ and 0.100 , respectively; Table 4.5). Under the model including nest initiation date, hens were predicted to take fewer daily recesses the later they initiated nests ($\hat{\beta} = -0.100$, SE = 0.076; Table 4.4, Figure 4.3). I did not detect an effect of habitat covariates on recess frequency (Table 4.5). The Lincoln-Petersen estimator did not identify a substantial difference in recess frequency for nests at which observations of recesses were missed. Therefore I did not adjust recess frequency for any hens.

Recess Duration

The average recess duration was 86.5 minutes (SD = 102.3; Range = 2-1352). Human disturbance caused 19 of the 341 recesses observed, most of which were the initial nest visits to conduct camera set up. The mean duration of investigator-caused recesses was significantly longer than that of naturally occurring recesses (t = 8.47, p-value = <0.001), averaging 260.3

minutes (Range = 5-1352) compared to 76.3 minutes (Range = 2-394), respectively. The top model for recess duration included an interaction between nest age and time of day (Table 4.6), with hens on younger nests (i.e., earlier in incubation) taking longer recesses in the early morning and late evening than their older counterparts (Figure 4.4). Habitat covariates did not appear to influence recess duration (Table 4.6).

Incubation Constancy

Hens spent an average of 89.2% of the day on the nest (SD = 7.81%). The most parsimonious model explaining the percentage of time hens spent on the nest included an additive effect of nest age and ambient temperature (Table 4.7). Hens spent a lower proportion of the day on the nest in warmer ambient temperatures ($\hat{\beta} = -0.003$, SE = 0.001; Table 4.4, Figure 4.4.5), and hens with older nests that were closer to hatching spent more time on the nest overall ($\hat{\beta} = 0.003$, SE = 0.001; Table 4.4, Figure 4.4.5).

Nest Survival

Ten of the 47 nests monitored with a camera were unsuccessful in hatching ≥ 1 egg, but only three of those nests resulted in usable footage. Hens with successful nests spent on average 86.6 minutes (SD = 102.3) off the nest during a given recess and took 2.95 recesses per day (SD = 1.43), whereas the unsuccessful hens spent an average of 78.6 minutes off (SD = 52.4) and took 2.86 recesses per day (SD = 1.83). Unsuccessful hens also had slightly higher incubation constancy (95.4%, SD = 0.994%) compared to the successful hens (89.3%, SD = 7.84%). When I included recess frequency, duration and incubation constancy as covariates of nest survival during the incubation stage, they exhibited varying relationships with daily nest survival rate (Figure 6). Higher rates of nest survival were weakly associated with hens that took infrequent ($\hat{\beta} = -0.109$, SE = 0.757) and longer recesses ($\hat{\beta} = 0.027$, SE = 0.028) in the directions consistent

with my predictions. Incubation constancy, however, exhibited an apparent relationship with nest survival opposite the direction I predicted ($\hat{\beta} = -0.339$, SE = 0.295). Camera-monitored nests exhibited higher nest survival rates than their counterparts monitored via investigator checks ($\hat{S}_{\text{Camera}} = 0.356$, SE = 0.184 and $\hat{S}_{\text{NoCamera}} = 0.114$, SE = 0.089).

DISCUSSION

General

Nest attendance strategies play a vital role in determining whether or not a nest is successful and the nesting individual maintains proper body condition to survive the breeding season. I observed variability within and among individual cinnamon teal nest attendance strategies during incubation in the San Luis Valley of Colorado. This study is one of only two studies available evaluating cinnamon teal nest attendance patterns and is the most complete dataset to date. Hohman (1991) observed two hens throughout incubation in California and found slightly lower incubation constancy than I did ($79.9\% \pm 0.1\%$ and $77.0\% \pm 0.1\%$ compared to my $89.2 \pm 7.81\%$), but mine was consistent with other waterfowl species nesting in the prairies (Miller 1976, Gloutney 1989, Afton and Paulus 1992). Using video surveillance cameras not only allowed me to identify more precise attendance patterns than previous studies using temperature loggers (Hoover et al. 2004), but also captured predation events and interspecific interactions (Ellis-Felege et al. 2012). In addition, it provided a valuable means of reducing investigator-caused nest abandonment, which is consistently high among cinnamon teal (Setash Chapter 2, Josh Vest, unpublished data).

Recess Frequency, Duration, and Constancy

Cinnamon teal took recesses at a frequency consistent with other small-bodied gamebirds with fast life-history strategies (Hohman 1991, Afton and Paulus 1992, Burnam et al. 2012). Although the support for the model including nest initiation date was weak, the finding that

incubating hens take fewer incubation recesses as nest initiation date increases is consistent with the idea that foraging opportunities are seasonally variable (Krapu and Reinecke 1992). Previous studies have shown the importance of energy reserves for birds initiating nests early in the season and the speed at which incubating birds lose weight (Harvey et al. 1989, Hepp et al. 1990, Manlove and Hepp 2000, Hepp et al. 2005). Given the limited capacity of cinnamon teal to store nutrients, the earliest nest initiators, having just arrived on the breeding grounds in depleted body condition, likely have to leave frequently to forage and improve their body condition, especially during periods of low ambient temperature (Hepp et al. 2005). In addition, teal respond opportunistically to daily and seasonal patterns of variation in food abundance or availability, so their behavioral patterns are likely more dynamic than could be captured here.

Contrary to my predictions, microhabitat conditions in the area surrounding the nest did not appear in the top models explaining variation in recess frequency, duration, or incubation constancy for cinnamon teal. I included distance to water as an index of how long it would take incubating birds to access foraging areas and thus the duration of their recess, but it may be that water sources are so ephemeral, this does not accurately capture the variation in the distance a nest is from water throughout the nesting period, and therefore does not act as an appropriate index of recess duration. Neither temperature nor vegetation structure (e.g., visual obstruction rating, percent aerial cover) exhibited a strong relationship with recess duration. Birds select their nest sites based on the perceived safety of the microhabitat characteristics surrounding the nest (Setash Chapter 2, Conway and Martin 2000b), which might preempt the need to adjust incubation behavior based on the daily variation in perceived safety.

Although neither recess duration nor frequency were correlated with ambient temperature, the combination of the two, measured as incubation constancy, was negatively

correlated with temperature. This pattern is commonly exhibited across bird species; incubating females of many species take advantage of high ambient temperatures to forage when the chance of embryo hypothermia is lowest (Skutch 1962, Caldwell and Cornwell 1975, Afton 1980, Ringelman and Longcore 1982, Afton and Paulus 1992, Mallory and Weatherhead 1993, Eichholz and Sedinger 1999, McClintock et al. 2014). Incubation constancy also exhibited a positive relationship with nest age, with hens on older nests (i.e., closer to hatch) displaying higher incubation constancy than those in early, post-laying incubation. This is also a common phenomenon among birds as they are forced to make tradeoffs between energy requirements and embryo development early in incubation, and as their investment in the nest increases throughout incubation (Drent 1970, Loos and Rohwer 2004, Hepp et al. 2005, Wang and Beissinger 2011, Burnam et al. 2012). Birds that are in higher body condition and therefore have the ability to incubate with increased constancy early in the incubation stage can reduce their incubation time (Deeming and Ferguson 1991, Zicus et al. 1995, Hepp et al. 2005, Kim and Monaghan 2006), increase hatchability (Skutch 1962, Arnold 1993), and increase duckling condition (Kim and Monaghan 2006). Given the small body size of teal and their income breeding strategy, they likely do not have the capacity to maintain high incubation constancy during early incubation and therefore increase constancy as incubation progresses and they replenish their energy reserves.

The duration of incubation recesses differed according to the age of the nest and the time of day females took the recess. Hens on nests close to hatching took their longest recesses during the afternoon, but hens early in the incubation process took longer recesses during the morning and evening. In arid climates such as the San Luis Valley of Colorado, temperatures can vary by more than 20 degrees Celsius throughout the day (Mix et al. 2011). Daily variation in

temperature has been shown to influence nest attendance patterns in other bird species including wild turkeys (*Meleagris gallopavo*; Spohr 2001), black-necked cranes (*Grus nigricollis*; Zhang et al. 2017), and Carolina chickadees (*Poecile carolinensis*; Walters et al. 2016). In addition, eggs become increasingly susceptible to fluctuations in temperature as they approach hatch, necessitating increased attentiveness or strategic timing of nest recesses to correspond with high ambient temperatures (Romanoff and Romanoff 1949, Burnam et al. 2012). Hens with nests early in incubation likely had more flexibility in when they took long recesses and therefore took bimodal recesses to avoid diurnal predators (Coates and Delehanty 2008) and take advantage of food availability, while hens with nests close to hatch needed to ensure they maintained a highly regulated embryonic temperature and therefore timed their longest recesses to occur during the warmest part of the day.

Nest Survival

With the caveat that sample size was limited and few nests monitored via camera failed, I observed variation among individuals in nest attendance strategy that resulted in differential rates of nest survival. The strategies ranged from short, frequent recesses to long, infrequent recesses, the latter being associated with the highest nest survival. Given that the microhabitat surrounding the nests monitored by cameras did not affect nest attendance patterns, hens may have been using this nest attendance strategy to reduce the probability that they will attract the attention of nest predators by leaving and returning to the nest as infrequently as possible. Longer, infrequent recesses reduce trails through the vegetation and movement that might draw attention. The intraspecific variation in attendance strategy and nest survival might also be correlated with hen age, experience, and body condition, although I did not measure any of these qualities in this study. Hens with few energetic reserves or in poor condition are already inherently less likely to

succeed in producing offspring, and if their condition necessitates that they leave the nest more frequently to forage, activity near the nest might lead to a further reduction in the probability of nest survival.

Cameras provided a convenient method to monitor cinnamon teal nesting behavior, but further research is necessary to evaluate the indirect effects of cameras on nest survival. Cameras have been shown to impact nest survival to varying degrees in a variety of bird species (reviewed by Richardson et al. 2009), but more specific investigations into the impacts on waterfowl nests are warranted given the discrepancies in nest survival detected in this study.

Conclusions

Advances in video technology have improved the ability of researchers to accurately monitor nest attendance activities in a minimally invasive way (Burnam et al. 2012, Coates and Delehanty 2008). This has been an especially important development for gamebirds, whose reproductive choices and behaviors are of particular interest to better understand the processes that scale up to affect demographic parameters and have implications for the management of harvested populations (Ellis-Felege and Carroll 2012). Little research has focused specifically on cinnamon teal, however, and additional research is needed to expand the evidence for adaptive patterns of nest attendance provided in this study. Increasing sample sizes of camera-monitored nests should be a high priority in future studies as conservation actions are limited by the insubstantial inferences resulting from small sample sizes (Ellis-Felege and Carroll 2012). Additional work is also needed to improve implementation of cameras for birds utilizing dense nesting cover. Fewer than half of my deployed cameras resulted in usable footage, mostly due to views obstructed by vegetation. Research ascertaining an appropriate mix of camera size, stand structure, and camera angle would mitigate sample size issues and minimize camera effects on

the study species. I encourage future researchers to utilize an estimator for detection (i.e., a Lincoln-Petersen estimator), especially for nests monitored in dense vegetation, to account for the possibility of a recess being missed because neither departure nor return of the hen was detected. This will ensure unbiased counts of recess frequency and provide reliable information for future studies.

Table 4.1: Covariate definitions and predicted relationships with three response variables associated with cinnamon teal nest attendance: recess frequency, duration, and incubation constancy for nests monitored in 2016 and 2017 on Monte Vista NWR.

Covariate Group	Covariate	Description	Predicted Relationship with Recess Frequency	Predicted Relationship with Recess Duration	Predicted Relationship with Inc. Constancy	Citations
Temporal	Time of day	Minute of the day from 0 to 1440 (60 minutes x 24 hours)	-	+	0	Zicus and Hennes 1995; MacCluskie and Sedinger 1999; Manlove and Hepp 2000
	Nest age	Age of the nest from 1-35	-	-	+	Loos and Rohwer 2004; Zicus and Hennes 1995
	Season Stage (Early, Mid, Late)	Early: 15 April-15 May Mid: 16 May-10 June	-	-	-	Burnam et al. 2012

		Late: 11 June- 30 June				
	Incubation stage (Early, Mid, Late)	Early: Age 7-15 Mid: Age 16-23 Late: Age 24-35	-	-	+	Burnam et al. 2012
	Nest Initiation Date	Date first egg was laid	0	0	-	Loos and Rohwer 2004
Intrinsic/Hen Related	Clutch size	Largest number of eggs being incubated (even if ≥ 1 gets depredated, I still use the most eggs the nest had at any point in time)	-	+	+	Wiebe and Martin 2000, Loos and Rohwer 2004, Hepp et al. 2015, Nord and Williams 2015
Environmental	Distance to water	Distance (m) from the nest to the closest water deeper than 3 cm	0	+	0	Miller 1976

Ambient high temperature	Daily high temperature recorded by a weather station in Monte Vista, CO.	+	+	-	MacCluskie and Sedinger 1999, Conway and Martin 2000a
% Aerial Cover	Visual estimate of the percentage of the nest obstructed by vegetation from directly overhead	+	+	-	Miller 1976
VOR	The height of vegetation (in cm) that visually obstructed the nest bowl. Measurements were taken from each cardinal direction at a distance of 4 m	+	+	-	Winder et al. 2016

and then
averaged.

Other

Investigator-
Caused?

Was the recess
caused by
human
disturbance?

0

+

-

Meixell and
Flint 2017

Table 4.2: Predictions of the effects of nest attendance parameters on cinnamon teal daily nest survival rate during incubation.

Covariate	Description	Predicted Relationship with Nest Survival	Citations
Frequency of recesses	How many times in a 24 hour period a hen leaves the nest	-	Powell et al. 2012
Duration of recesses	How long (in minutes) a hen is gone from the nest during a given recess	+	Powell et al. 2012
Incubation Constancy	The percentage of a 24-hour day a hen spends incubating the nest	+	Erikstad 1986, Wiebe and Martin 2000, Wilson et al. 2007
Camera	Whether or not a camera was used to monitor the nest	+	Richardson et al. 2009

Table 4.3: Summary of cinnamon teal nest monitoring videos and photos from nests found in 2016 and 2017 on Monte Vista NWR.

Year	Number of Photos Recorded	Hours of Video Recorded	Number of Nests with Usable Photos/Video	Average Recess Duration in minutes (SD)	Average Recess Frequency (SD)	Average Incubation Constancy (SD)
2016	208,779	0	9	92.3 (117.8)	2.79 (1.41)	0.902 (0.075)
2017	83,256	2,541	12	75.8 (59.0)	3.23 (1.47)	0.883 (0.082)
Total	292,035	2,541	21	86.5 (102.3)	2.95 (1.43)	0.892 (0.078)

Table 4.4: β coefficient estimates corresponding to covariates used to evaluate cinnamon teal nest attendance patterns on Monte Vista NWR from 2016-2017. Covariates were included in generalized linear mixed-effects models and were assessed for three response variables: recess duration, recess frequency, and incubation constancy.

Covariate	Recess	SE	Recess	SE	Incubation Constancy	SE
	Duration β		Frequency β		β Estimate	
	Estimate		Estimate			
Nest Age	0.071	0.051	-0.0003	0.008	0.003	0.001
Ambient Temperature	0.005	0.005	0.015	0.059	-0.003	0.001
Season Stage						
Early	3.73	0.344	0.784	0.474	1.20	0.058
Mid	4.31	0.353	0.729	0.486	1.27	0.059
Late	4.23	0.345	0.744	0.475	1.27	0.058
Nest Initiation Date	0.017	0.008	-0.091	0.075	0.001	0.002
Precipitation	0.400	1.65	-0.027	0.053	0.171	0.265
Distance to Water	4.60×10^{-4}	3.00×10^{-3}	-0.002	0.004	1.54×10^{-5}	5.90×10^{-4}
Percent Aerial Cover	-0.0002	0.002	0.0004	0.003	3.19×10^{-4}	4.13×10^{-4}
Visual Obstruction	0.004	0.005	0.002	0.006	-0.0002	0.0009
Rating						

Investigator-Caused	0.695	0.163	NA	NA	-0.063	0.027
Disturbance						
Time of Day	0.052	0.044	NA	NA	NA	NA
Time of Day ²	-0.101	0.039	NA	NA	NA	NA

Table 4.5: AICc table showing top models explaining frequency of recesses during cinnamon teal incubation on Monte Vista NWR from 2016-2017.

Model Structure	Df	LogLik	AICc	Delta AICc	Model Weight
Null	2	-254.868	513.8	0	0.220
Nest Initiation Date	3	-254.166	514.5	0.67	0.157
(Nest Initiation Date) ²	4	-253.567	515.4	1.58	0.100
Precipitation	3	-254.715	515.6	1.77	0.091
Distance to Water	3	-254.791	515.7	1.92	0.084
VOR	3	-254.814	515.8	1.97	0.082
Temperature	3	-254.837	515.8	2.01	0.080
Percent Aerial Cover	3	-254.855	515.9	2.05	0.079
Nest Age	3	-254.868	515.9	2.07	0.078
Season Stage	4	-254.856	518.0	4.15	0.028

Table 4.6: AICc table showing top models explaining duration of recesses during cinnamon teal incubation on Monte Vista NWR from 2016-2017.

Model Structure	Df	LogLik	AICc	Delta AICc	Model Weight
(Nest Age) * (Time of Day) ²	7	-371.938	758.2	0.00	0.405
(Time of Day) ²	5	-374.331	758.8	0.063	0.295
Investigator-Caused	4	-375.835	759.8	1.58	0.183
(Nest Age) * (Time of Day)	6	-374.791	761.8	3.62	0.066
(Time of Day)	4	-377.429	763.0	4.77	0.037
(Time of Day) + (Nest Age)	5	-377.428	765.0	6.83	0.013
Nest Initiation Date	4	-382.643	773.4	15.20	0
Null	3	-384.634	775.3	17.13	0
Season Stage	5	-383.123	776.4	18.22	0
Temperature	4	-384.271	776.7	18.46	0
VOR	4	-384.306	776.7	18.53	0
Nest Age	4	-384.593	777.3	19.10	0
Precipitation	4	-384.604	777.3	19.12	0
Distance to Water	4	-384.622	777.4	19.16	0
Percent Aerial Cover	4	-384.629	777.4	19.17	0
Incubation Stage	5	-384.180	778.5	20.33	0

Table 4.7: AICc table showing top models explaining incubation constancy during cinnamon teal incubation on Monte Vista NWR from 2016-2017.

Model Structure	Df	LogLik	AICc	Delta AICc	Model Weight
(Nest Age) + (Temp)	5	267.291	-524.4	0	0.596
(Nest Age) * (Temp)	6	267.436	-522.6	1.78	0.245
Temp	4	263.519	-518.9	5.48	0.038
Null	3	262.232	-518.4	6.01	0.029
Nest Age	4	263.055	-518.0	6.41	0.024
Precipitation	4	262.438	-516.8	7.65	0.013
Nest Initiation Date	4	262.425	-516.7	7.67	0.013
VOR	4	262.258	-516.4	8.01	0.011
Percent Aerial Cover	4	262.235	-516.4	8.05	0.011
Distance to Water	4	262.232	-516.4	8.06	0.011
Season Stage	5	263.035	-515.9	8.51	0.008
Clutch Size	4	185.883	-363.6	160.8	0.000

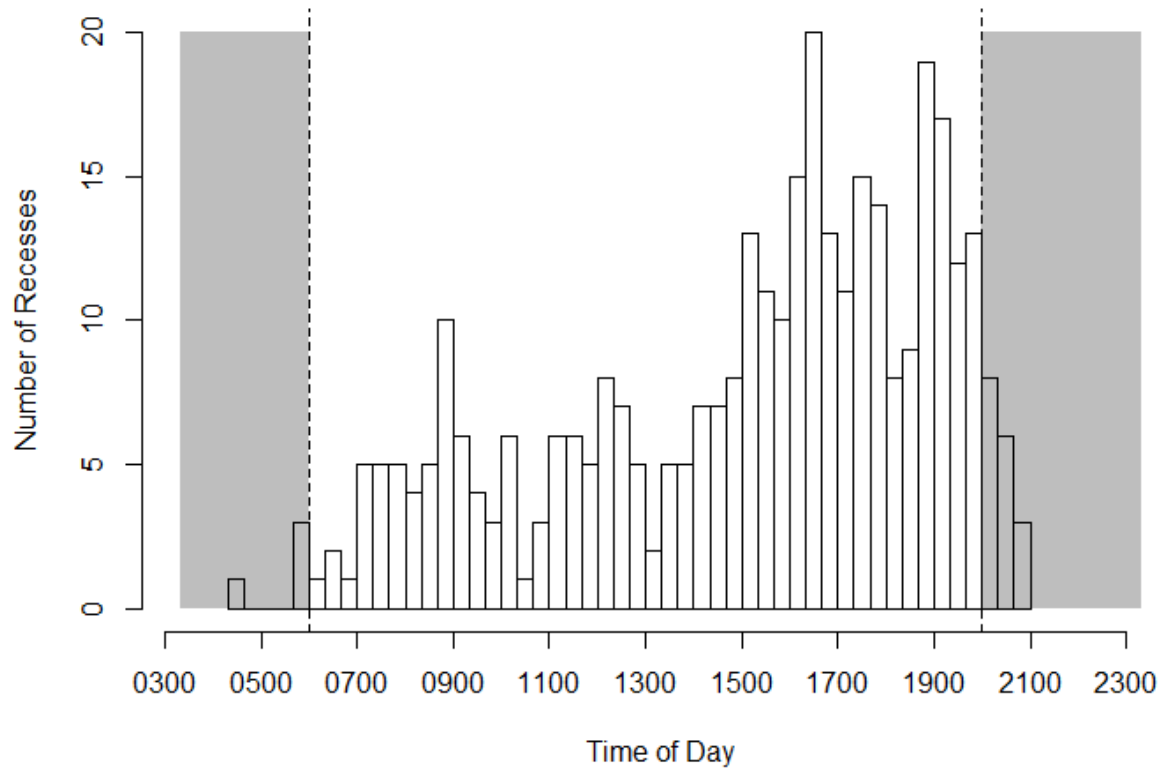


Figure 4.1: Histogram showing the distribution of recesses during cinnamon teal incubation on Monte Vista NWR from 2016-2017. Shaded areas represent hours of darkness in between average sunset and sunrise from May through August in the San Luis Valley.

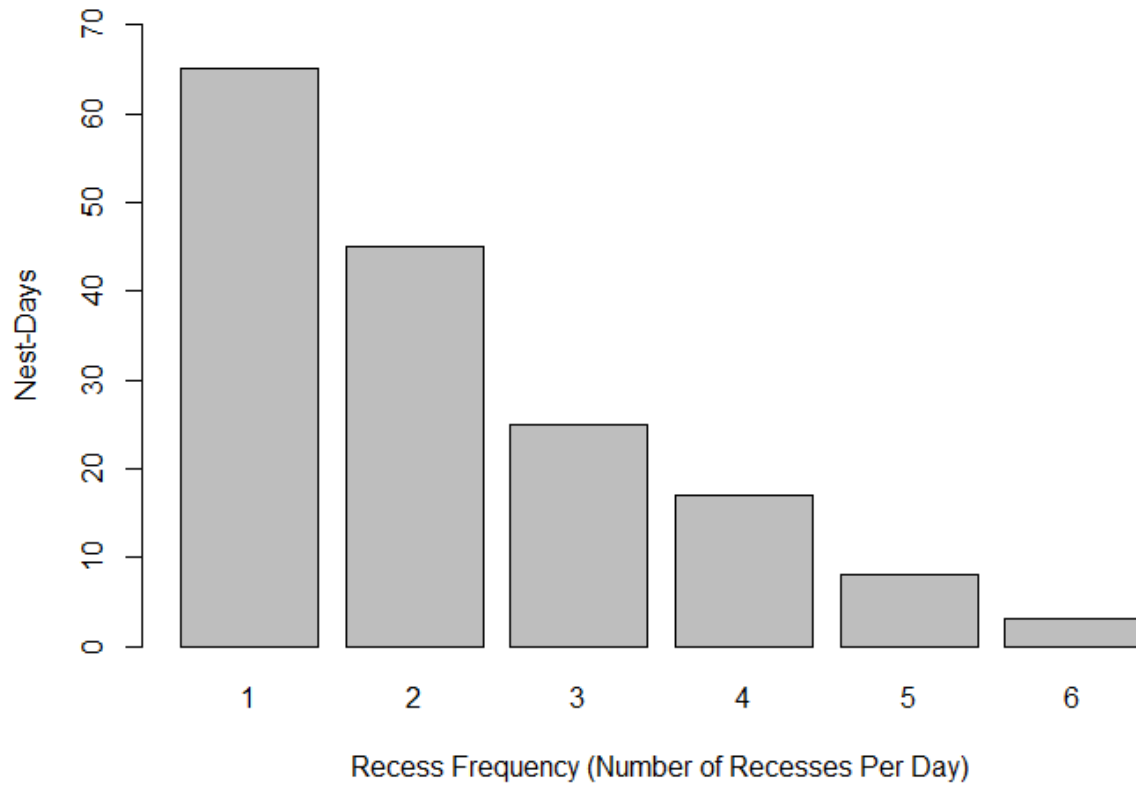


Figure 4.2: Barplot of the most commonly observed recess frequencies across 155 total cinnamon teal nest-days from 2016-2017 on Monte Vista NWR.

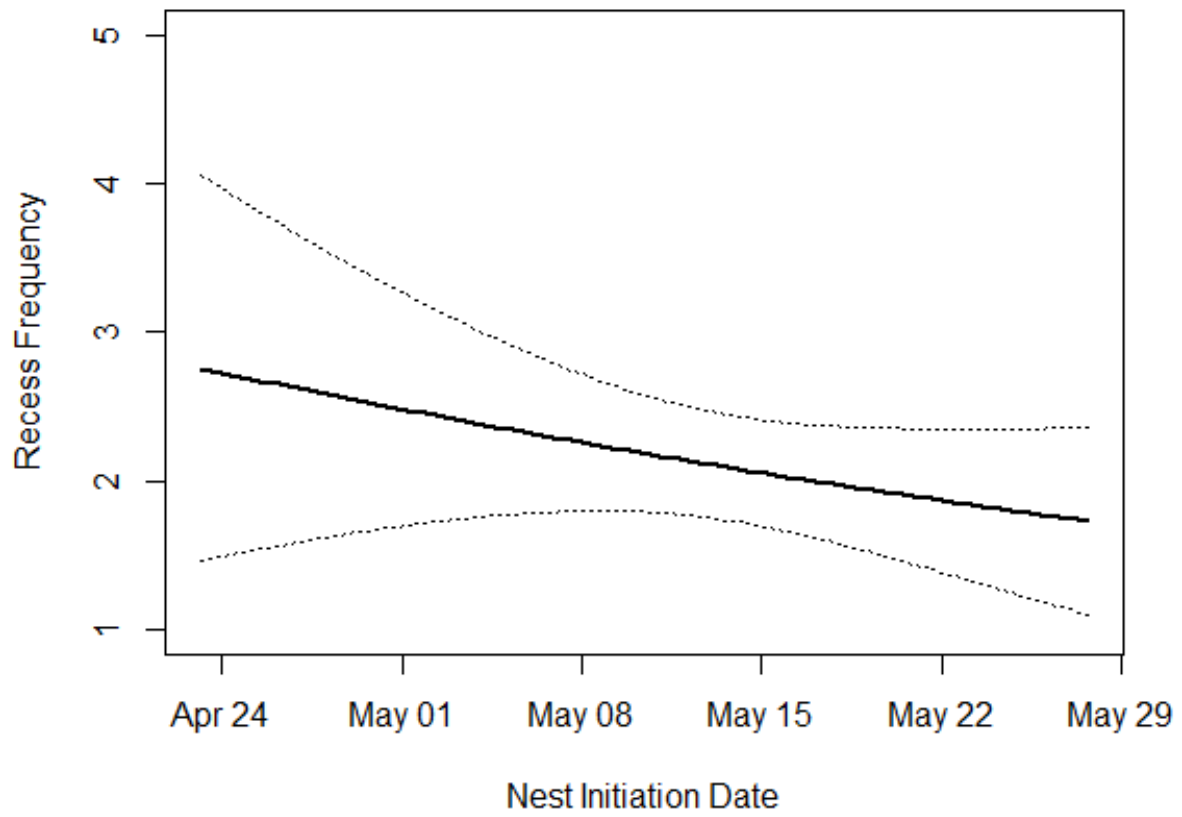


Figure 4.3: Predicted relationship between recess frequency and nest initiation date for incubating cinnamon teal hens monitored in 2016 and 2017 on Monte Vista NWR.

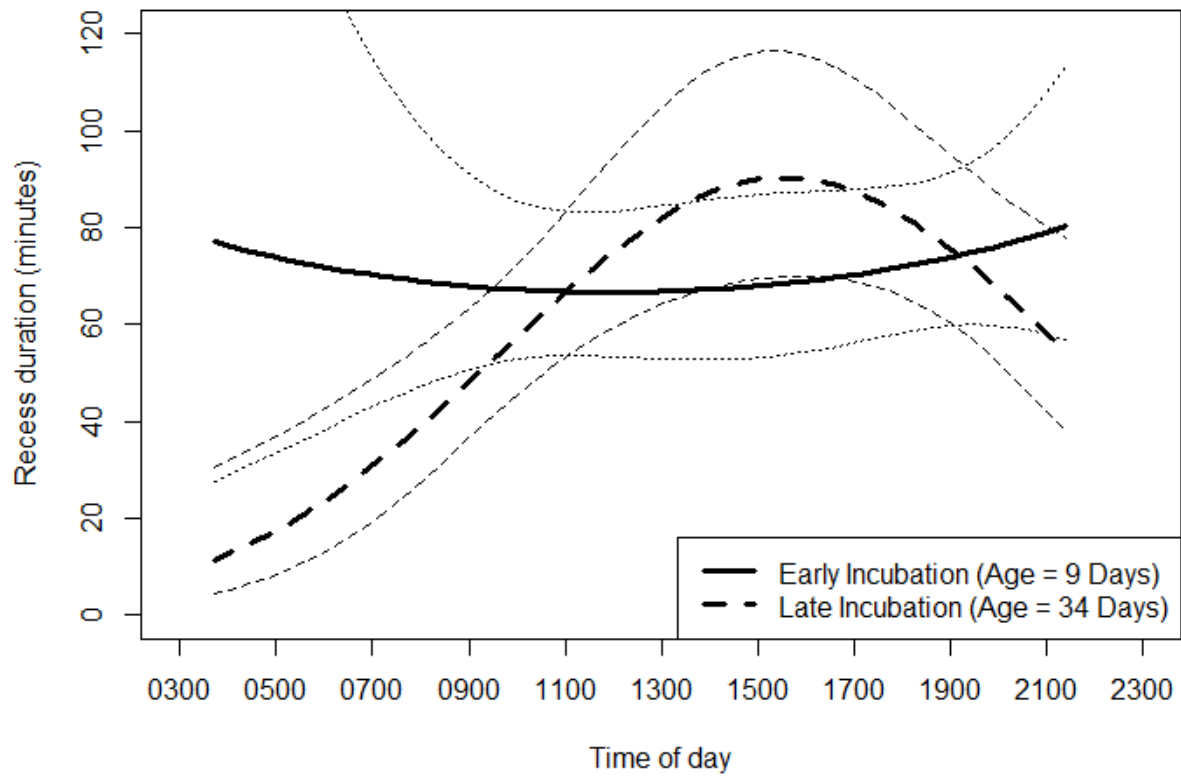


Figure 4.4: Relationship between recess duration and time of day for cinnamon teal hens with nests early in incubation and late in incubation. All nests were monitored in 2016 and 2017 on Monte Vista NWR.

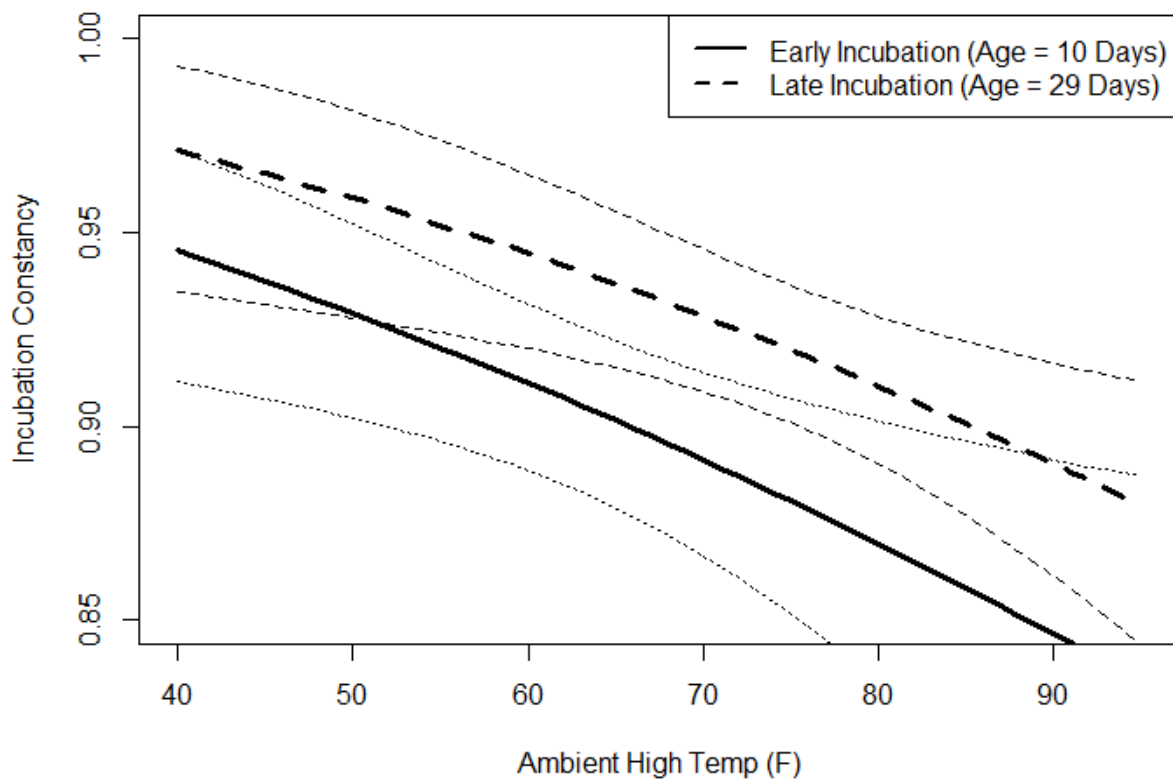


Figure 4.5: Relationship between incubation constancy and ambient temperature with an additive effect of nest age for incubating cinnamon teal monitored in 2016 and 2017 on Monte Vista NWR.

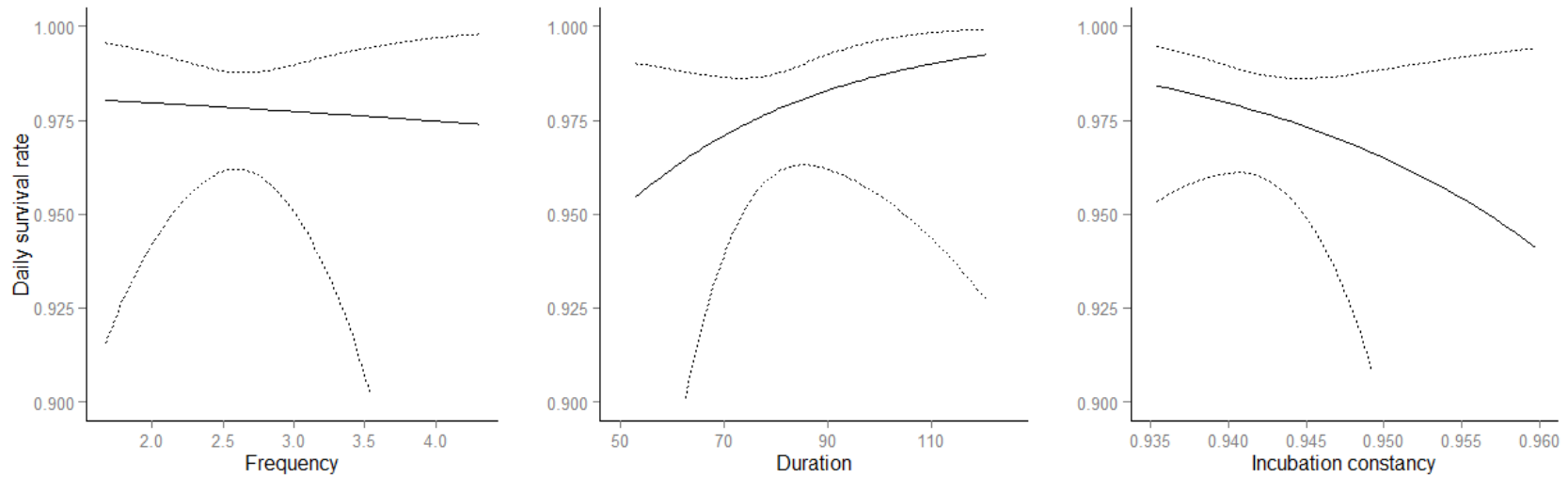


Figure 4.6: Relationship between daily nest survival rate and three response variables characterizing nest attendance of cinnamon teal hens monitored in 2016 and 2017 on Monte Vista NWR. The solid line represents the predicted response and dashed lines represent 95% confidence intervals. The figure on the left represents the negative relationship between daily survival rate during incubation and recess frequency (the number of times a hen leaves the nest on a given day). The figure in the middle is the positive relationship between daily incubation survival and recess duration (in minutes). The figure on the right is the negative relationship between daily incubation survival and incubation constancy (the proportion of the day spent incubating eggs)

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Chapter 5 - HEN AND DUCKLING SURVIVAL OF CINNAMON TEAL IN COLORADO

SUMMARY

Breeding season vital rates constitute an important component of annual waterfowl demography and aid in the analysis and management of waterfowl populations. Breeding season survival rates for hens and ducklings are unavailable for the cinnamon teal (*Spatula cyanoptera*) and an assessment of these rates is necessary to properly inform management. I web tagged 290 cinnamon teal ducklings and radiomarked 43 hens from 2015-2017 on Monte Vista NWR in the San Luis Valley of Colorado. I estimated duckling survival from hatch until the start of preseason banding (approximately 60 days on average) and hen survival throughout the 93-day study period corresponding to the time hens arrived on the breeding grounds until the start of preseason banding. Duckling survival was 0.802 (SE = 0.752) in 2015, 0.210 (SE = 0.045) in 2016, and was inestimable in 2017 (survival averaged across years = 0.506, SE = 0.107). Only one telemetered hen died over the course of the study period and my estimate of daily breeding season hen survival was 0.9963 (SE = 0.004) in 2016 when the hen died. These results are the only available estimates of cinnamon teal hen and duckling survival available, and represent substantial evidence for the need to improve banding protocols for all waterfowl species.

INTRODUCTION

The breeding season poses unique risks and decisions for female waterfowl in North America. Hens face tradeoffs between their own survival and the survival of their offspring, which result in variability in where individuals nest (Miller et al. 2007) and how invested they are in their nest/offspring (Blums et al. 2002, Liker and Székely 2005). Breeding hens are frequently more vulnerable to sources of mortality during this time than any other part of the annual cycle (Sargeant and Raveling 1992). They often face stochastic environmental conditions,

especially species that breed in the arctic or at higher elevations (Johnson et al. 1992), have diverse sets of predators (Johnson et al. 1989, Amundson and Arnold 2011), and must contend with the limitations of their own experience, condition, and genetic adaptations during this time of increased energetic demand. Offspring of breeding waterfowl also depend on a wide array of biotic and abiotic factors to survive until fledging. Ducklings are subject to heavy predation, extreme weather events, and large overland movements in areas where water sources are ephemeral and inconsistent (Talent et al. 1983, Ringelman 1992, Mehl and Alisauskas 2006, Amundson and Arnold 2011). The conditions ducklings face in early life have the potential to not only determine whether or not they are recruited into the breeding population (Pöysä et al. 2017), but also to affect their future breeding performance and predilection to return to their natal breeding grounds (Gauthier 1990).

Hen and duckling survival have been studied thoroughly for many waterfowl species historically. Many studies focus on ascertaining how these vital rates are influenced by local landscape covariates and estimating these parameters reliably at varying scales (Davis et al. 2017, Garrick et al. 2017, Boyer et al. 2018). Both hen survival and duckling survival have been shown to contribute substantially not only to reproductive success parameters (e.g., recruitment), but also to overall population growth rate (Hoekman et al. 2002, Coluccy et al. 2008). Cinnamon teal (*Spatula cyanoptera*) have been largely excluded from the population ecology literature, however, due to the lack of banding samples and the difficulty in differentiating them from their close relatives, the blue-winged teal (*Spatula discors*; USFWS 2013). Therefore, to date, estimates of hen and duckling survival are lacking, as is information regarding how these parameters have changed over time. Hens are particularly secretive and difficult to observe during the breeding season, making estimates of breeding season hen survival and duckling

survival even scarcer. The traditional methods of estimating duckling survival require frequent relocations of entire broods, which is rarely possible with cinnamon teal since they utilize dense emergent vegetation during the brood-rearing stage (Gammonley 2012).

Cinnamon teal breed in high densities on Monte Vista National Wildlife Refuge, which holds critical wetland habitat in the arid San Luis Valley of Colorado for breeding waterfowl and other waterbirds (USFWS 2015). A large portion of the cinnamon teal banded across the Intermountain West from 2012-2017 were captured in this region (57.0% of known cinnamon teal; D. Olson, unpublished report), and at one point it was estimated that specific areas on Monte Vista NWR were home to the highest breeding density of waterfowl in the country (Gilbert et al. 1996). It is therefore an ideal location to evaluate breeding season survival for both ducklings and hens to provide baseline data to inform future research as climate conditions change in the arid west. My objectives during this study were to estimate cinnamon teal hen survival and duckling survival during the breeding season in a system characterized by relatively high breeding density. Due to limited sample size, my goal was mainly to provide baseline estimates rather than to describe the ecological mechanisms underlying the variation in these estimates.

STUDY AREA

I conducted this study on Monte Vista National Wildlife Refuge in the San Luis Valley of Colorado. This 6,003 hectare study area sits at approximately 2,255 meters of elevation and receives less than 20 centimeters of precipitation annually (USFWS 2015). The primary vegetation throughout the study area consists of bulrush (*Schoenoplectus sp.*), cattails (*Typha latifolia*), Baltic rush (*Juncus arcticus*), and sedges (*Carex sp.*) in the semi-permanent and permanent wetlands, as well as rabbitbrush (*Ericameria nauseosa*), greasewood (*Sarcobatus*

vermiculatus), saltgrass (*Distichlis spicata*), and alkali sacaton (*Sporobolus airoides*) in the upland areas (USFWS 2015). Under their 2015 Comprehensive Conservation Plan, the San Luis Valley NWR Complex included cinnamon teal as a focal species for their chosen plan alternative, linking their life history and population dynamics directly to their habitat-based objectives (USFWS 2015).

METHODS

Nest Searching and Marking Birds

In 2015-2017, I searched for nests using a combination of systematic searches and rope-dragging (Wiens 1969) on foot through all areas of the refuge containing appropriate teal nesting habitat. These included flooded or potentially flooded meadows of Baltic rush, bulrush, and grasses. I also specifically searched areas near cinnamon teal drakes on waiting sites (Bellrose 1980). In 2017, I systematically searched 18 randomly selected 8.5-hectare plots every one to two weeks in addition to opportunistically searching other wetland habitats. I selected these plots from the aforementioned appropriate habitat and did so to ensure a representative sample of teal nests. I trapped cinnamon teal hens before breeding commenced using decoy traps (Sharp and Lokemoen 1987), baited swim-in traps (Hunt and Dahlka 1953), and on the nest using bownets during late incubation (i.e., after day 19 of incubation; Salyer 1962). I attached a prong-and-suture VHF radio transmitter (Model A4350 or A4420 weighing 12g and 8g respectively; Advanced Telemetry Systems, Isanti, MN, USA) or individually identifiable nasal discs (Lokemoen and Sharp 1985) and a metal leg band (U.S. Geological Survey (USGS)), to search for nests via telemetry and to follow hens with broods. All trapping and handling of cinnamon teal followed protocols approved by the Colorado State University Animal Care and Use Committee (Protocol #15-5756A). I located nests of radiomarked birds by homing in on their

approximate location until I could conclude that they had likely entered the incubation stage to reduce investigator-caused nest abandonment. I relocated telemetered hens on an irregular basis and for varying amounts of time each year after ducklings had hatched, recording the number of ducklings seen (if any) and the status of the hen (i.e., dead or alive).

On the day of estimated hatch, I returned to the nest to attach a web tag to the foot of each hatching duckling (Model 1005-1, National Band and Tag, Newport, Kentucky, USA; Alliston 1975). I then returned to the nest a final time to determine how many ducklings had hatched and which web tag numbers were associated with ducklings that did not hatch. From August until two weeks prior to the start of the waterfowl hunting season, refuge staff conducted banding operations, capturing ducks using baited swim-in traps and fitting all duck species with a US Geological Survey aluminum leg band. Cinnamon teal were visually examined for web tags or torn webbing indicating a web tag had been lost, and all recaptures from previous banding seasons were recorded. Within-season recaptures were not recorded.

Duckling Survival

I calculated seasonal survival for hatch year birds during the breeding season (ranging from mid-April to mid-August) and the non-breeding season. This survival probability is not estimable without supplementary recapture and recovery data in addition to the web tag recaptures, so I included all recapture and recovery data from cinnamon teal banded at Monte Vista NWR for 2015-2017. I therefore had data from recaptured and recovered birds that had been web tagged only, web tagged and banded, and banded only. I used Burnham's joint model for live recapture and dead recovery (Burnham 1993) in Program MARK (White and Burnham 1999) to estimate summer survival of ducklings while accounting for subsequent detection and annual survival. This method allowed for increased precision in survival estimates compared to

those that would result from an analysis of band recovery or live recapture data alone. This model estimates four parameter types: S_t , survival at time t ; p_t , the probability that an individual is detected at time t , given it is alive and in the study area at time t ; r_t , the probability, given an individual dies in the interval $(t, t + 1)$ that it is reported; and F_t , the probability that an individual using the study area at time t is faithful to the study area at time $t + 1$, given it survives to $t + 1$. I included six time periods in these models, one for each breeding season and non-breeding season across the three year study period. I fixed breeding season recapture probabilities (p_{BS}) to zero because the only opportunity to recapture birds occurred during banding, which marked the end of the breeding season. I also fixed breeding season recovery rates (r_{BS}) to zero because birds were not susceptible to hunting during the breeding season and were therefore not recovered if they died. I fixed breeding season fidelity (F_{BS}) to one because it was confounded with survival and I did not have the recovery data needed to estimate it separately. Given my limited sample of web tagged ducklings, the uncertainty of a bird's sex upon hatching, and the small proportion of recaptured individuals, I pooled estimates of duckling survival and adult survival, respectively, across sex. I created an *a priori* list of candidate models to evaluate whether survival was constant or varied across years and seasons (Table 1).

Recapture and recovery data were not yet available for the 2017-2018 hunting season or the 2018 banding season at the time of this analysis (i.e., future information), so all parameters that I allowed to vary by year were inestimable for 2017. I used the top model to calculate an average breeding season duckling survival for the study period.

Hen Survival

I estimated breeding season hen survival using a nest survival model (Dinsmore et al. 2002) since my telemetry data could be considered “ragged” (Rotella et al. 2004). I implemented this modeling approach in Program MARK (White and Burnham 1999) and compared these estimates to those derived from the joint live recapture and dead recovery analysis (see previous section; Burnham 1993) for breeding season survival of after hatch year birds. This model estimates a daily survival rate (DSR_t) that can be rescaled to estimate survival for the entire time period birds were monitored. I monitored birds over varying time periods each year, and calculated overall breeding season hen survival by rescaling daily survival rate to the entire monitoring period ($S^{Monitoring\ Period}$). I calculated the variance for survival on the breeding season scale using the delta method (Powell 2007).

RESULTS

Duckling Survival

I web tagged 290 cinnamon teal ducklings from 2015-2017. Seasonal variability in nesting phenology introduced variability in the timing of web tagging, but my web tagging effort was constant across years (Setash Chapter 2; Figure 1). A total of 234 ducklings hatched after being web tagged and were available for recapture during banding operations ($n = 57$ in 2015, $n = 81$ in 2016, and $n = 96$ in 2017; Table 1). I recaptured five web tagged birds in 2015, 18 in 2016, and two in 2017. In addition, I caught four hatch year individuals with torn webbing in 2017 that were thought to have lost a web tag. Refuge staff banded 332 hatch year and 54 after hatch year cinnamon teal in 2015, 1,082 hatch year and 248 after hatch year in 2016, and 509 hatch year and 96 after hatch year in 2017 (Table 1). Summer survival estimates of ducklings was 0.802 (SE = 0.752), and 0.210 (SE = 0.045) for 2015 and 2016, respectively (since 2017 was

inestimable; Table 2). When averaged across years, breeding season duckling survival was 0.506 (SE = 0.107). The estimate of breeding season duckling survival from the model that pooled survival across years was 0.432 (SE = 0.355), but it performed considerably worse than the model in which survival varied by year ($\Delta\text{AICc} = 26.0074$).

Hen Survival

I radio tagged nine cinnamon teal hens in 2015, 16 in 2016 and 18 in 2017. I censored five individuals in 2015, three in 2016 and five in 2017 either because the transmitters fell off or because I could not relocate their transmitter signals and I could not be certain whether this was due to mortality, transmitter failure, or emigration from the study area. In 2015, I monitored telemetered birds for a period of 27-45 days (varied by individual), all of which were captured on their nests towards the end of incubation (Figure 2). In 2016, I monitored birds over a 93-day period from the day they were marked during decoy trapping through the brood rearing period, and in 2017 I monitored them over a 61-day period from decoy trapping until peak nest initiation had ended (Figure 2). I also marked 22 hatch year birds with nasal discs in 2015 and 133 in 2016 during operational banding procedures, and I resighted seven in subsequent years. One of the 16 telemetered birds in 2016 was killed by an avian predator, and I recorded no deaths of telemetered cinnamon teal in 2015 or 2017. The best-approximating model indicated breeding season survival varied by year (Table 3). Daily survival rate estimates from the nest survival model (1.00, SE = 0.00 in 2015, 0.9963, SE = 0.004 in 2016 and 1.00, SE = 0.00 in 2017) were comparable to those estimated by the Burnham model (1.00, SE = 0.00 for each estimable year) given only one individual died during the study period. When rescaled to encompass the entire 93-day study period, the estimate of breeding season survival using the daily survival rate from 2016 was 0.708 (SE=0.289)

DISCUSSION

Hen survival and duckling survival are two of the most influential parameters to recruitment and population growth rate in waterfowl (Hoekman et al. 2002, Coluccy et al. 2008, Amundson et al. 2012). Despite limited sample sizes and restricted geographic scope, the estimates of breeding season survival presented here are the only available estimates for cinnamon teal of which I am aware. These estimates have the potential to inform future analyses of cinnamon teal demographics (e.g., sensitivity analyses, population viability analyses), but I advise the reader that estimates should be used with caution given the variability in survival estimates across years and the limited timeframe of monitoring. Among waterfowl, hen survival is typically lowest during the breeding season relative to the remainder of the year (Hammond and Johnson 1984, Sargeant and Raveling 1992, Arnold et al. 2016). My estimate of breeding season hen survival (93-day survival in 2016 = 0.708, SE=0.289) was consistent with this phenomenon and with breeding season survival estimates of comparable species (90-day survival = 0.76, SE=0.004 for mallards in the Prairie Potholes; Devries et al. 2003, 133-day survival = 0.764, SE = 0.090 for mottled ducks in Texas; Rigby and Haukos 2012). Because ducklings hatched and were web tagged throughout the breeding season, the estimates of duckling survival provided here represent an average cinnamon teal survival rate from hatch until the start of banding, regardless of when that hatch occurred. Because my nest searching effort and the timing of web tagging was relatively constant across years and was distributed evenly with regards to the peak hatch date within years (Figure 1), these estimates should be reliable without accounting for the time-to-banding variability. In addition, they were comparable to estimates of duckling survival until fledging for other waterfowl species (0.56 for mallards in Minnesota; Ball et al 1975, 0.65 for mallards in North Dakota; Talent et al. 1983).

Suggestions for Future Research

I recommend careful forethought and creativity when planning future studies focused specifically on ascertaining breeding cinnamon teal vital rates. This study emphasized the inherent difficulties in monitoring cinnamon teal breeding populations, and I encourage the use of advancing technology to monitor these birds in the future. Drones are becoming an increasingly common method for monitoring waterbird survival, reproductive success, and movement (McEvoy et al. 2016), and have the potential to access wetlands that are difficult to traverse and use heat sensitive equipment to conduct duckling counts that would otherwise be challenging. In addition, search efforts for telemetered birds would be greatly improved by the use of aerial survey techniques, as the densely vegetated habitat used by cinnamon teal during the breeding season is especially susceptible to signal bounce and interference, and an overhead perspective would likely increase detection considerably. Given the low recovery rate for banded cinnamon teal, managers could greatly increase the value of the data they collect through small changes in banding protocols. Recording individual recapture information within season in addition to across seasons (Lindberg et al. 2001) would provide the information necessary to calculate survival and detection estimates without having future recapture and recovery data information. I therefore encourage recording daily recapture information for all studies and banding protocols in the future. In addition, methods that could augment the reporting rate of auxiliary markers on ducks might aid in advancing our knowledge of more enigmatic species like the cinnamon teal. For example, several individuals marked with nasal discs ($n = 2$) or web tags ($n = 1$) were reported through social media outlets tailored to birders and waterfowl hunters throughout the course of this study, and it is likely that they would not have been reported to the Bird Banding Laboratory otherwise. Nasal disc resightings were relatively infrequent, but have

the potential to provide migration information, especially if more systematic searches are conducted.

With limited data, my analysis was somewhat restricted, precluding my ability to estimate sex-specific survival rates. The use of web tagged ducklings to estimate duckling survival is a promising avenue for future studies, especially in locations that are conducive to drive trapping or have easily accessible areas of brood habitat (Stetter 2014). Locations of traps used to recapture web tagged ducklings and banded birds should be carefully considered, however, to ensure the banding effort is universal enough to encompass all ducks breeding in the study area. Obtaining higher recovery rates than I observed here would allow for the use of hidden Markov models (*sensu* Nichols et al. 2004, Pradel 2005, Kendall et al. 2012, Johnson et al. 2015) to estimate sex-specific duckling survival rates originating from ducklings that cannot be assigned to a sex upon hatching/web tagging. I encourage future researchers to consider this technique as a possible avenue for estimating duckling survival rates. Building on the information presented here to evaluate variation in seasonal survival rates over greater temporal and spatial scales and assessing the impacts of environmental covariates on cinnamon teal survival rates is the next step in ascertaining a more comprehensive understanding of this enigmatic species.

Table 5.1: Recapture history for cinnamon teal marked from 2015-2017 at Monte Vista NWR and recaptured or recovered through August 2017. Web tag recaptures also include recaptured HY birds with torn webbing believed to indicate tag loss.

Year	Web tags released	HY bands released	AHY bands released	Webtags recaptured	HY bands recaptured	AHY bands recaptured	HY bands recovered	AHY bands recovered
2015	57	332	54	6	1	2 ^a	7	2
2016	81	1,082	248	17	0	13	16	7
2017	96	509	96	6	NA	NA	NA	NA
Total	234	1923	398	29	1	15	23	9

^aRecaptures and recoveries denote birds banded in the listed year, not birds recaptured that year. For example, two AHY birds that were banded in 2015 were recaptured in either 2016 or 2017.

Table 5.2: Candidate model set for estimating cinnamon teal duckling survival on Monte Vista NWR, 2015-2017, using Burnham's (1993) joint live recapture and dead recovery model. **Age** = parameter is allowed to vary by age of the duck (hatch year or after hatch year), **Seas** = parameter is allowed to vary between breeding season and non-breeding season, **Year** = parameter is allowed to vary by year of the study (2015-2017).

Model	AICc	Delta AICc	Weights	Model Likelihood	Num. Par	Deviance
S(Age*Seas*Year) p(Age*Seas*Year) r(Age*Seas*Year) F(Age*Seas)	653.9022	0	0.40747	1	13	627.759
S(Age*Seas*Year) p(Age*Seas*Year) r(Age*Seas) F(Age*Seas)	653.9444	0.0422	0.39896	0.9791	13	627.8012
S(Age*Seas*Year) p(Age*Seas) r(Age*Seas*Year) F(Age*Seas)	656.0436	2.1414	0.13967	0.3428	12	631.9209
S(Age*Seas*Year) p(Age*Seas*Year) r(Age*Seas*Year) F(Age*Seas*Year)	657.9479	4.0457	0.0539	0.1323	15	627.759
S(Age*Seas) p(Age*Seas*Year) r(Age*Seas) F(Age*Seas)	679.9096	26.0074	0	0	11	657.8058
S(Age*Seas) p(Age*Seas) r(Age*Seas) F(Age*Seas)	684.6023	30.7001	0	0	8	668.5458

Table 5.3: AICc table indicating performance of models estimating breeding season hen survival for cinnamon teal breeding on Monte Vista NWR from 2015-2017.

Model	AICc	Delta AICc	AICc	Model	Num. Par	Deviance
			Weights	Likelihood		
S(year)	12.8213	0	0.50866	1	2	8.806
S(.)	12.9635	0.1422	0.47375	0.9314	1	10.9584
S(day+year)	19.55	6.7287	0.01759	0.0346	7	5.4067

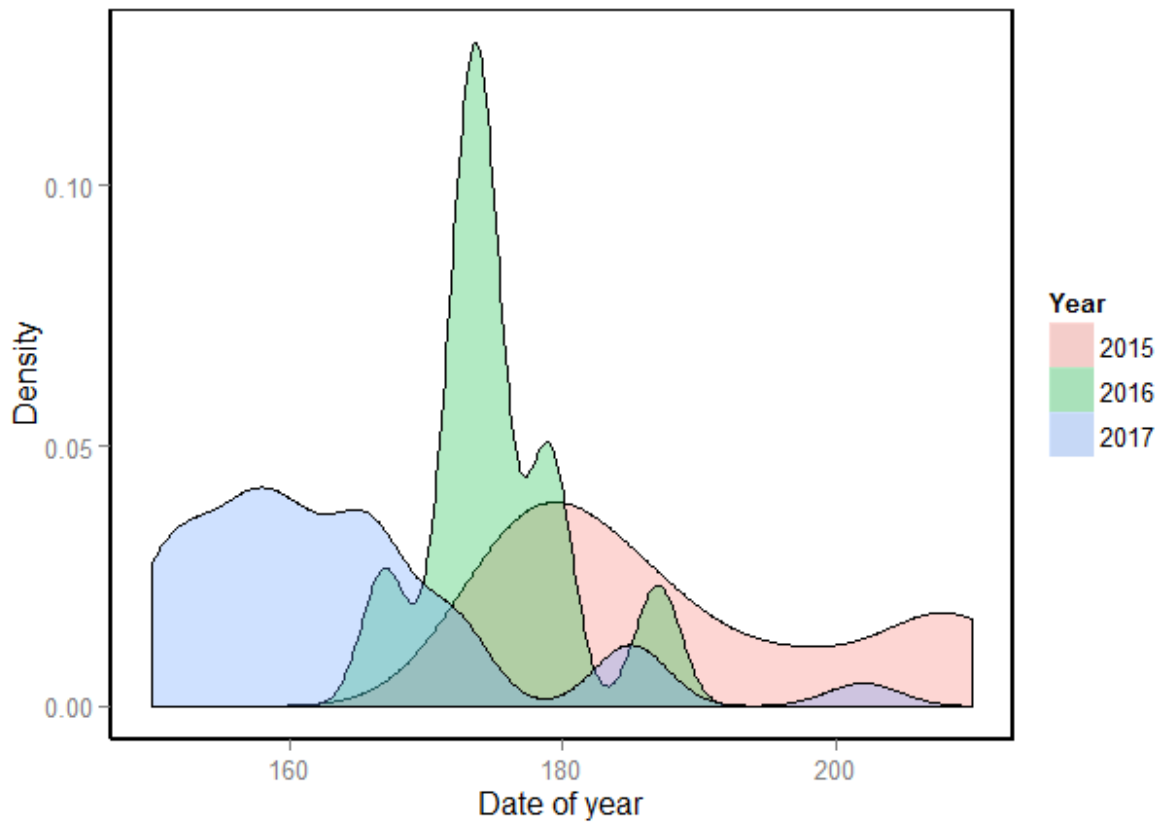


Figure 5.1: The distributions of cinnamon teal web tagging effort from 2015-2017 on Monte Vista NWR. Density measures the relative number of web tags placed on ducklings on a given date.

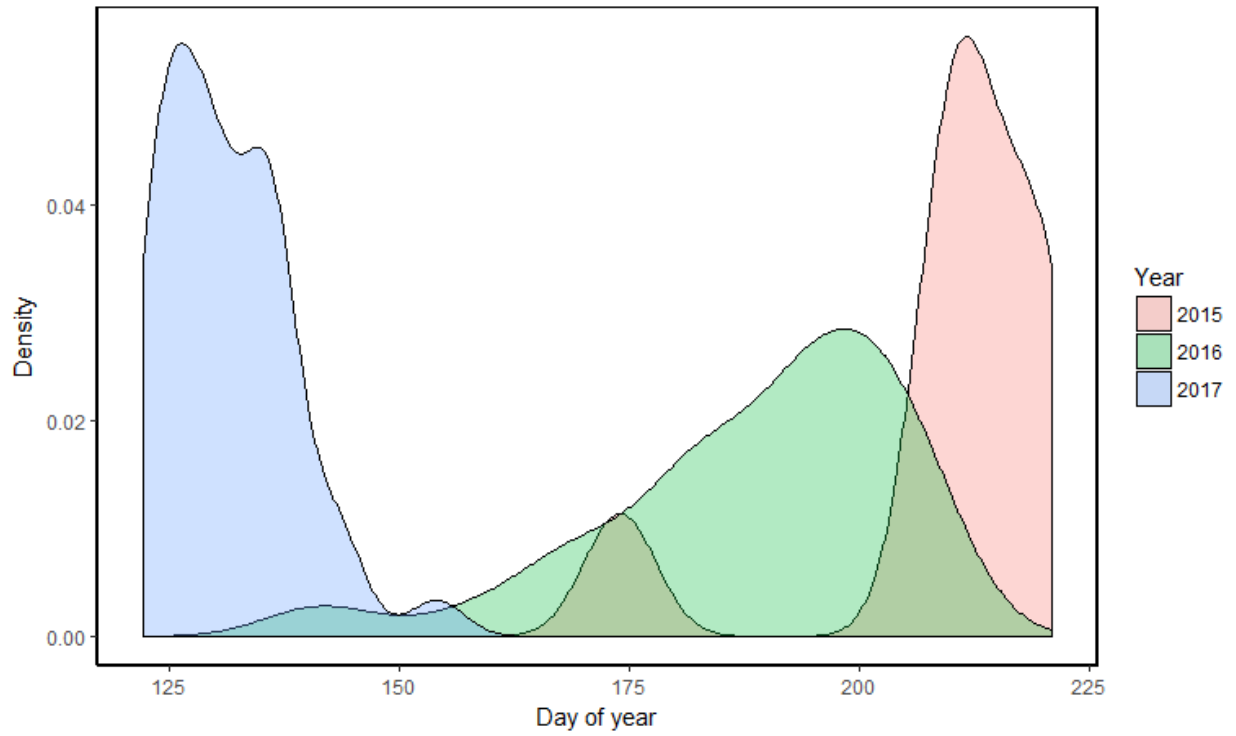


Figure 5.2: The distributions of telemetry monitoring effort for cinnamon teal hens from 2015-2017 on Monte Vista NWR. Density measures the number of birds relocated on a given date relative to other days of searching.

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Chapter 6 - CONCLUSIONS

Waterfowl are unique among wildlife in the ways they are managed and the population level questions that remain unanswered for many species. The cinnamon teal is one of those species and remains the least studied and least abundant duck species in North America. My objective in this study was to partially bridge the information gap between cinnamon teal and other closely related species, beginning with an understanding of breeding demographics. Although observational in nature, this study provided insight into mechanisms driving nest site selection and nest survival, a potential method for surveying reproductive success, evidence for nest attendance patterns similar to other species of waterfowl during the incubation stage of nesting, and hen and duckling survival rates during the breeding season. While there is work to be done to improve methods used to study cinnamon teal, I provided suggestions throughout this thesis that will offer future researchers potential considerations regarding study design, analysis, and field logistics. In an increasingly arid west and changing climatic conditions worldwide, this research has the potential to not only enhance the understanding of the basic population ecology of this species, but also to provide baseline estimates of vital rates to which future researchers can refer as species and habitats continue to adapt and change.

Cinnamon teal nest throughout the Intermountain West in semi-permanent and seasonal wetlands (Gammonley 2012). My research emphasizes the importance of wetland graminoid communities to cinnamon teal habitat use and reproductive success throughout this region, as well as the importance of considering the effect of invasive plant species on this success. Although my estimate of overall nest survival (0.194, SE = 0.076) is comparable to other fast-lived waterfowl species (Johnson 1979, Lokemoen et al. 1990, Skone et al. 2016), it is important to continue monitoring this vital rate across scales and regions to obtain a better understanding of

the cinnamon teal and to ensure its longevity. More research is also necessary to ascertain the importance of varying hydrological regimes and ephemeral water sources to its reproductive success. My research did not find a relationship between the distance of a nest to water and nest survival, but the variation in this distance throughout the duration of a single bird's nesting period necessitates more research to truly capture that variation and determine its effect, if any.

In the future, reproductive monitoring might be possible on a larger scale using social index surveys (Hochbaum et al. 1987, Serie and Cowardin 1990, Arnold et al. 2008, Setash Chapter 3). In this thesis, I showed strong correlations between several social indices and other metrics of reproductive success that, if verified over a longer time scale, show promise for monitoring cinnamon teal and other waterfowl in a time-efficient manner. This method is also an excellent tool for gaining an understanding of the reproductive phenology of a system, as my research and others' show that using social indices allows researchers and managers to pinpoint pivotal events throughout the breeding season (i.e., peak nest initiation, timing of renesting, etc.). As budgets among the wildlife management community become more restricted, social index surveys offer an alternative method for monitoring parameters of waterfowl populations necessary to assess the population. Although not frequently monitored, patterns in nest attendance offer a unique perspective on waterfowl behavior in relation to the more frequently evaluated population parameters such as nest survival. In this thesis, I showed that cinnamon teal nest attendance patterns vary by nest age, time of day, and ambient temperature, and that they are making use of the variation in their daily thermal environment to ensure the success of their nests (Setash Chapter 3). These results not only provide inference into the behavior of this secretive species, but potentially offer explanations for variations in seasonal survival of breeding hens, nests, and ducklings.

Estimates of waterfowl survival during specific stages of the annual cycle are often important components of their management, especially given their status as game birds (Hoekman et al. 2002). Breeding season survival of hens and ducklings drives the following year's breeding population levels and can indicate variation in habitat quality or management actions (Ringelman 1992, Stetter 2014). My estimates of cinnamon teal hen and duckling survival during the breeding season contribute directly to management of the species as they are the only estimates currently available that do not combine cinnamon and blue-winged teal survival. They therefore act as a baseline on which future researchers can build and generate future research questions regarding the mechanisms driving breeding season survival. Most importantly, this research provides guidance to future cinnamon teal researchers regarding banding protocols and web tagging efforts that can be implemented across species to provide the most robust information available. Cinnamon teal research is often considered behind that of other species (USFWS 2013), but the work presented here will provide a foundation upon which others can construct the complete story of this species' population dynamics and trajectory amidst a changing world.

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Appendix A - HIDDEN MARKOV MODEL STRUCTURES CONSIDERED TO DESCRIBE THE VARIABILITY IN CINNAMON TEAL NEST SURVIVAL AND ASSOCIATED AICc VALUES.

Model Number	Model Structure	K	Model Likelihood	AICc	Delta AICc	Model Weight	Deviance
1	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2+\text{Pforbs}) \psi^{25}(\text{Age})$ $\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	13	1.00	351.34	0.00	0.25	324.79
2	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2+\text{Pforbs}) \psi^{24}(\text{NID}^2+\text{Pforbs}) \psi^{25}(\text{Age})$ $\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	14	0.55	352.52	1.19	0.14	323.89
3	$\psi^{12}(\text{Age}) \psi^{13}(\text{Age}+\text{NID}^2) \psi^{24}(\text{NID}^2+\text{Pforbs}) \psi^{25}(\text{Age})$ $\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	14	0.55	352.55	1.21	0.14	323.91
4	$\psi^{12}(\text{Age}) \psi^{13}(\text{Age}+\text{NID}^2) \psi^{24}(\text{Age}+\text{NID}^2+\text{Pforbs})$ $\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	15	0.36	353.40	2.06	0.09	322.67
5	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$ $\delta_{\text{Inc}}(\text{Age})$	12	0.17	354.88	3.54	0.04	330.40
6	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2+\text{Pgrass}) \psi^{25}(\text{Age})$ $\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	13	0.16	354.95	3.62	0.04	328.40
7	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2+\text{Clutch}) \psi^{24}(\text{NID}^2+\text{Clutch})$ $\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	14	0.15	355.20	3.86	0.04	326.56

	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{robel}) \psi^{24}(\text{NID}^2 + \text{robel}) \psi^{25}(\text{Age})$	14	0.11	355.78	4.45	0.03	327.15
8	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{Pshrub}) \psi^{24}(\text{NID}^2 + \text{Pshrub})$	14	0.10	355.90	4.56	0.03	327.26
9	$\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Age}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$	13	0.09	356.25	4.91	0.02	329.70
10	$\delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{Pforbs}) \psi^{24}(\text{Age} + \text{Pforbs}) \psi^{25}(\text{Age})$	11	0.07	356.61	5.27	0.02	334.21
11	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{Pgrass}) \psi^{24}(\text{NID}^2 + \text{Pgrass}) \psi^{25}(\text{Age})$	14	0.07	356.74	5.40	0.02	328.10
12	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Dshrub}) \psi^{25}(\text{Age})$	13	0.07	356.76	5.43	0.02	330.21
13	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{Clutch}) \psi^{25}(\text{Age})$	13	0.07	356.81	5.47	0.02	330.25
14	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2) \psi^{24}(\text{NID}^2 + \text{robel}) \psi^{25}(\text{Age})$	13	0.06	356.92	5.58	0.02	330.37
15	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}) \psi^{24}(\text{NID}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$	10	0.05	357.22	5.88	0.01	336.89
16	$\delta_{\text{Inc}}(\text{Age})$						

	$\psi^{12}(\text{Age}) \psi^{13}(\text{Age}+\text{NID}^2) \psi^{24}(\text{Age}+\text{NID}^2) \psi^{25}(\text{Age})$	14	0.05	357.24	5.90	0.01	328.60
17	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2+\text{PLive}) \psi^{24}(\text{NID}^2+\text{PLive}) \psi^{25}(\text{Age})$	15	0.05	357.28	5.95	0.01	326.55
18	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}^2) \psi^{13}(\text{Age}^2+\text{NID}^2) \psi^{24}(\text{Age}+\text{NID}^2) \psi^{25}(\text{Age})$	14	0.04	357.56	6.22	0.01	328.92
19	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}^2) \psi^{13}(\text{Age}^2+\text{NID}) \psi^{24}(\text{Age}+\text{NID}) \psi^{25}(\text{Age})$	12	0.03	358.06	6.72	0.01	333.59
20	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}) \psi^{24}(\text{Age}+\text{NID}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$	11	0.03	358.31	6.97	0.01	335.91
21	$\delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2+\text{Weight}) \psi^{24}(\text{NID}^2+\text{Weight})$	14	0.03	358.56	7.22	0.01	329.92
22	$\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2+\text{PWater}) \psi^{24}(\text{Age}+\text{NID}^2+\text{PWater})$	15	0.01	359.86	8.53	0.00	329.14
23	$\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2+\text{Year}) \psi^{24}(\text{Age}+\text{NID}^2+\text{Year})$	17	0.01	360.13	8.79	0.00	325.20
24	$\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{Age}+\text{NID}) \psi^{24}(\text{Age}+\text{NID}) \psi^{25}(\text{Age})$	12	0.01	360.37	9.03	0.00	335.90
25	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						

26	$\psi^{12}(\text{Age}) \psi^{13}(\text{Age}^2) \psi^{24}(\text{Age}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$ $\delta_{\text{Inc}}(\text{Age})$	8	0.01	361.05	9.71	0.00	344.83
27	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{DShrub}) \psi^{24}(\text{Age} + \text{NID}^2 + \text{DShrub})$ $\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	15	0.01	361.40	10.06	0.00	330.67
28	$\psi^{12}(\text{Age}) \psi^{13}(\text{Year}) \psi^{24}(\text{Year}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$ $\delta_{\text{Inc}}(\text{Age})$	13	0.00	362.04	10.71	0.00	335.49
29	$\psi^{12}(\text{Age}) \psi^{13}(\text{Age}^2) \psi^{24}(\text{Age}^2) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$ $\delta_{\text{Inc}}(\text{Age})$	10	0.00	362.06	10.73	0.00	341.73
30	$\psi^{12}(\text{Age}) \psi^{13}(\cdot) \psi^{24}(\text{Age}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	9	0.00	362.23	10.89	0.00	343.95
31	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2 + \text{Year}) \psi^{24}(\text{NID}^2 + \text{Pforbs} + \text{Year})$ $\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	19	0.00	362.67	11.33	0.00	323.51
32	$\psi^{12}(\text{Age}) \psi^{13}(\text{PGrass}) \psi^{24}(\text{Age} + \text{PGrass}) \psi^{25}(\text{Age})$ $\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	11	0.00	362.98	11.64	0.00	340.58
33	$\psi^{12}(\text{Age}) \psi^{13}(\cdot) \psi^{24}(\text{Age}^2) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	9	0.00	363.10	11.76	0.00	344.83
34	$\psi^{12}(\text{Age}) \psi^{13}(\text{Robel}) \psi^{24}(\text{Age} + \text{Robel}) \psi^{25}(\text{Age})$ $\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$	11	0.00	363.16	11.82	0.00	340.76
35	$\psi^{12}(\text{Age}) \psi^{13}(\text{Age}) \psi^{24}(\text{Age}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$ $\delta_{\text{Inc}}(\text{Age})$	10	0.00	363.34	12.01	0.00	343.01

	$\psi^{12}(\text{Age}^2) \psi^{13}(\text{Age}^2) \psi^{24}(\text{Age}^2) \psi^{25}(\text{Age}^2) \delta_{\text{Lay}}(\text{Age}^2)$	10	0.00	363.81	12.47	0.00	343.48
36	$\delta_{\text{Inc}}(\text{Age}^2)$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{Year+NID}^2) \psi^{24}(\text{Year+NID}^2) \psi^{25}(\text{Age})$	18	0.00	364.00	12.66	0.00	326.96
37	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{DWater}) \psi^{24}(\text{Age+DWater}) \psi^{25}(\text{Age})$	11	0.00	365.29	13.95	0.00	342.89
38	$\delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
	$\psi^{12}(\text{Age}) \psi^{13}(\text{NID}^2+\text{PBG}) \psi^{24}(\text{Age+NID}^2+\text{PBG})$	17	0.00	367.38	16.04	0.00	332.45
39	$\psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age}) \delta_{\text{Inc}}(\text{Age})$						
40	$\psi^{12}(\text{Age}) \psi^{13}(\cdot) \psi^{24}(\cdot) \psi^{25}(\text{Age}^2) \delta_{\text{Lay}}(\text{Age}^2) \delta_{\text{Inc}}(\text{Age}^2)$	10	0.00	367.48	16.14	0.00	347.14
41	$\psi^{12}(\text{Age}) \psi^{13}(\text{Age}) \psi^{24}(\text{Age}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\cdot) \delta_{\text{Inc}}(\cdot)$	9	0.00	377.22	25.88	0.00	358.95
42	$\psi^{12}(\cdot) \psi^{13}(\cdot) \psi^{24}(\cdot) \psi^{25}(\cdot) \delta_{\text{Lay}}(\cdot) \delta_{\text{Inc}}(\cdot)$	5	0.00	482.88	131.54	0.00	472.79
43	$\psi^{12}(\text{Age}) \psi^{13}(\text{Year}) \psi^{24}(\text{Age+Year}) \psi^{25}(\text{Age}) \delta_{\text{Lay}}(\text{Age})$	13	0.00	511.65	160.31	0.00	485.17
	$\delta_{\text{Inc}}(\text{Age})$						
