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Factors Affecting Songbird Nest Survival and Brood Parasitism in the Rainwater Basin Region of Nebraska

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FACTORS AFFECTING SONGBIRD NEST SURVIVAL AND BROOD PARASITISM IN THE RAINWATER BASIN REGION OF NEBRASKA

by

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FACTORS AFFECTING SONGBIRD NEST SURVIVAL AND BROOD PARASITISM IN THE RAINWATER BASIN REGION OF NEBRASKA

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One way to think about a bird's nest is as a commitment to a location. Once the nest is built, it can't just be moved. This means that birds should choose habitats that allow their nests to be safe from predators, such as raccoons (*Procyon lotor*) or brood parasites, such as brown-headed cowbirds (*Molothrus ater*), that lay eggs in the nests of other birds. Both nest predation and brood parasitism can lower the number of young a songbird can produce.

I studied the patterns of nest predation and brood parasitism in red-winged blackbird (*Agelaius phoeniceus*) nests in the Rainwater Basin region of south central Nebraska. Of the 591 nests I studied from 2002 to 2004, approximately 8 of every ten nests failed. I found that failure risk increased when nests were closer to the ground, or when rainfall or temperature increased. I also found that nests earlier in the nesting season had a lower risk of failing compared to later in the season. Interpreted another way, these results suggest that nest predators prey on lower nests, tend to forage during periods of higher rainfall or higher temperature, and increase foraging later in the year.

Aside from predators, I found that 5 of ten nests were the victim of a brood parasite. However, I also found that red-winged blackbirds decrease their risk of being parasitized by nesting at the same time - probably because more birds can deter cowbirds

from laying their eggs. Unlike the predation study, my results also suggest that birds can lower the risk of parasitism by building a nest closer to the ground and later in the year.

My results suggest that we need to know more about what kinds of predators songbirds must avoid to be successful, and why the factors I found here increase or decrease nest survival. The results from the parasitism analysis suggest that research is needed to determine the trade-offs between avoiding parasitism vs. predation.

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CHAPTER 1. Factors affecting the survival of red-winged blackbird (*Agelaius phoeniceus*) nests in the Rainwater Basin region of central Nebraska.

Abstract: My study focused on the assessment of songbird nest survival in a subset of Rainwater Basin wetlands in south-central Nebraska. I used an information-theoretic approach to compare hypotheses about the role of habitat-level characteristics, nest-site variables, climate, and time on explaining variation in red-winged blackbird (*Agelaius phoeniceus*) daily nest survival (DNS). I analyzed 591 nests from 2002-2004. The pooled DNS estimate for this region was 0.944 (CI: 0.938-0.949). Assuming that 23 days are needed for a successful nest, this estimate yields a nest success rate of 0.24 (CI: 0.23-0.30). My results showed little support for the habitat-level model, weak support for the nest-site model and strong support for the climate and temporal models. Model-averaged predictions showed a weak positive effect of increasing nest height on DNS. Increasing daily mean precipitation had a negative effect on DNS, and daily mean high temperature showed a similar negative effect. Stage also explained some variation with survival being lower in the egg stage than the nestling stage. DNS also decreased with increasing day during the nesting season, and annual fluctuations explained some variation. The impact of time and weather could reflect responses of predator and prey communities and further research is needed to understand the composition of those communities in this region.

INTRODUCTION

Wetlands provide habitat for a wide variety of breeding birds (Burger 1985). On a regional scale, the playa wetlands of the Great Plains are especially important for birds that use these playas as migratory habitat while traversing the central fly-way (Smith 2003). Playa wetlands are also thought to function as islands of biodiversity because they occur within homogeneous agricultural landscapes (Haukos and Smith 1994). This view of playas makes assessing their quality a vital component for the management of breeding birds.

Wetland quality is determined in numerous ways, which can range from assessments of species richness and abundance (Hemesath and Dinsmore 1993, Naugle et al. 1999) to nest success (Yerkes 2000; Esler and Grand 1993). Although some evidence exists to suggest that species abundance may be a good indicator of breeding habitat quality (Bock and Jones 2004), demographic parameters, such as nest success, are considered more direct (Van Horne 1983, Vickery et al. 1992).

Breeding birds seem to select habitats based on factors that decrease the risk of predation and increase nest success (Martin 1993a). For example, birds may choose to build nests at varying heights to avoid certain types of predators. Mesopredators, for example are more likely to find a nest near the ground (Burhans et al. 2002), whereas a aerial predators or brown-headed cowbirds may be more likely to find nests further from the ground (Filliater et al. 1994; Martin 1993b).

In addition, a bird may select a larger habitat because nests can be built further from the habitat's edge. Studies looking at the effect of the distance of a nest from the edge of a wetland vary with some studies demonstrating an edge effect on nest success

(Pasitschniak-Arts and Messier 1995; Crabtree et al. 1989), while others failed to find any effect (Hanski et al. 1996; Berg et al. 1992). The variability in edge effects could be related to landscape context (Donovan et al. 1997) or to the presence of grassland buffers, which might change the type of habitat edge, thus making nests more difficult to find (Paton 1994). However, species specific differences between predators and nesting birds could also explain some of this variation (Lahti 2001).

Despite the efforts of birds to avoid predation by selecting "safer" habitats, there are other variables that could influence nest survival that are outside of the bird's control. For example, it has been hypothesized that increased precipitation and temperature may lead to lower nest survival because microbial growth on the plumage of an incubating adult might provide olfactory cues to predators (Roberts et al. 1995, Roberts and Porter 1998). However, for aquatic systems that rely on runoff, such as playas, precipitation may fill wetlands making it difficult for mammalian mesopredators to access the wetland. Some have found that nests built over deeper water have a lower risk of predation (Picman et al. 1993). In addition, weather related variables might also cause direct failure by affecting incubation temperatures or causing structural damage to the nest or its contents.

Birds selecting nesting habitats also contend with temporal factors that may influence nest survival rates as predators respond to nest cues or as nesting densities increase throughout the season. This may be reflected in the responses of predators to changes in resources (i.e. alternative prey; Jones et al. 2002) or to the cues used by predators to locate nests, such as increased activity after eggs have hatched (Eichholz and Koenig 1992).

In this study, I sought to determine the multiple factors that might influence songbird nesting success in the Rainwater Basin region of central Nebraska. I focused on red-winged blackbirds (*Agelaius phoeniceus*; hereafter RWBL), one of the most abundant songbirds in North America (Beletsky 1996, Yasukawa and Searcy 1995). The high levels of RWBL abundance in the Rainwater Basin provided me with an opportunity to amass a large dataset of natural nests within a short period of time.

Earlier work by Kocer (2004) showed that RWBL nest survival in the Rainwater Basin varies between wetlands. Her results suggested that this variation may be driven by mammalian mesopredator abundance, which was found to be negatively correlated with daily nest survival. However, her study was not focused on the relationship between nesting habitats or other variables that may have influenced the daily survival probability of nests.

I used an information-theoretic approach to determine the effects of habitat characteristics, nest-site, climate and temporal covariates on daily nest survival. I proposed *a priori* models as hypotheses concerning the impact of the amount of grassland buffer area, mesopredator abundance, nest height, distance to edge, mean high temperature, mean rainfall, year, day and stage of the nest. By comparing models and model-averaged predictions, I was able to assess which factors had the greatest impact on daily nest survival. I predicted that temporal and climate effects would have the greatest impact on nest survival because failure rates would be more or less constant between habitats and nest-sites in a highly agricultural landscape.

METHODS

Study Area

My study was conducted in the Rainwater Basin region of central Nebraska, an important stopping point for migrating waterfowl and breeding habitat for species of non-game birds (Gersib et al. 1989; see Appendix I). Identified as an endangered habitat (LaGrange 1997), the Rainwater Basin is a complex of playa wetlands that occupies roughly 4,200 square miles in south-central Nebraska. Almost 100,000 acres of wetland are believed to have been present at the time of settlement. Recent estimates suggest 34,103 acres remain (LaGrange 1997).

My sample wetlands were located in a 13-by-18 km area southeast of Clay Center, NE in Clay County. I sampled 11 wetlands that varied in size, ownership and the amount of upland buffer (Table 1). Wetlands made up approximately 17% of my study area, whereas roads and agricultural fields made up about 72% (Kocer 2004).

Dominant plant communities among wetlands were composed of cattail (*Typha* spp.), river bulrush (*Scirpus fluvailtalis*), reed canary grass (*Phalaris arundinacea*) and smart weed (*Polygonum* spp.). The relative abundance of each plant species varied between wetlands.

Sampling Methods

Nest searching- I began searching for nests in the second or third week of May; I terminated searches at the end of July each year. At the beginning of the 2002 season random transects were established in wetlands exceeding 1 ha, and covered both wetland and upland habitat. I adjusted these transects in 2003 so that only the wetland was searched (see Appendix II), and used these same transects in 2004. I searched the entire wetland if it was smaller than 1 ha.

On larger wetlands I searched for nests within 100 meters on either side of the transect. I identified each nest with a number by writing on vegetation near the nest with a felt-tip marker. I also tied plastic flagging to vegetation > 10 meters from the nest and I wrote the distance and direction to the nest on the flag.

I re-visited nests every 3-4 days until the young successfully fledged or the nest failed. When I left the nest site I tried to avoid leaving dead-end trails in the vegetation that might be used by predators to locate a nest. For analysis, I considered a nest successful if ≥ 1 young, host or parasite, fledged. I considered a nest a failure if its contents were lost before fledging. I attributed predation as the cause of failure if there was physical evidence near the nest (i.e. tracks, fur) or if there was significant damage to the nest or surrounding substrate. I regarded the cause of failure as unknown if the eggs or nestlings were prematurely removed from the nest, but no significant damage was seen.

Nest-site characteristics- At the time of discovery, I identified the avian species that built the nest, the species of nest substrate, and I quantified nest height and vegetation density. I measured nest height (from the ground to the top edge of the nest) and vegetation density using a Robel pole. Both were measured to the nearest 0.5 dm. In addition, I collected the UTM coordinates for each nest using a WAAS-ready Garmin Etrex Vista GPS receiver.

I measured the distance between the nest and the edge of the wetland using DOQQ and NWI data in ESRI's ArcGIS (version 8.x). I delineated the wetland edge with a GPS unit in the field; I considered the edge to be the zone where obligate wetland plant species changed to obligate upland species. I modified the National Wetlands Inventory (NWI) coverage with the edge data, then overlaid the nest coordinates and measured the shortest distance from each nest to the wetland edge in meters.

Mesopredator abundance- To quantify relative differences in mammalian predator abundance among wetlands, I used trap indices published in Kocer (2004). These indices were calculated for each wetland as the number of mesopredators captured divided by the number of trap nights. These indices were only available for 2002 and 2003, so I had to rely on track stations to estimate predator abundance in 2004. I set up six track stations for each wetland over 1 ha. I placed three stations in the upland habitat, 30 m apart and perpendicular to the transect. For wetlands less than 1 ha in size, I randomly placed three track stations parallel to the wetland-upland edge.

I constructed each 1-m^2 station with a 5:1 mixture of fine-grained masonry sand to mineral oil. I placed a plaster egg at the center of each station to act as novel cue for a foraging predator (Kocer 2004). I monitored each station every 3-5 days, and quantified predator abundance by dividing the total number of individuals identified by the total number of exposure nights for each wetland. Kocer (2004) found that track stations did a reasonably good job of predicting trap index results, so I feel that the use of track stations as supplemental data for 2004 is justified.

Habitat Characteristics- I delineated the amount of upland grassland/shrub buffer by collecting UTM coordinates around the interior and exterior perimeters of the upland habitat buffer. These coordinates were used to create polygons in ArcGIS, which were merged with the NWI coverage (Appendix II). From this, I calculated the total upland area around each wetland in ha.

Climate Measurements- I accessed the High Plains Climate Research Center database (University of Nebraska-Lincoln, Lincoln, Nebraska) and obtained climate data from a weather station in Clay Center, NE, within ten miles of my study site. The station provided daily high temperature (C) and daily precipitation (cm).

Statistical Analyses

I used the statistical program R (version 2.0.1) to estimate daily nest survival with the logistic exposure method outlined in Shaffer (2004). I used the GLM (generalized linear model) package with a binomial distribution (0 = failure, 1 = successful) and a modified logit link function: $g(\theta) = \mathrm{Log}_e\,(\theta^{1/t}/[1 - \theta^{1/t}])$, where θ is the survival estimate for the monitoring interval and t is the interval length in days (Shaffer 2004). Appendix III shows the code I used to modify the logit link function. This model uses the nest monitoring interval as the sampling unit, and thus does not require an assumption about the timing of nest losses. In addition, the age of the nest need not be known. This method also assumes that the survival rate associated with each covariate is constant within a nest observation interval.

I fit models composed of covariates related to conditions of the nesting habitat, nest-site, daily climate conditions, and time. My first model, the habitat model, was composed of two parameters, the amount of buffer area around each wetland (BUF) and a year-specific mesopredator index (PRED) for each wetland. My nest-site model included two parameters, nest height (HT) and distance from edge (DIST).

My time specific models included a year effect (YR), an effect of day in the nesting season (DAY), and a stage effect (STAGE). For the DAY parameter I used the mid point of the monitoring interval. For STAGE, I used nest data to assign one of three stages to the midpoint of each observation interval: laying, incubation or nestling stage. My sample for the laying stage was quite small compared to the other stages so I merged the laying and incubation stages into an "egg" stage.

I also fit climate models that included daily precipitation (PR) and average daily high temperature (TEMP). For both parameters, I used the mean value for the entire monitoring interval. I also composed pairwise combinations of each of these models, a global model (GLOBAL) with all parameters and a constant survival (CONSTANT) model for a total of 12 models.

I used an information-theoretic approach to rank my candidate models using Akaike's Information Criterion (AIC, Burnham and Anderson 2002). I determined the best models by calculating the difference (ΔAIC) between the AIC value with the lowest score and all other models. Lower values of ΔAIC indicate better fitting models (Burnham and Anderson 2002). I also used Akaike weights (AIC_w) to determine the best set of models and to contend with modeling uncertainty.

I made DNS predictions by allowing one parameter to vary and holding all other parameters at their average values. I then model-averaged these predictions over all the models according to Burnham and Anderson (2002). I calculated model-averaged regression coefficients using the same methods.

RESULTS

Over the three years of this study I monitored and analyzed 591 active RWBL nests. I estimated that about 27% of the nests in this study failed as a result of predation, and about 33% failed due to unknown causes. The daily nest survival (DNS) estimate for my entire study area over all three years was 0.944 (95% CI: 0.938-0.949), which results in a 23-day nest success rate of 0.24 (95% CI: 0.23-0.30). DNS ranged from 0.942 (95% CI: 0.928-0.953) to 0.939 (95% CI: 0.930-0.946) during 2002-2004 (Figure 1).

The logistic exposure model that explained the most variation in daily nest survival (DNS) was the model that included climate and temporal effects (AIC = 1929.16, $k = 7$; Table 2). There was some support for my global model (AIC = 1930.76, $k = 11$), but the nest-site and habitat models seemed to explain less of the variation (Table 2). Model averaged parameter coefficients are presented in Table 3.

Model averaged predictions were made using the range of values from my field data (Table 3). Daily survival did not vary according to the amount of upland buffer (β = 0.00004, SE = 0.0005; Figure 2) or the mesopredator index (β = -0.70091, SE = 1.67844; Figure 3). In terms of nest-site parameters, nest height seemed to show a weak trend of increasing DNS with increasing nest height (β = 0.02644, SE = 0.037781.67844; Figure 4), but there was no trend for distance from edge (β = -0.00001, SE = 0.0005; Figure 5).

Mean high temperature showed a negative effect on DNS (β = -0.04396 , SE = 0.02014; Figure 6), as did mean rainfall (β = -0.11300, SE = 0.07036; Figure 7). Day in the nesting season also shows a declining trend in DNS over the course of the nesting season (β = -0.00989, SE = 0.00402; Figure 8). Predictions for the stage parameter show a consistently higher survival rate in the nestling stage [2002: 0.972 (95% CI: 0.979-

0.961), 2003: 0.979 (95% CI: 0.985-0.972), 2004: 0.968 (95% CI: 0.975-0.959)] compared with the egg stage [(2002: 0.925 (95% CI: 0.942-0.903), 2003: 0.944 (95% CI: 0.955-0.930), 2004: 0.916 (95% CI: 0.927-0.903)] (Figure 9).

DISCUSSION

The pooled DNS estimate for my study area is lower than for red-winged blackbirds nesting in other wetland systems. For example, Vierling (2000) estimated a DNS estimate for RWBL in Colorado of about 0.962 (23-day success rate: 0.41). Fletcher and Koford (2004) estimated a DNS estimate of 0.984 (23-day success rate: 0.69) for RWBL in the Prairie Pothole Region. Clotfelter and Yasukawa (1999) reported a nest success rate of 0.315 (DNS $\approx$0.951) for wet-meadow prairie nesting RWBL in southern Wisconsin. Perhaps the lower rate that I found was related to the impact of agriculture in my study region.

Roughly 72% of my study area is composed of agricultural land (Kocer 2004). Other studies have attributed lower nest success rates to agricultural land use adjacent to forest habitats, suggesting that these systems might be of lower quality for breeding birds (Donovan et al. 1997, Peak et al. 2004). Further evidence for lower habitat quality in my study may be found in the lack of effect for habitat buffer. Initially, I hypothesized that the predominance of agricultural land use in the region probably homogenized the available habitat so that differences between habitats might not be evident. I found that DNS did not vary according to grassland buffer area around each wetland. Grassland buffers are thought to increase nest success by "softening" the edge between a habitat and an agricultural field (Paton 1994). However I cannot rule out the fact that red-winged blackbirds may not be as sensitive to edge effects because of their generalized habitat preferences (Yasukawa and Searcy 1995).

I also did not find any effect of mesopredator index, suggesting that mesopredator abundance does not help to explain variation in DNS. Kocer (2004) suggested that mesopredator abundance tended to have a negative relationship with DNS; her analysis covered all songbird nests in the same wetlands that I studied in 2002-2003, and she compared the average nest survival rate for each wetland with the predator index for that wetland during the given year with a regression analysis. I used the annual predator index for each wetland as a model covariate, which is at a different time scale than my interval-specific nest data. Although my β value for the effect of predator abundance is negative, I was not able to conclude that relative mesopredator abundance among wetlands affects nest survival. It appears that during 2002-2004 other predators such as other birds or snakes may have played a much larger role in nest failure.

The role of other predators may explain why I found a weak trend of increasing survival for taller nests, but no variation in DNS for distance from the wetland edge. Others have suggested that increasing RBWL nest height might be a response to terrestrial predation (Beletsky 1996; Beletsky and Orians 1996). Perhaps the lack of strong nest-site effects could be explained by the behavior of the incubating adult.

Red-winged blackbirds are known to be aggressive and nest success has been found to positively correlate with the degree and type of defensive behavior of males and females (Knight and Temple 1988). It is entirely possible that this behavior swamped any potential effect of the location of the nest or of the chosen nesting habitat. Cresswell (1997) found that blackbirds (*Tardus merula*) apparently compensated for the vulnerability of a nest by being more vigilant, making nest survival independent of the nest's physical location.

This behavioral influence of nest-site effects might also explain why factors such as climate, which an incubating adult has little control over, explain more variation in DNS. I found that increasing mean high temperature tended to decrease DNS, and that a similar trend existed for precipitation. Pleasant et al. (2003) tested for evidence of moisture-facilitated nest predation in scaled quail (*Callipepla squamata*) and found no effect of precipitation. They suggested that the lack of humidity in their study system may have led to a positive effect of precipitation on habitat quality and a reduction of bacterial growth that could have attracted predators. My results suggest that there might be some support for moisture-facilitated nest predation (Roberts and Porter 1998).

Still, another way to look at the effect of climate is from the point of view of reptilian predators. Some evidence suggests that snakes may become more active foragers following periods of rainfall (Dinsmore et al. 2002) and may be more likely to prey upon nestlings compared to eggs (Eicholtz and Koenig). However, the real effect of precipitation may be difficult to interpret. Confidence intervals around the DNS predictions for rainfall were so large, that I included a rug plot of data points for each year in the graph. This plot shows that outliers in 2004 could have more influence over the estimated trend in the model, which might overestimate the effect of precipitation.

By far, the strongest effect on DNS was for the nest stage, with the egg stage having a consistently lower survival rate than the nestling stage in all three years. Other studies looking at nest stage have found similar results (Sockman 1997; Peak et al. 2004), while some have found survival to be lower during the nestling stage (Burhans et al.

2002). This variation might be reflective of changes in the predator community or the cues that predators use to find nests (Eicholz and Koenig 1992). However, for colonial species such as red-winged blackbirds, defensive behavior increases following hatching, which might be explain my observed increase in survival during the nestling stage (Knight and Temple 1988).

As for the year effect, some have suggested that fluctuations between years could reflect changes in predator populations (Burhans et al. 2002). Predators select prey from the larger prey community of which RWBL nests are a part. Thus, annual changes might be reflective of changes in the presence of alternative prey (Jones et al. 2002).

But some evidence suggests that selection of bird nests as prey items may be correlated with foraging for a more abundant prey item (Vickery et al. 1992). This switching between prey items could explain why survival rates change over the course of the nesting season. For my study, the effect of day in the nesting season has a negative impact on nest survival. Perhaps as other prey becomes less available or as predators develop search images, the reliance on nests as prey might go up toward the end of the season.

On the other hand, predation may have had little to do with this decline in survival rate over the season. Red-wings may nest up to 2 times (Yasukawa and Searcy 1995), so the decline toward the end of the year might reflect last ditch renesting attempts on the part of physiologically stressed adult females (Haas 1998). This might lead to more nest failures because eggs are less viable or because nestlings are more susceptible to starvation as resources become less abundant.

SUMMARY

My study demonstrates the importance of using nest survival to assess habitat quality, and the need to examine multiple causes of variation in nest survival. Most importantly, my study shows that nest-site and habitat variables may not be very useful for managers in focusing research on the causes of such variation. However, my choice of habitat and nest-site variables may not have been reflective of this variation. Climatic and temporal models do seem to explain much of the variation, but the effect of precipitation is unclear. This suggests that further research is needed to determine the relationship between climatic variables and nest survival, with particular emphasis on the influence of climate on predator behavior. My results also suggest that mesopredators may not be the most important nest predator in the area. In addition, research should also examine the role bird nests play in the overall prey community. Thus, future research in the Rainwater Basin will focus on placing cameras on nests to determine the composition of the predator community and temporal fluctuations in the types of predators that cause nest failure.

LITERATURE CITED

Beletsky, L. and G. H. Orians (1996). Red-winged blackbirds: decision-making and reproductive success. Chicago, University of Chicago Press.

Beletsky, L. D. (1996). The Red-winged Blackbird: the biology of a strongly polygynous songbird. San Diego, CA, Academic Press.

Berg, A., S. G. Nilsson and U. Bostrom (1992). Predation on Artificial Wader Nests on Large and Small Bogs Along a South-North Gradient. *Ornis Scandinavica* **23**(1): 13-16.

Bock, C. E. and Z. F. Jones (2004). Avian habitat evaluation: should counting birds count? *Frontiers in Ecology* **2**(8): 403-410.

Burger, J. (1985). Habitat Selection in Temperate Marsh-nesting Birds. Habitat Selection in Birds. M. L. Cody. Orlando, Academic Press: 253-278.

Burhans, D. E., D. Dearborn, I. F.R. Thompson and J. Faaborg (2002). Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management* **66**(1): 240-249.

Burnham, K. P. and D. R. Anderson (2002). Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. New York, Springer-Verlag.

Clotfelter, E. D. and K. Yasukawa (1999). The effect of aggregated nesting on Red-winged Blackbird nest success and brood parasitism by Brown-headed Cowbirds. *Condor* **101**(4): 729-736.

Crabtree, R. L., L. S. Broome and M. L. Wolfe (1989). Effects of habitat characteristics on gadwall nest predation and nest-site selection. *Journal of Wildlife Management* **53**(1): 129-137.

Cresswell, W. (1997). Nest predation: The relative effects of nest characteristics, clutch size and parental behaviour. *Animal Behaviour* **53**: 93-103.

Dinsmore, S. J., G. C. White and F. L. Knopf (2002). Advanced techniques for modeling avian nest survival. *Ecology* **83**(12): 3476-3488.

Donovan, T. M., P. W. Jones, E. M. Annand and F. R. T. III (1997). Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* **78**(7): 2064-2075.

Eichholz, M. W. and W. D. Koenig (1992). Gopher Snake Attraction to Birds Nests. *Southwestern Naturalist* **37**(3): 293-298.

Esler, D. and J. B. Grand (1993). Factors influencing depredation of artificial duck nests. *Journal of Wildlife Management* **57**(2): 244-248.

Filliater, T. S., R. Breitwisch and P. M. Nealen (1994). Predation on northern cardinal nests: does choice of nest site matter? *Condor* **96**: 761-768.

Fletcher, R. J. and R. R. Koford (2004). Consequences of rainfall variation for breeding wetland blackbirds. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **82**(8): 1316-1325.

Gersib, R. A., R. R. Raines, W. S. Rosier and M. C. Gilbert (1989). A functional assessment of selected wetlands within the Rainwater Basin of Nebraska. Lincoln, NE, Nebraska Game and Parks Commission.

Haas, C. A. (1998). Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk* **115**(4): 929-936.

Hanski, I. K., T. J. Fenske and G. J. Niemi (1996). Lack of edge effect in nesting success of breeding birds in managed forest landscapes. *Auk* **113**(3): 578-585.

Haukos, D. A. and L. M. Smith (1994). The Importance of Playa Wetlands to Biodiversity of the Southern High-Plains. *Landscape and Urban Planning* **28**(1): 83-98.

Hemesath, L. M. and S. J. Dinsmore (1993). Factors affecting bird colonization of restored wetlands. *Prairie Naturalist* **25**(1): 1-11.

Johnsgard, P. A. (1997). The Avian Brood Parasites: Deception a the Nest. New York, Oxford University Press.

Jones, D. D., L. M. Conner, R. J. Warren and G. O. Ware (2002). The effect of supplemental prey and prescribed fire on success of artificial nests. *Journal of Wildlife Management* **66**(4): 1112-1117.

Knight, R. L. and S. A. Temple (1988). Nest-defense behavior in the red-winged blackbird. *Condor* **90**: 193-200.

Kocer, C. J. (2004). Mesopredator movement, abundance, and habitat selection in the Rainwater Basins of Nebraska. Graduate College. Lincoln, NE, University of Nebraska- Lincoln: 84.

LaGrange, T. (1997). Guide to Nebraska's wetlands and their conservation needs. Lincoln, NE, Nebraska Game and Parks Commission.

Lahti, D. C. (2001). The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* **99**(3): 365-374.

Martin, T. E. (1993a). Nest predation and nest sites: new perspectives on old patterns. *Bioscience* **43**(8): 523-532.

Martin, T. E. (1993b). Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* **141**: 897-913.

Naugle, D. E., K. F. Higgins, S. M. Nusser and W. C. Johnson (1999). Scale-dependent habitat use in three species of prairie wetland birds. *Landscape Ecology* **14**: 267-276.

Pasitschniak-Arts, M. and F. Messier (1995). Risk of Predation on Waterfowl Nests in the Canadian Prairies - Effects of Habitat Edges and Agricultural Practices. *Oikos* **73**(3): 347-355.

Paton, P. W. C. (1994). The Effect of Edge on Avian Nest Success - How Strong Is the Evidence. *Conservation Biology* **8**(1): 17-26.

Peak, R. G., F. R. I. Thompson and T. L. Shaffer (2004). Factors affecting songbird nest survival in riparian forests in a midwestern agricultural landscape. *Auk* **121**: 726-737.

Picman, J., M. L. Milks and M. Leptich (1993). Patterns of predation on passerine nests in marshes: effects of water depth and distance from edge. *Auk* **110**(1): 89-94.

Pleasant, G. D., C. B. Dabbert and R. B. Mitchell (2003). Evaluation of the moisture-facilitated nest depredation hypothesis in a semiarid environment. *Wilson Bulletin* **115**(3): 343-346.

Roberts, S. D., J. M. Coffey and W. F. Porter (1995). Survival and Reproduction of Female Wild Turkeys in New-York. *Journal of Wildlife Management* **59**(3): 437-447.

Roberts, S. D. and W. F. Porter (1998). Influence of temperature and precipitation on survival of wild turkey poults. *Journal of Wildlife Management* **62**(4): 1499-1505.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. *Auk* **121**(2): 526-540.

Smith, L. M. (2003). Playas of the Great Plains. Austin, University of Texas Press.

Sockman, K. W. (1997). Variation in life-history traits and nest-site selection affects risk of nest predation in the california gnatcatcher. *Auk* **114**: 324-332.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**(4): 893-901.

Vickery, P. D., M. L. Hunter and J. V. Wells (1992). Incidence of incidental nest predation and its effects on nests of threatended grassland birds. *Oikos* **63**: 281-288.

Vickery, P. D., M. L. Hunter and J. V. Wells (1992). Is density an indicator of breeding success? *Auk* **109**: 706-710.

Vierling, K. T. (2000). Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. *Ecological Applications* **10**(4): 1211-1218.

Yasukawa, K. and W. A. Searcy (1995). Red-winged Blackbird (*Agelaius phoeniceus*). Birds of North America, No. 184. A. Poole and F. Gill, The Academy of Natural Sciences, Philadelphia. The American Ornithologists Union, Washington, D.C.

Yerkes, T. (2000). Nest-site characteristics and brood-habitat selection of redheads: an association between wetland characteristics and success. *Wetlands* **20**(4): 575-580.

Table 1. All study wetlands including ownership, size (hectares) and amount buffer surrounding each wetland (hectares). Wetlands are organized according to ownership; federal Waterfowl Production Area (WPA) and state Wildlife Management Areas (WMA).

Harms WPA	Public- Federal	12.48	12.08
Massie WPA	Public- Federal	193.86	140.67
Meadowlark WPA	Public- Federal	6.48	25.54
Smith WPA	Public- Federal	92.32	65.51
Greenacres WPA	Public- State	21.23	4.15
Greenhead WMA	Public- State	20.77	2.80
Private 1	Private	4.86	1.92
Private 2	Private	0.49	0.00
Private 3	Private	12.26	2.68
Private 4	Private	6.13	0.39
Private 5	Private	0.31	0.00

Table 2. *A priori* candidate models explaining nest survival of 591 red-winged blackbird nests in the Rainwater Basin of Nebraska for 2002-2004. The number of parameters (*k*) includes an intercept and all the covariates in each model. Models with lower ΔAIC values and larger Akaike weights (w_i) have more support. Values for the best models are in bold. Abbreviations for each parameter are defined in the text.

Model	*k*	*AIC*	ΔAIC	w_i
PREC+TEMP+YR+DAY+STAGE	**7**	**1929.16**	**0.00**	**0.62**
BUF+PRED+HT+DIST+PREC+TEMP+YR+DAY+STAGE	**11**	**1930.78**	**1.63**	**0.28**
HT+DIST+YR+DAY+STAGE	7	1933.40	4.24	0.07
YR+DAY+STAGE	5	1935.67	6.51	0.02
BUF+PRED+YR+DAY+STAGE	7	1938.73	9.58	0.01
HT+DIST+PREC+TEMP	5	2002.66	73.51	0.00
PREC+TEMP	3	2002.88	73.73	0.00
BUF+PRED+PREC+TEMP	5	2005.38	76.23	0.00
CONSTANT	1	2006.43	77.27	0.00
HT+DIST	3	2007.47	78.31	0.00
BUF+PRED	3	2009.36	80.21	0.00
BUF+PRED+HT+DIST	5	2010.97	81.82	0.00

Table 3. Model averaged intercepts and regression coefficients (β) (+/- 1 SE), as well as the average values (+/- 1SD) calculated from field data and used for each quantitative model variable.

Parameter	B	SE	Mean (sd)	Range
Intercept	3.97113	0.64177	-	-
Buffer Area	0.00004	0.00047	31.24 (40.63)	0.00-140.70
Predator Index	-0.70091	1.67844	0.03 (0.02)	0.00-0.07
Nest Height	0.02644	0.03778	6.13 (1.86)	1.50-13.00
Distance from Edge	-0.00001	0.00053	55.92(36.86)	0.00-278.70
Daily Precipitation (cm)	-0.11300	0.07036	28.14 (3.96)	8.57-38.02
Daily High Temperature (°C)	-0.04396	0.02014	0.30 (0.73)	0.00-11.90
Year: 2003	0.30788	0.17627	-	-
Year: 2004	-0.12485	0.16583	-	-
Day	-0.00989	0.00402	-	-
Stage: Nestling	1.03044	0.12950	-	-

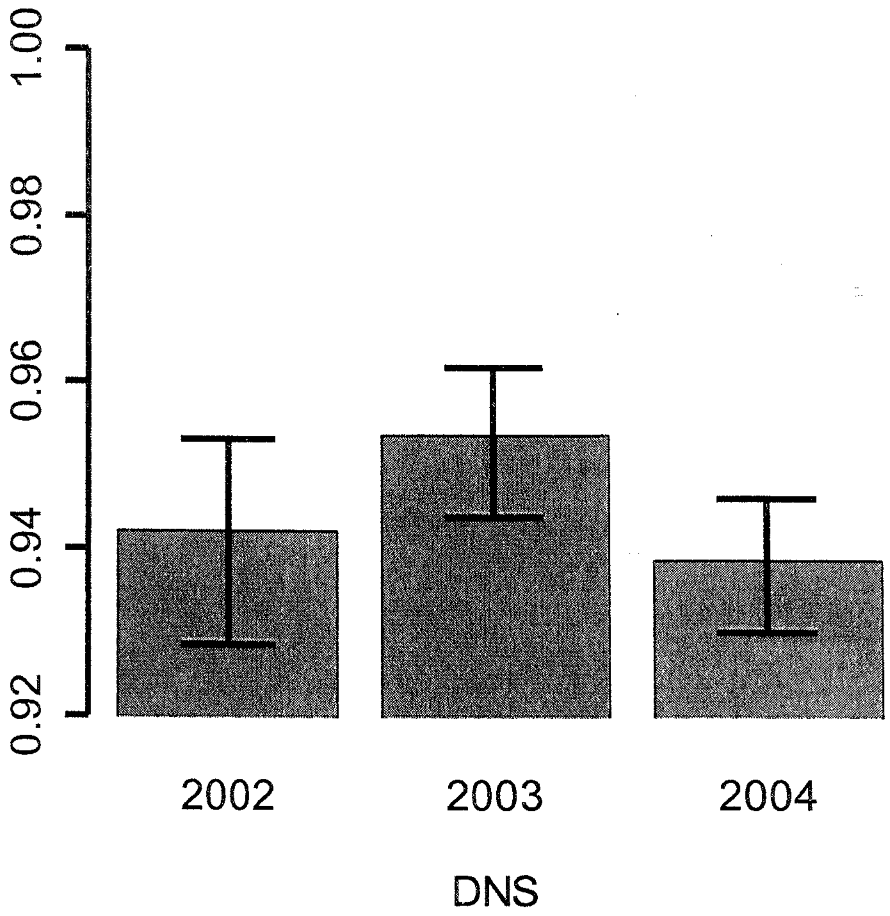

Figure 1. Pooled daily nest survival (DNS) for all wetlands over three years: 2002, 2003, 2004. Error bars represent 95% CI.

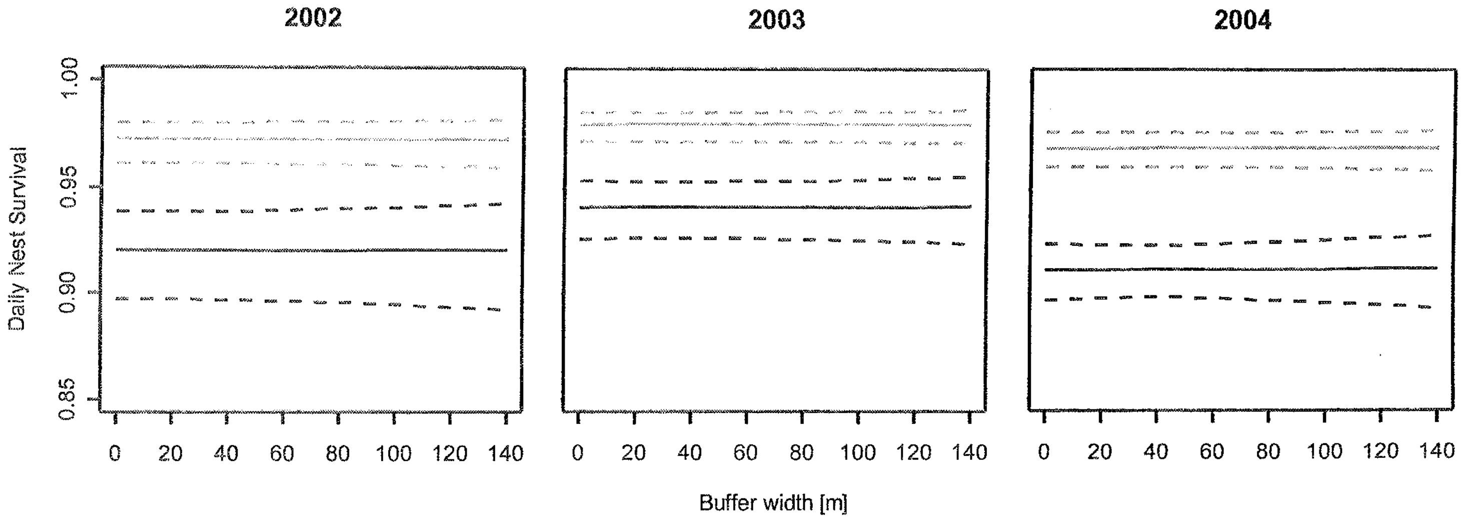

Figure 2. Model-averaged predictions for DNS for different amounts of buffer width (ha) over three years (2002-2004). Gray lines are predictions for the nestling stage and black lines are the predictions for the egg stage. Dashed lines represent 95% confidence intervals

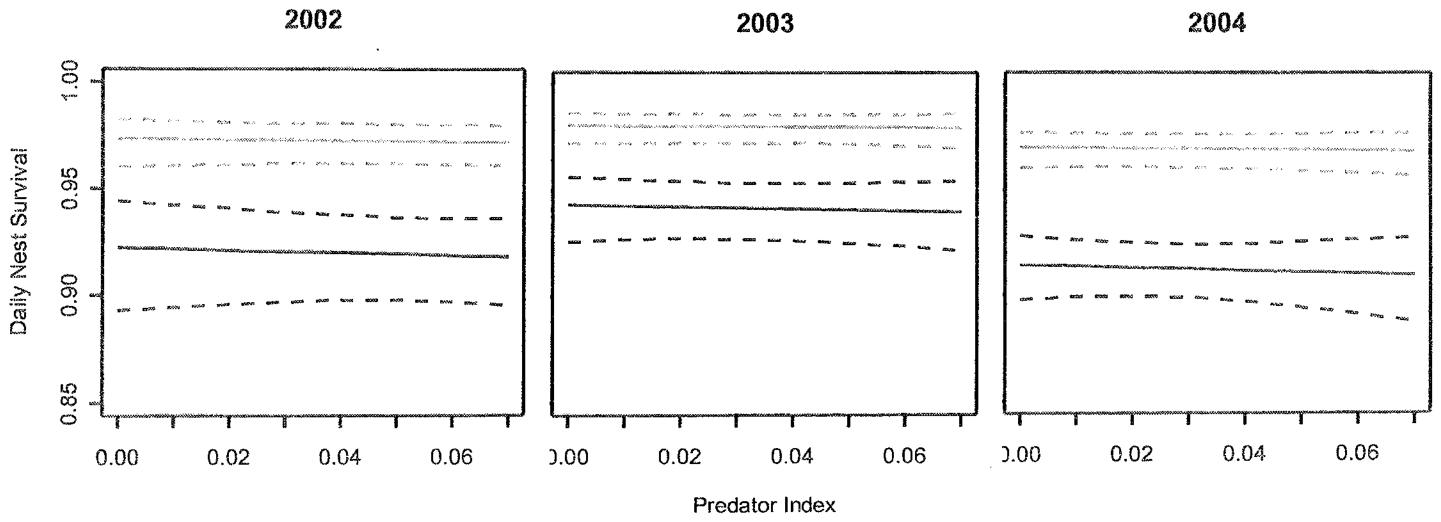

Figure 3. Model-averaged predictions for DNS for different amounts of predator abundance over three years (2002-2004). Gray lines are predictions for the nestling stage and black lines are the predictions for the egg stage. Dashed lines represent 95% confidence intervals.

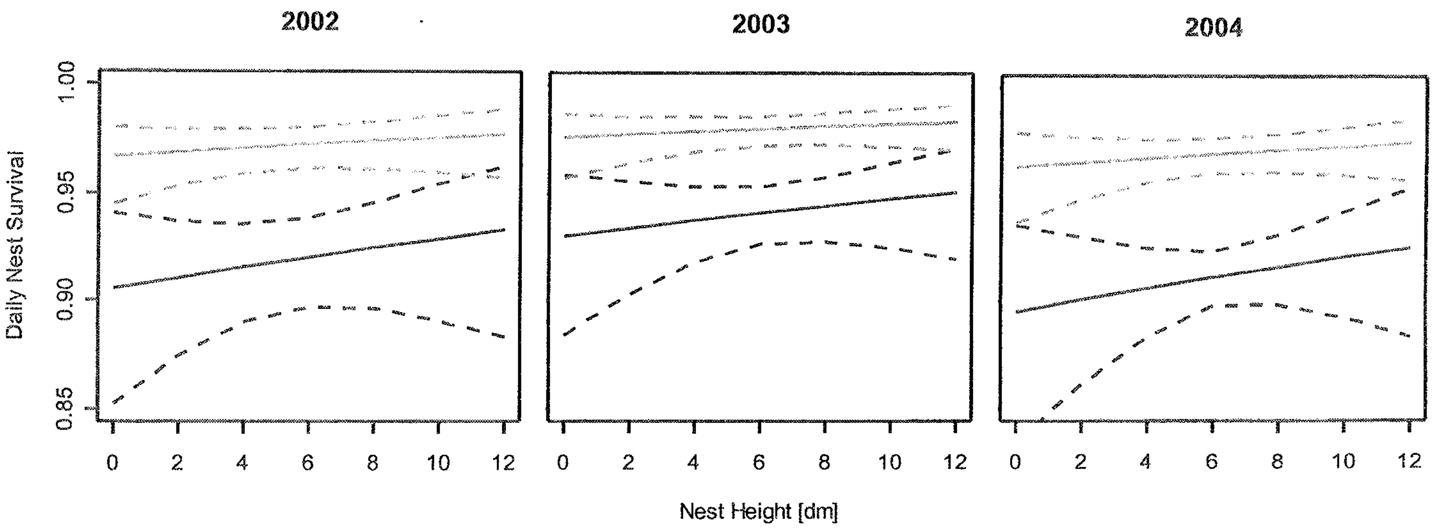

Figure 4. Model-averaged predictions for DNS for different nest heights (dm) over three years (2002-2004). Gray lines are predictions for the nestling stage and black lines are the predictions for the egg stage. Dashed lines represent 95% confidence intervals.

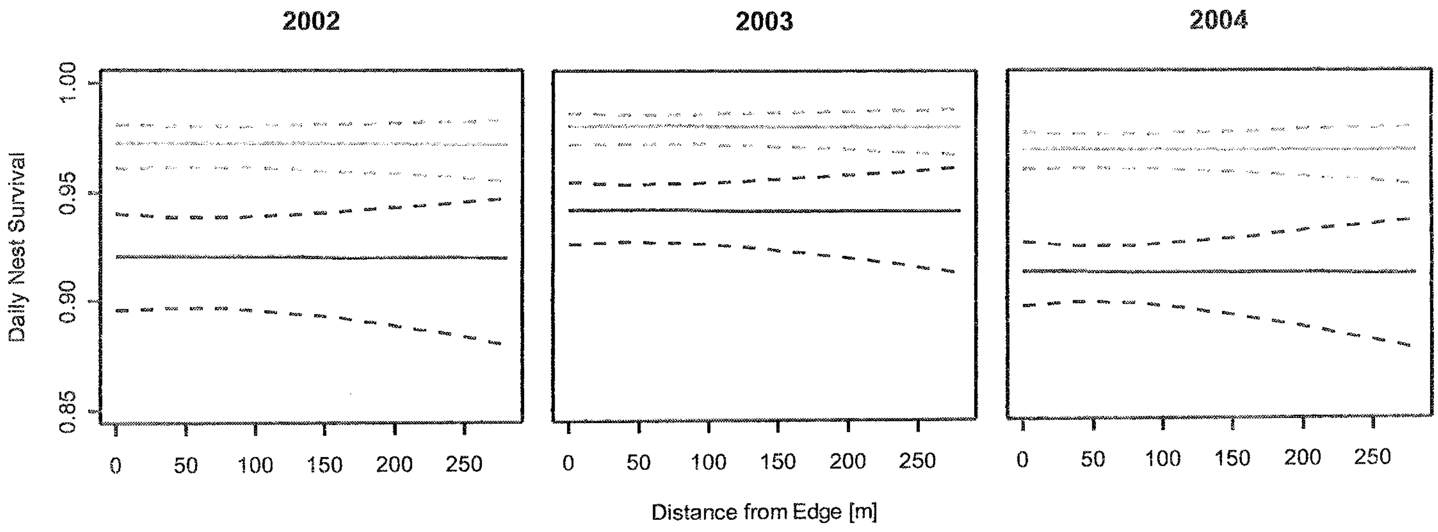

Figure 5. Model-averaged predictions for DNS for nests at different distances from a wetlands edge (m) over three years (2002-2004). Gray lines are predictions for the nestling stage and black lines are the predictions for the egg stage. Dashed lines represent 95% confidence intervals.

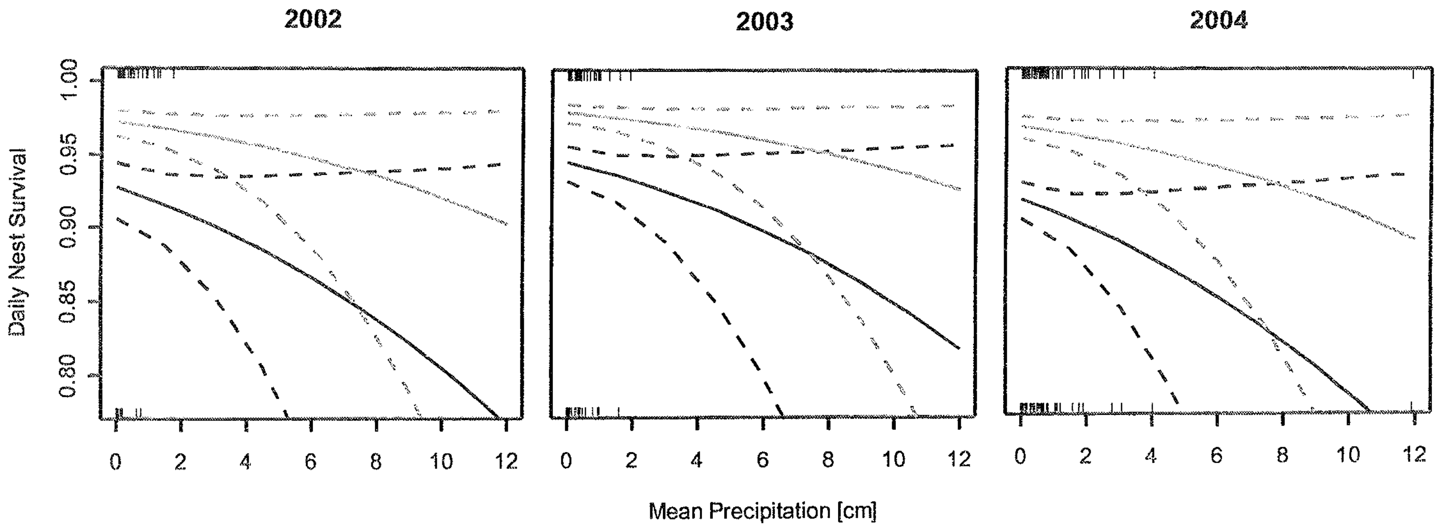

Figure 6. Model-averaged predictions for DNS at different amounts of mean interval rainfall (cm) over three years (2002-2004). Gray lines are predictions for the nestling stage and black lines are the predictions for the egg stage. A rug plot was also included to show the distribution of data points for successful (top) and unsuccessful (bottom) intervals. Dashed lines represent 95% confidence intervals.

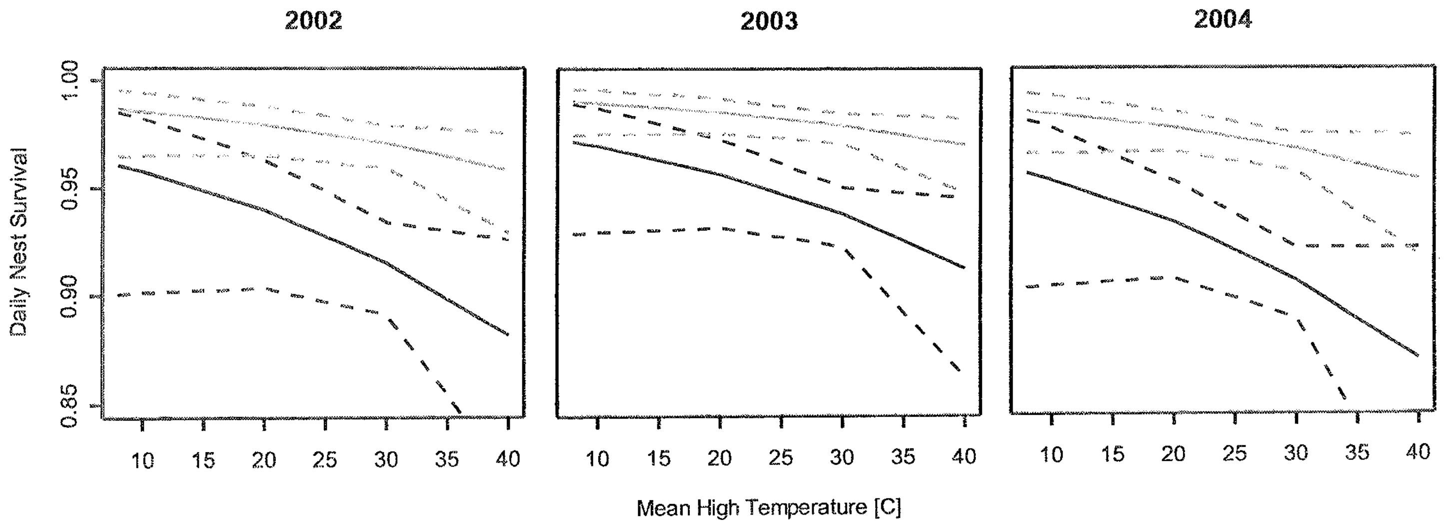

Figure 7. Model-averaged predictions for DNS at various levels mean interval high temperature (C) over three years (2002-2004). Gray lines are predictions for the nestling stage and black lines are the predictions for the egg stage. Dashed lines represent 95% confidence intervals.

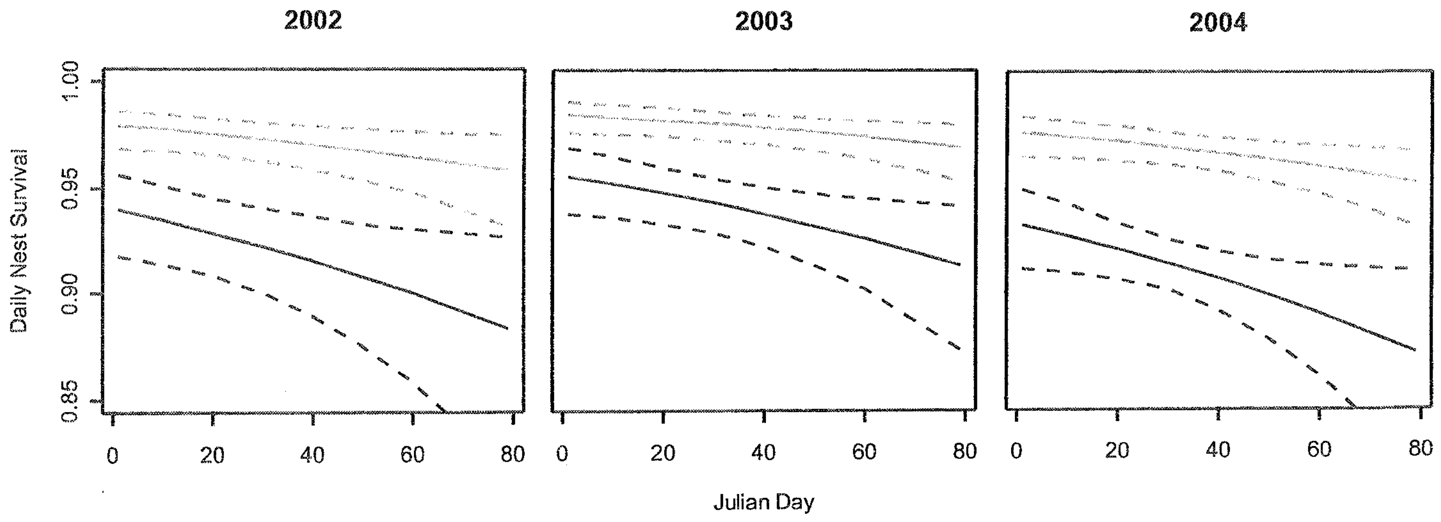

Figure 8. Model-averaged predictions for DNS during the breeding season over three years (2002-2004). Gray lines are predictions for the nestling stage and black lines are the predictions for the egg stage. Dashed lines represent 95% confidence intervals.

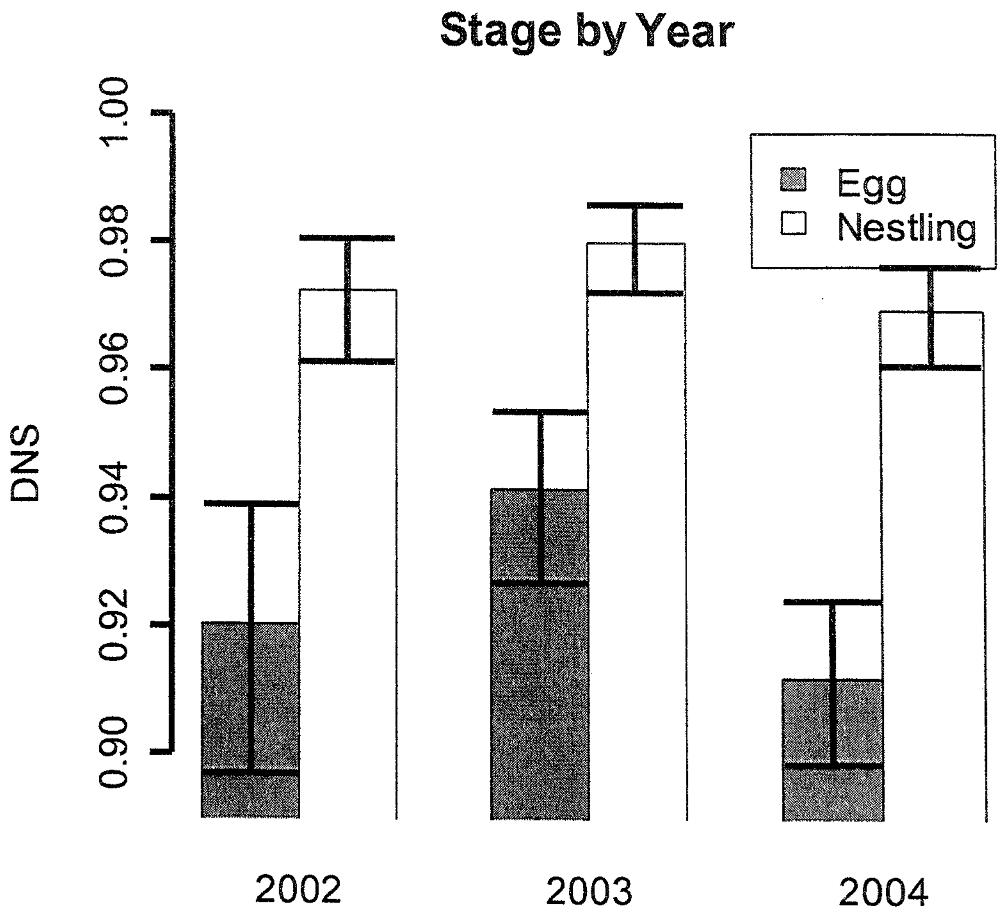

Figure 9. Daily nest survival (DNS) estimates during 2002-2004 by stage. Egg stage (black bars), nestling stage (gray bars). Error bars represent 95% confidence intervals.

CHAPTER 2. Factors that determine the daily probability of avoiding brown-headed cowbird (*Molothrus ater*) parasitism by red-winged blackbirds (*Agelaius phoeniceus*) in the Rainwater Basin region of central Nebraska.

Abstract: My study focused on the assessment of brown-headed cowbird (*Molothrus ater*) parasitism of red-winged blackbird (*Agelaius phoeniceus*) nests in a subset of Rainwater Basin wetlands in south-central Nebraska. I compared the daily nest survival probability and host clutch size of parasitized and unparasitized nests to examine the effects of cowbirds on red-winged blackbird reproductive success. I also used an information-theoretic approach to compare hypotheses about the role of nest-site characteristics, host abundance and density, and time on explaining variation in the daily probability of avoiding parasitism (PAP). Of 591 nests analyzed, I estimated that 51% were parasitized and that pooled PAP was 0.953 (0.946-0.960). The best model in my comparison was the global model, which suggested that all covariates played some role in accounting for variation in PAP. Model-averaged predictions showed that nest height had a weak positive effect on PAP, distance to edge had no impact, whereas abundance had a strong positive influence and density had a negative influence. Year also accounted for some of the variation. Overall my results suggest that habitats that can sustain large numbers of simultaneously active nests should help in reducing parasitism rates, and that parasitism could be influenced by the presence of alternative hosts. However, more research is needed concerning that host community in the Rainwater Basin and the population fluctuations of cowbirds themselves.

INTRODUCTION

The brown-headed cowbird (*Molothrus ater*) is a well-known species of brood parasite that is historically common in the Great Plains of the United States (Johnsgard 1997). Despite their ubiquity, cowbirds are a subject of concern for wildlife managers and conservation biologists because of their potential impact on host demography. Parasitized nests often fail completely (i.e. lose both host and parasite eggs) or produce fewer host offspring (Ortega and Cruz 1991, Johnson and van Riper 2004).

Red-winged blackbirds (*Agelaius phoeniceus*; RWBL) are one of the most abundant cowbird hosts in North America and are considered parasite egg “acceptors” (Ortega and Cruz 1988). This may make parasitism in RWBL a point of concern because abundant hosts may increase brood parasitism rates for more sensitive species (Barber and Martin 1997). For example, high RWBL abundance could be responsible for an increase in cowbird parasitism of yellow warbler nests (Weatherhead 1989).

However, a particular host may not act as a reservoir for cowbirds if parasitized host nests experience higher rates of failure. The predation facilitation hypothesis suggests that the act of parasitism could provide a cue for searching predators, thereby lowering host nest success (Arcese et al. 1996, Payne and Payne 1998). Since cowbird eggs are deposited during the laying or incubation stage of the host nest, one would expect markedly lower nest survival during the early stages of a parasitized nest. However, the apparent acceptance behavior of RWBL may be considered an attempt to lower the chance of nest failure following parasitism (Beletsky 1996). Rejection may be costly for RWBL because the act of trying to remove the parasite egg could damage host eggs (Ortega and Cruz 1988). This suggests that the true impact of parasitism should be seen in the reduction of host reproductive output (e.g. smaller host clutch size or lower fecundity) rather than outright failure of the nest (Ortega and Cruz 1988; Beletsky 1996).

With that in mind, there are a variety of factors that could increase the risk of a bird's nest being parasitized by a cowbird. Among them, nest-site characteristics such as nest height or distance from the edge of a habitat may increase parasitism. Some evidence suggests that nests further off the ground experience greater parasitism risk in grassland habitats (Martin 1993). The risk of parasitism for RWBL nests in prairie nesting populations does not seem to be affected by nest height, however (Clotfelter 1998). How generalized this pattern is for marsh-nesting RWBL is unknown.

The location of a nest relative to a habitat edge is also thought to contribute to increased predation and parasitism risk (Paton 1994). Some evidence from grassland systems suggests that increasing distance from shrublands lowers parasitism rate (Winter et al. 2000). Similarly, nests further from woodland-grassland edges also experience lower rates of parasitism (Jensen and Finck 2004).

Similar data suggests that RWBL nests are more likely to be parasitized around the perimeter of wooded marshes (Friedmann 1963). Nests further from wooded edges should be more difficult to locate for searching cowbirds. But even if host nests are easier to locate, species that have a long history of coping with nest parasitism could reduce negative impacts by nesting colonially (Picman et al. 1988). In prairie nesting RWBL, individual parasitized nests tended to be further from simultaneously active nests (Clotfelter and Yasukawa 1999b). But for marsh nesting RWBL, aggregated nests have lower parasitism rates because cowbirds are more likely to be molested by vigilant adult hosts (Straussberger 2001).

Aside from spatial factors, temporal covariates might also help to explain changes in parasitism risk. For example, parasitism could fluctuate from year to year with changes in parasite abundance (Clotfelter and Yasukawa 1999a), or changes in the number of host nests over the course of the breeding season. Clotfelter and Yasukawa (1999b) found that parasitism rate tracks with the number of initiated nests and the highest proportion of parasitized nests occurred during the height of the reproductive season (Clotfelter and Yasukawa 1999b; Ortega and Cruz 1991).

As of yet, I am aware of no other data concerning songbird nest parasitism in the Rainwater Basin Region of Central Nebraska, a breeding site for migratory songbirds (see Appendix I). My study provides much needed preliminary information about nest parasitism dynamics in the region and compares hypotheses about the influence of cowbird parasitism on reproductive success and the factors that influence how likely a nest is to avoid being parasitized.

First, since cowbirds are thought to increase nest predation via increased activity at the nest, I decided to test whether daily nest survival was higher for unparasitized nests compared with parasitized nests. I also sought to test whether survival varied according to the stage of unparasitized and parasitized nests. These estimates were then used to compare host clutch sizes and fecundity between parasitized and unparasitized nests.

Second, because hosts presumably try to avoid parasitism I sought to compare hypotheses about how factors such as nest placement, host nest abundance and density, or time affected the daily probability of avoiding parasitism (PAP). I built *a priori* models and used an information-theoretic approach to rank my candidate models. I expected that host nest abundance and density would account for most of the variation in PAP, and that covariates of nest height and distance would account for less variation. I also expected that PAP would increase over the course of the nesting season as fewer host nests become available.

METHODS

Study Area

My study was conducted in the Rainwater Basin region of central Nebraska. A site description can be found in the methods section of Chapter 1. My nest sampling strategy and protocol for nest-site measurements can also be found in Chapter 1.

Host abundance and density- I determined the host abundance for each wetland as the absolute number of monitored RWBL nests that were active at the same time. Density was calculated as host abundance divided by the total area searched on each wetland. These values were calculated independently for each nest monitoring interval.

Clutch Size and Fecundity- I calculated the maximum host clutch size as the largest number of host eggs observed during a monitoring interval to determine whether parasitized nests had smaller clutches. To determine whether cowbirds selected nests with smaller clutches or removed eggs I also compared clutch size in the interval prior to the parasitism event to clutch size in the interval following parasitism.

I used the PopTools extension for Microsoft Excel to estimate fecundity using the pooled 23-day nest success estimate from Chapter 1 and mean clutch size (+/- 1 SD). Using methods similar to those in Donovan et al (1995), I estimated fecundity as the product of nest success rate multiplied by a randomly chosen clutch size for 10,000 trials. Since red-winged blackbirds are capable of renesting after a failure I assumed that the proportion of renesting females was 1.0, minus the nest success rate, and that the range of clutch sizes stayed the same for each renesting attempt. Thus fecundity was the sum of first and second nesting attempts.

Statistical Analyses- I used the statistical program R (version 2.0.1) to compare host and parasite clutch size, using a two-tailed t-test. I estimated daily nest survival using the same program, but with the logistic exposure method outlined in Shaffer (2004). I used the GLM (generalized linear model) package with a binomial distribution (0 = failure, 1 = successful) and a modified logit link function: $g(\theta) = \text{Log}_e\, (\theta^{1/t}/[1 - \theta^{1/t}])$, where θ is the interval survival rate and t is the nest observation interval length in days (Shaffer 2004). This model uses the nest monitoring interval as the sampling unit, and thus does not require an assumption about the timing of nest losses. In addition, the age of the nest need not be known. This method also assumes that the survival rate values for each covariate is constant within a nest observation interval. I compared models using covariates of parasitism status (1=parasitized, 0=not parasitized), year and stage of the nest (egg or nestling).

To estimate the daily probability of avoiding parasitism (PAP) I used the same logistic exposure method, except I considered parasitism instead of survival (1 = avoidance, 0 = parasitized). For the analysis I only considered intervals up to the point when the nest became parasitized. In essence this treated a parasitized nest as a failed nest (T. Shaffer, USGS, *personal communication*).

I compared models with covariates relating to the placement of a nest, host availability and time. My first model included nest height (NH) and distance from edge (DIST) as covariates. I also composed a model to look at the impact of simultaneously active host nests by using the number (AB) and density (DEN) of RWBL nests that were active during an interval. My temporal model included a year effect (YR) and an effect of day in the nesting season (DAY). For the parameter DAY, I used the midpoint of the observation interval to assign a day in the breeding season. I also constructed three models that were additive pairwise combinations of each of the above models, plus a global model (GLOBAL) and a constant probability model (CONSTANT). All told, I compared a total of 8 models.

I used an information-theoretic approach to rank my candidate models using Akaike's Information Criterion (AIC, Burnham and Anderson 2002). I determined the best models by calculating the difference (ΔAIC) between the AIC value with the lowest score and all other models. Lower values of ΔAIC indicate better fitting models (Burnham and Anderson 2002). I also used Akaike weights (AIC_w) to determine the best set of models and to contend with modeling uncertainty.

I then made predictions by holding all the parameters at their average values and allowing one parameter to vary at a time. I then model averaged these predictions over all the models according to Burnham and Anderson (2002). I calculated model-averaged regression coefficients using the same methods.

RESULTS

Over the three years of this study I monitored 591 red-winged blackbird nests. Nesting began in late and May in all years and reached its peak by early to mid- June. The greatest number of parasitism events also occurred during this peak nesting period. The observed percentage of parasitized nests over all three years was 0.32 (+/-0.19 SE). This percentage ranged from as high as 0.50 (+/-0.05, SE) in 2002 to as low as 0.23 (+/-0.03, SE; Figure 1) in 2003.

The daily probability of a nest avoiding parasitism (PAP) over the three years was 0.953 (95% CI: 0.946, 0.960). If this probability is exponentiated by an assumed 14-day laying and incubation period it suggests that 0.49 of my sample nests were not parasitized, and approximately 51% of my sample nests were parasitized.

Parasitism had little impact on overall daily nest survival [Parasitized: 0.945 (95% CI: 0.938-0.951); Unparasitized: 0.939 (95% CI: 0.928-0.949)] (Figure 2) or on daily survival during different stages [Parasitized egg: 0.927 (95% CI: 0.918-0.936); Unparasitized egg: 0.923 (95% CI: 0.908-0.935); Parasitized nestling: 0.969 (95% CI: 0.963-0.976); Unparasitized nestling: 0.968 (95% CI: 0.958-0.975)] (Figure 3). There was a significant difference between the average maximum host clutch size for parasitized nests (mean=2.07, SD=1.31) and unparasitized nests (mean=3.16, SD=1.07; t= -9.69, df=276, p<.001). But there was an insignificant difference between clutch sizes in the interval immediately before the parasitized interval (mean=2.00, SD=1.22) compared with host clutch size after parasitism (mean=2.12, SD=1.16; t = -0.4997, df = 98, p=0.62). My fecundity model predicted that females with parasitized nests produced 0.87 (95% CI: 0.24-1.51) fledglings per year, whereas females with unparasitized nests produced 1.27 (95% CI: 0.72-1.80) fledglings per year.

The logistic exposure model that explained the most variation in PAP was the global model (AIC = 1127.34, $k = 8$). The simpler model containing the additive main effects of host nest abundance, nest density and temporal effects explained less variation (AIC = 1122.95, $k = 6$). All the other models did very little to explain variation in PAP (Table 1). A list of model averaged regression coefficients can be found in Table 2.

A summary of the values that were calculated from field data, and used to make model-averaged predictions, can be found in Table 2. Model averaged predictions show a very weak positive trend for PAP with increasing nest height ($\beta = 0.05881$, SE = 0.06481; Figure 4). Distance from wetland edge did not have any effect on PAP ($\beta =$ .00148, SE = 0.00233; Figure 5). There was a stronger positive trend in PAP for the number of simultaneously active host nests ($\beta = 0.10011$, SE = 0.01594; Figure 6). This trend was reversed for host density ($\beta = -0.26313$, SE = 0.06305), with PAP being lower for nests in more densely occupied wetlands (Figure 7). A rug plot shows that outliers in 2002 are probably responsible for the strong decline in PAP at higher density values for model predictions. However, even at lower values for density there appears to be a weak negative effect of host nest density on PAP. Scatter plots of interval nest density against interval nest abundance show a generally positive relationship (Figure 8). However, the intervals with higher density values appear to have lower abundance values. A similar plot of interval host nest density by area shows that smaller wetlands generally have higher relative densities (Figure 8).

My models also predicted a positive trend in PAP for day in the nesting season ($\beta = 0.04154$, SE = 0.00689; Figure 9). Year seems to account for some variation with risk being higher in 2002 than in 2003 or 2004, which were very similar (Figure 10). However, because the confidence intervals overlap, the pooled PAP estimate is probably a more representative estimate.

DISCUSSION

Over the three years of this study, 32% of the nests I monitored were parasitized. However, the estimated parasitism rate was quite a bit higher at 51%. This suggests that I may have missed parasitized nests because they may have failed before I found them (T. Shaffer, USGS, *personal communication*). The overall parasitism rate I estimated is about consistent with reported rates (30.2% to 41.3%) for prairie nesting RWBL (Weatherhead 1989). For marsh nesting RWBL, others have found overall rates as low as 7-13% for Colorado (Ortega and Cruz 1991) or as high as 54.2 % for Nebraska (Hergenrader 1962). Reports from other portions of the RWBL's range suggest that there is a great deal of geographic variation in parasitism rates (Freeman et al. 1990, Beletsky 1996).

Despite the high rate of parasitism in the Rainwater Basin, I found that parasitized nests do not have a higher risk of failing compared with unparasitized nests. I also found no effect of parasitism on stage survival, which suggests that female cowbird behavior may not facilitate predation (Arcese et al. 1996). This is not surprising considering that other studies have found that brood parasitism has little impact on nest success, but probably has a greater impact on host clutch size (Beletsky 1996). For example, Weatherhead (1989) found no difference in nest success between parasitized and unparasitized nests, but found that parasitized nests had an average of 1 less host egg than unparasitized nests. My results were similar, and could be the result of cowbirds selecting nests with smaller clutch sizes or limiting host clutch size by depositing eggs early in the host laying period.

Lower clutch size may not reflect the laying and removal of eggs between observation intervals; in fact, it is possible that parasites might select nests with smaller clutches to begin with. Thus, the lower, but not statistically significant, host fecundity in parasitized nests might reflect this initially lower clutch size or the effect of cowbird nestlings which might compete with host nestlings. Regardless, females with parasitized nests tend to have lower fecundity than those without parasitism effects.

In my attempts to explain variation in the probability of avoiding parasitism, I found that nests built higher above the ground have a lower daily risk of being parasitized. This is unusual considering that the expectation would be lower PAP values for taller nests (Martin 1993). The explanation for this pattern might be that higher nests afford the host female with a better view of searching cowbirds, and more opportunity to defend the nest. This trend is so weak, though, that it is difficult to determine how significant nest height is to parasitism avoidance.

Other work has found that the proportion of parasitized nests declines with increasing distance from trees and possible perch sites (Freeman et al. 1990). Since many of the trees in my study wetlands are around the edge, I expected that distance might explain some of the variation in parasitism risk. The distance of a nest from the wetland's edge does very little to explain variation in PAP, which suggests that all nests, regardless of distance from the edge have similar parasitism risk.

However, Strausberger (2001) suggested that nests in marshes are not necessarily difficult for cowbirds to find and that behavioral responses, such as colonial nesting, may be more important in reducing parasitism risk. Clotfelter and Yasukawa (1999a) found more parasitized nests when a larger number of nests were simultaneously active, which they attributed to high rates of parasitism during the peak nesting season. However, they also found that parasitized nests tended to be further from other active nests, suggesting that aggregated nesting might be advantageous in reducing parasitism. My analysis shows that parasitism probability declines with a greater number of simultaneously active nests. This might be because there are more individuals to aggressively deter searching cowbirds (Straussberger 2001).

One might then expect that more dense aggregations of simultaneously active nests would show a similar pattern. Others have found that more active nests and more densely occupied nesting territories have lower parasitism rates (Straussberger 2001, Freeman et al. 1991). This is not the case for my data. Instead, one sees a marked decrease in parasitism avoidance at higher densities. A scatter plot of abundance and density of simultaneously active nests shows that, although there is a positive relationship between abundance and density, the relationship is strongest for lower risk density numbers. The high density areas in my study were outliers associated with small wetlands (Fig. 8), which also had a higher risk of being parasitized (Fig. 7). Nests in smaller wetlands might be at a higher risk because the wetland actually contains smaller numbers of host nests, even though they may have relatively high nest densities throughout the breeding season. But this still does not explain why PAP generally tends to decrease with increasing density.

There has also been some suggestion that host or parasite abundance could help to account for annual variation in parasitism rates (Beletsky 1996). From my analysis, year seems to be an important factor explaining parasitism rates. My results suggest that parasitism was higher in 2002 compared to 2003 or 2004. This pattern might be the result of changes in cowbird abundance, for which I have no data. However, because I changed the sampling design in 2003, I cannot rule out the possibility that this pattern is simply reflective of a difference in sampling design. It is also possible that this pattern is driven by changes in alternate host abundance (i.e. hosts other than RWBL; Barber and Martin 1997).

In terms of changes in PAP over the course of the nesting season, my results show an increase as the season progresses. This finding is consistent with other studies that found parasitism tended to decline along with the relative number of active RWBL nests (Ortega and Cruz 1991; Clotfelter and Yasukawa 1999a). For my study, it is also interesting to note that daily nest survival decreases over the nesting season (Chapter 1, Fig. 8), which might suggest that cowbirds avoid parasitizing nests that have high probability of failing.

SUMMARY

Parasitism seems to have little impact on red-winged blackbird nest success and annual parasitism rates seem to vary. However, parasitized nests also appear to produce fewer offspring than unparasitized nests. Variation in the daily probability of a nest being parasitized seems to be best explained by fluctuations in host abundance and density, with lower numbers of simultaneously active nests having a higher risk. Similarly, it appears that smaller habitats with higher densities, but relatively fewer nests are also at higher risk. Avoidance may also increase toward the end of the nesting season as failure rates for host nests increase. Another potential explanation may be that cowbirds shift their focus to more preferred hosts toward the end of the season. Therefore, future research in this region should focus on understanding more about the overall host community and population fluctuations in cowbirds, themselves. From a management angle, my results suggest that the removal of woody perches around wetlands may have little impact on parasitism rates in RWBL. However, more detailed data is needed on whether distance from perches influences parasitism probability. My results also suggest that maintenance of large wetlands that can handle large numbers of nesting red-winged blackbirds might help to reduce parasitism rates, and may thus help to reduce local cowbird populations.

LITERATURE CITED

Arcese, P., J. N. M. Smith and M. I. Hatch (1996). Nest predation by cowbirds and its consequences for passerine demography. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 4608-4611.

Barber, D. R. and T. E. Martin (1997). Influence of alternate host densities on brown-headed cowbird parasitism rates in black-capped vireos. *Condor* **99**: 595-604.

Beletsky, L. D. (1996). The Red-winged Blackbird: the biology of a strongly polygynous songbird. San Diego, CA, Academic Press.

Burnham, K. P. and D. R. Anderson (2002). Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. New York, Springer-Verlag.

Clotfelter, E. D. (1998). What cues do brown-headed cowbirds sue to locate red-winged blackbird host nests? *Animal Behaviour* **55**: 1181-1189.

Clotfelter, E. D. and K. Yasukawa (1999a). Impact of brood parasitism by brown-headed cowbirds on red-winged blackbird reproductive success. *Condor* **101**: 105-114.

Clotfelter, E. D. and K. Yasukawa (1999b). The effect of aggregated nesting on Red-winged Blackbird nest success and brood parasitism by Brown-headed Cowbirds. *Condor* **101**(4): 729-736.

Donovan, T. M., F. R. Thompson, J. Faaborg and J. R. Probst (1995). "Reproductive success of migratory birds in habitat sources and sinks." *Conservation Biology* 9(6): 1380-1395.

Freeman, S., D. F. Gori and S. Rohwer (1990). Red-winged blackbirds and brown-headed cowbirds: some aspects of a host-parasite relationship. *Condor* **92**: 336-340.

Friedmann, H. (1963). Host relations of the parasitic cowbirds. *United States National Museum Bulletin* **233**: 1-276.

Gersib, R. A., R. R. Raines, W. S. Rosier and M. C. Gilbert (1989). A functional assessment of selected wetlands within the Rainwater Basin of Nebraska. Lincoln, NE, Nebraska Game and Parks Commission.

Hergenrader, G. L. (1962). The incidence of nest-parasitism by the Brown-headed Cowbird on road-side nesting birds in Nebraska. *Auk* **79**: 85-88.

Jensen, W. E. and E. J. Finck (2004). Edge Effects on Nesting Dickcissels (*Spiza americana*) in Relation to Edge Type of Remnant Tallgrass Prairie in Kansas. *American Midland Naturalist* **151**: 192-199.

Johnsgard, P. A. (1997). The Avian Brood Parasites: Deception a the Nest. New York, Oxford University Press.

Johnson, M. J. and C. van Riper (2004). Brown-headed Cowbird parasitism of the Black-throated Sparrow in central Arizona. *Journal of Field Ornithology* **75**(3): 303-311.

Kocer, C. J. (2004). Mesopredator movement, abundance, and habitat selection in the Rainwater Basins of Nebraska. Graduate College. Lincoln, NE, University of Nebraska- Lincoln: 84.

LaGrange, T. (1997). Guide to Nebraska's wetlands and their conservation needs. Lincoln, NE, Nebraska Game and Parks Commission.

Martin, T. E. (1993). Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* **141**: 897-913.

McMaster, D. G. and S. G. Sealy (1998). Host-egg removal by Brown-headed Cowbirds: a test of the host incubation limit hypothesis. *Auk* **114**: 212-220.

Ortega, C. P. and A. Cruz (1988). Mechanisms of egg acceptance by marsh-dwelling blackbirds. *Condor* **90**: 349-358.

Ortega, C. P. and A. Cruz (1991). A comparative study of cowbird parasitism in yellow-headed blackbirds and red-winged blackbirds. *Auk* **108**: 16-24.

Paton, P. W. C. (1994). The Effect of Edge on Avian Nest Success - How Strong Is the Evidence. *Conservation Biology* **8**(1): 17-26.

Payne, R. B. and L. L. Payne (1998). Brood parasitism by cowbirds: risks and effects on reproductive success and survival in Indigo Buntings. *Behavioral Ecology* **9**: 64-73.

Picman, J., M. Leonard and A. Horn (1988). Anti-predation role of clumped nesting by marsh-nesting Red-winged Blackbirds. *Behavioral Ecology and Sociobiology* **22**: 9-15.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. *Auk* **121**(2): 526-540.

Straussberger, B. M. (2001). The relationship of habitat and spatial distribution of nests with brown-headed cowbird parasitism of red-winged blackbirds. *Wilson Bulletin* **113**(2): 129-133.

Weatherhead, P. J. (1989). Sex ratios, host-specific reproductive success, and impact of brown-headed cowbirds. *Auk* **106**: 358-366.

Winter, M., D. H. Johnson and J. Faaborg (2000). Evidence for edge effects on multiple levels in tallgrass prairie. *Condor* **102**: 256-266.

Table 1. ***A priori*** **candidate models explaining daily probability of parasitism for 591 red-winged blackbird nests in the Rainwater Basin of Nebraska for 2002-2004. The number of parameters (*k*) includes an intercept and all the covariates in each model. Models with lower ΔAIC values and larger Akaike weights (w_i) have more support. Values for the best models are in bold. Model parameters are described in the text.**

Model	k	AIC	ΔAIC	w_i
GLOBAL	**8**	**1122.34**	**0.00**	**0.58**
AB+DEN+YR+DAY	**6**	**1122.95**	**0.60**	**0.42**
HT+DIST+YEAR+DAY	6	1158.00	35.65	0.00
HT+DIST+AB+DEN	5	1160.51	38.17	0.00
YR+DAY	4	1166.32	43.98	0.00
AB+DEN	3	1174.48	52.14	0.00
HT+DIST	3	1192.17	69.82	0.00
CONSTANT	1	1212.40	90.06	0.00

Table 2. Model averaged intercepts and regression coefficients (β) (+/- 1 SE), as well as the average values (+/- 1SD) calculated from field data and used for each quantitative model variable.

Parameter	β	SE	Mean(sd)	Range
Intercept	1.38222	0.42576	-	-
Nest Height (HT)	0.05881	0.06481	6.16 (1.83)	2.00-13.00
Distance from edge (DIST)	0.00148	0.00233	56.61 (36.00)	0-278.70
Host Abundance (AB)	0.10011	0.01594	10.68 (7.66)	1.00-34.00
Host Density (DEN)	-0.26313	0.06305	1.93 (1.72)	0.04-12.78
Year: 2003	-0.42410	0.29448	-	-
Year: 2004	-0.51370	0.26280	-	-
Day	0.04154	0.00689	-	-

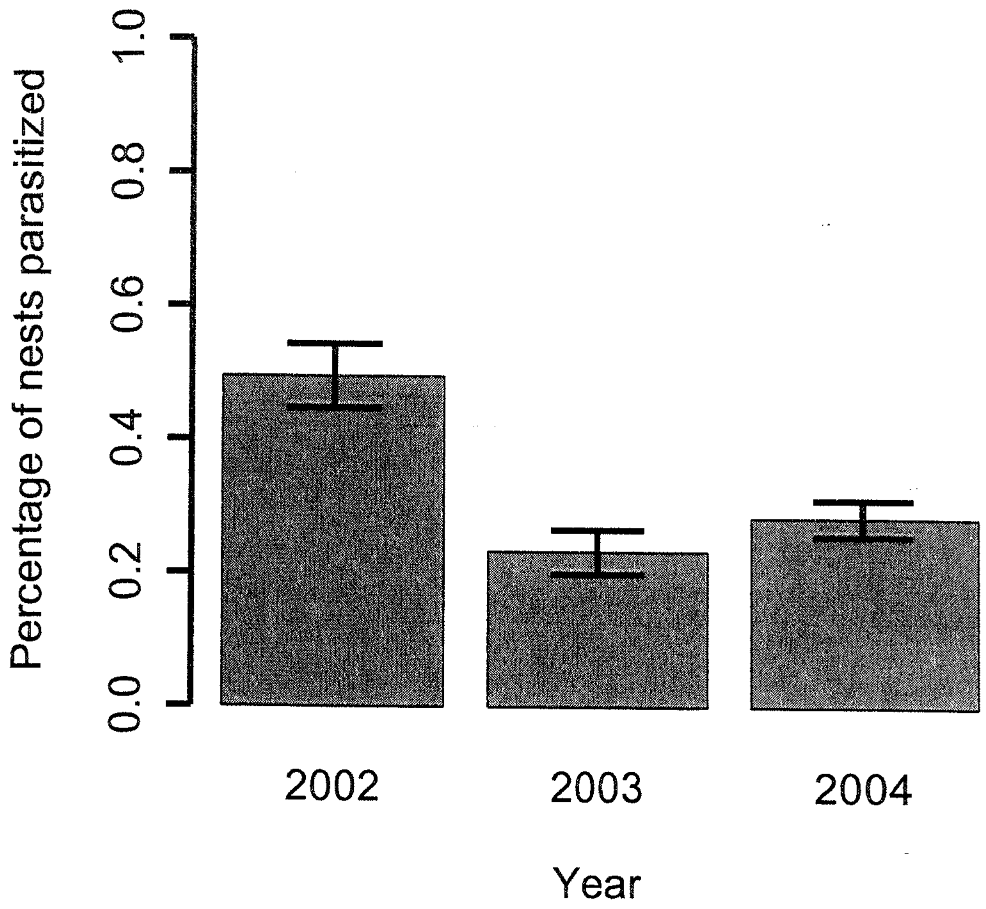

Figure 1. **The observed percentage of nests parasitized during the three years of my study. Error bars represent 1 SE.**

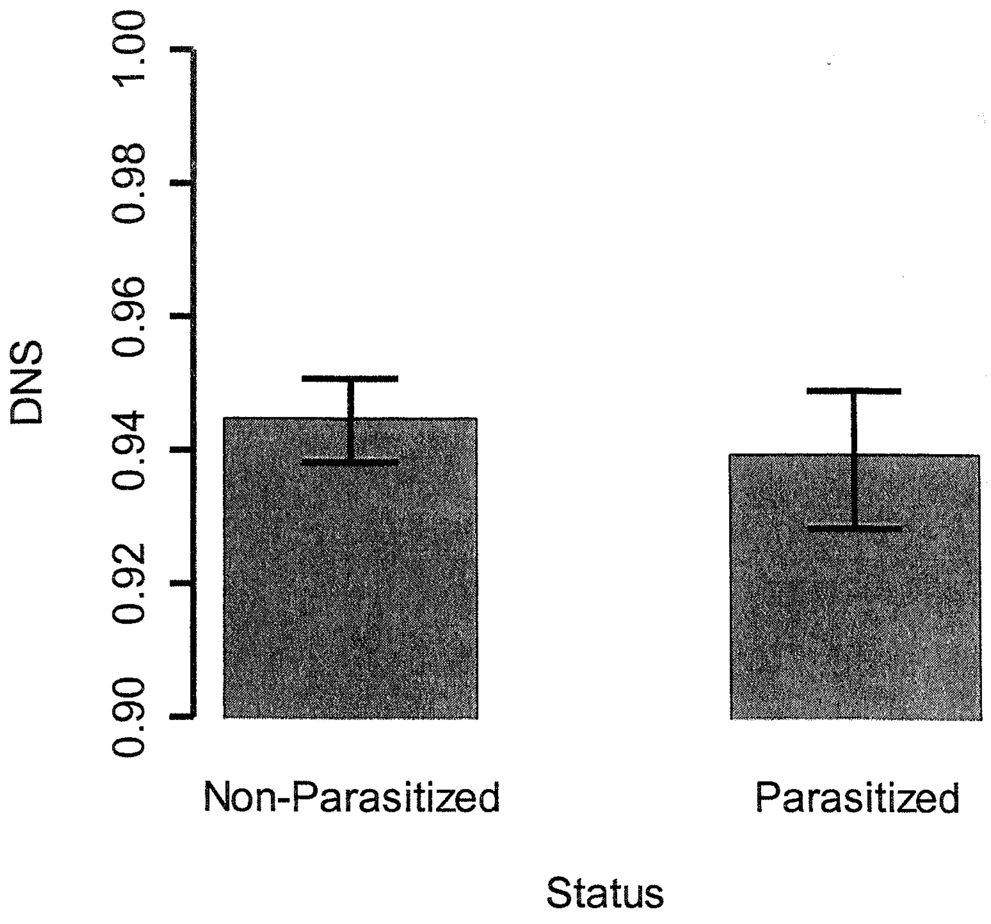

Figure 2. Daily nest survival (DNS) for all years combined according to whether the nest was parasitized or unparasitized. Error bars represent 95% CI.

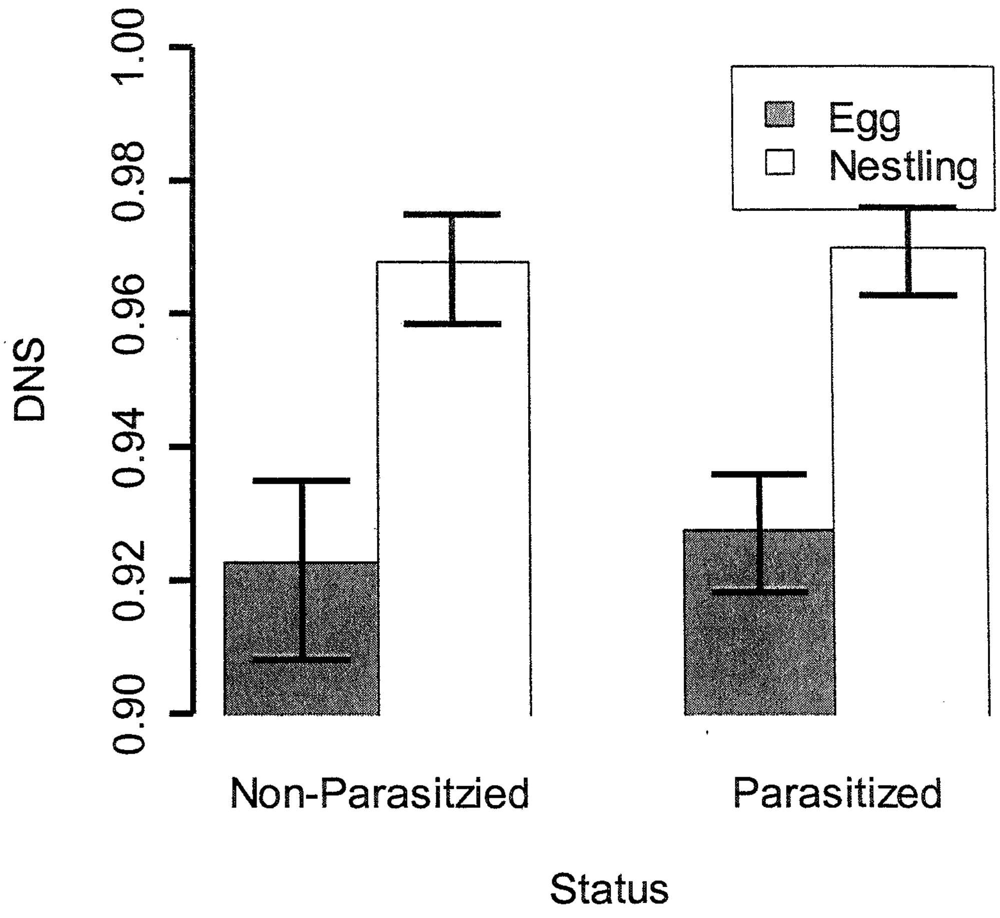

Figure 3. Daily nest survival (DNS) by stage over all three years (2002-2004) according to whether the nest was parasitized or unparasitized. Error bars represent 95% CI.

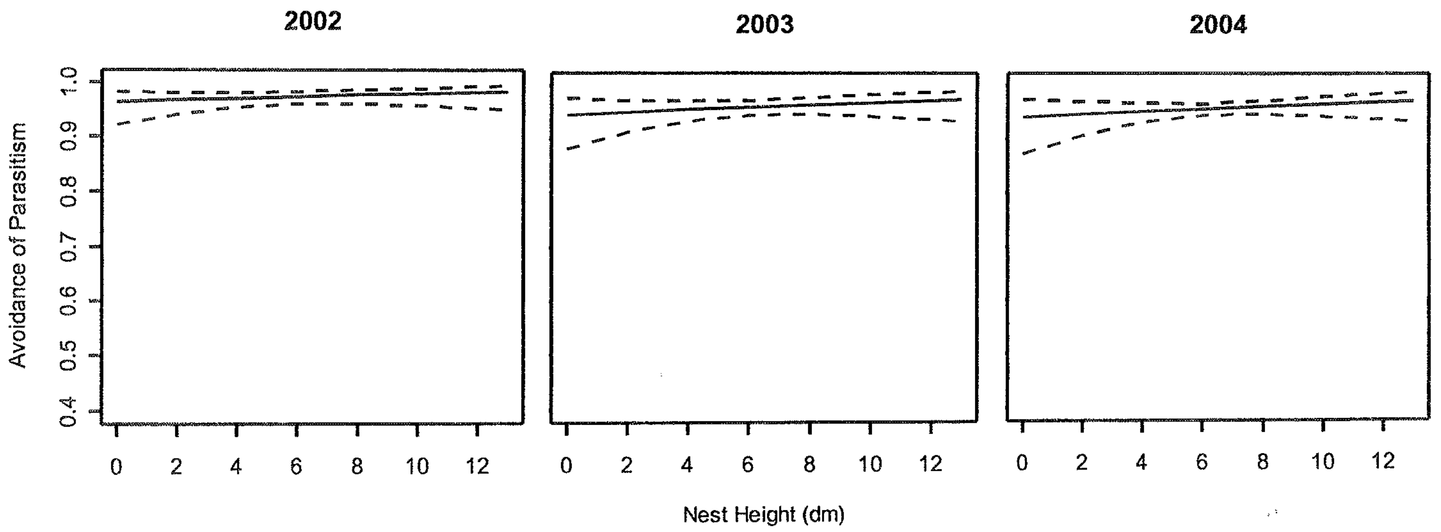

Figure 4. Model-averaged prediction for daily probability of parasitism avoidance at different levels of nest height (dm) for three years (2002-2004). Dashed lines represent 95% CI

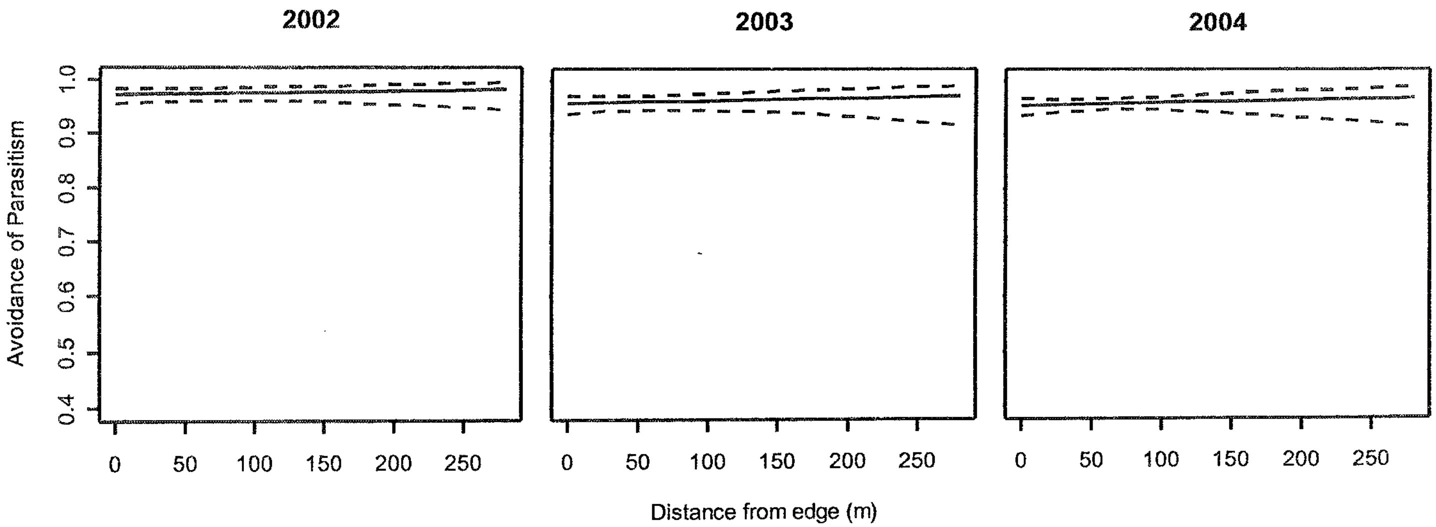

Figure 5. Model-averaged prediction for daily probability of parasitism avoidance at different levels of distance of the nest from wetland edge (m). Dashed lines represent 95% CI.

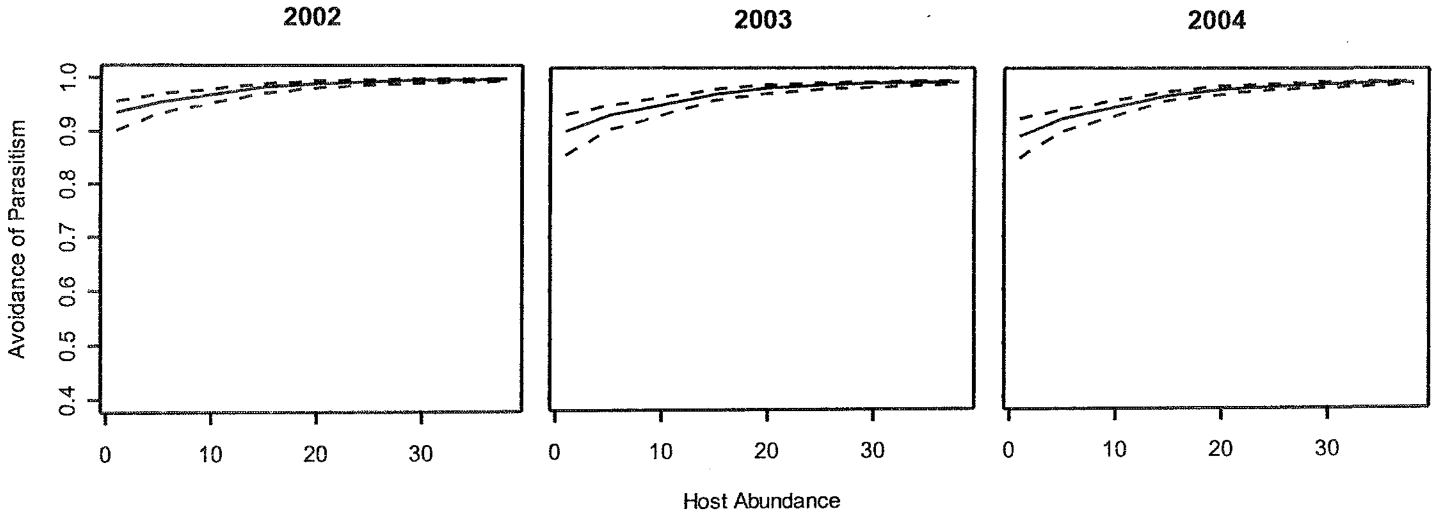

Figure 6. Model-averaged prediction for probability of parasitism avoidance at different levels of abundance of simultaneously active host nests. Dashed lines represent 95% CI

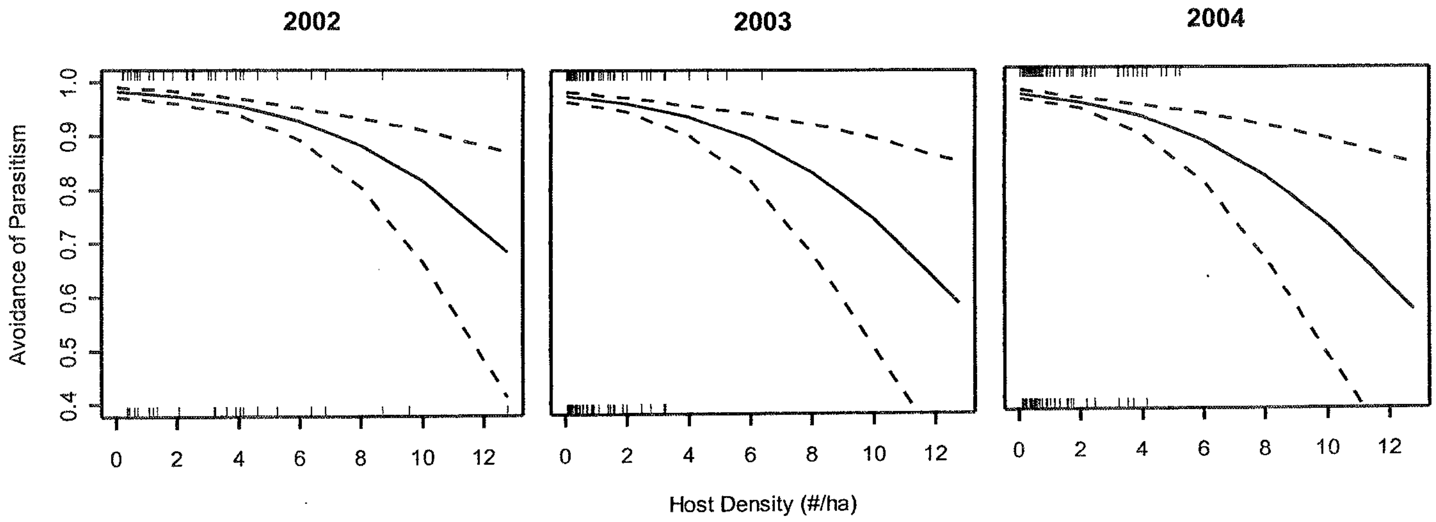

Figure 7. Model-averaged prediction for daily probability of parasitism avoidance at different levels of density of simultaneously active nests (#/ha). A rug plot was also included to show the distribution of data points for unparasitized (top) and parasitized (bottom) intervals. Dashed lines represent 95% CI

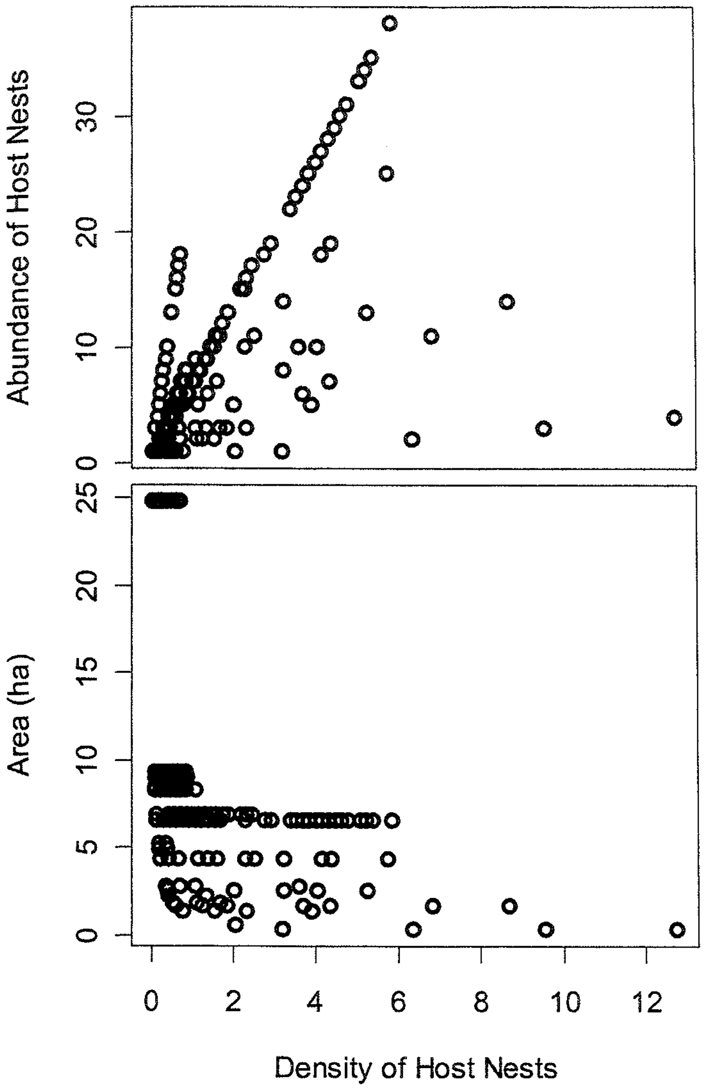

Figure 8. Scatter plots of the density of host nests (#/ha) plotted against abundance (top) and against the area searched (bottom).

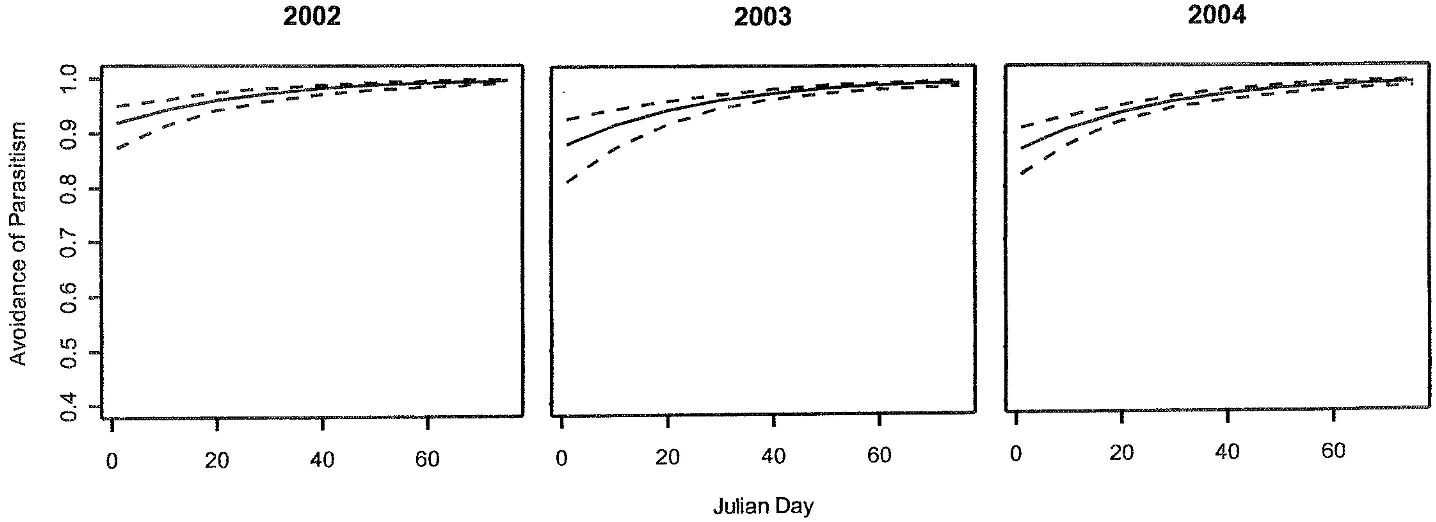

Figure 9. Model-averaged prediction for daily probability of parasitism avoidance during different times in the nesting season. Dashed lines represent 95% CI

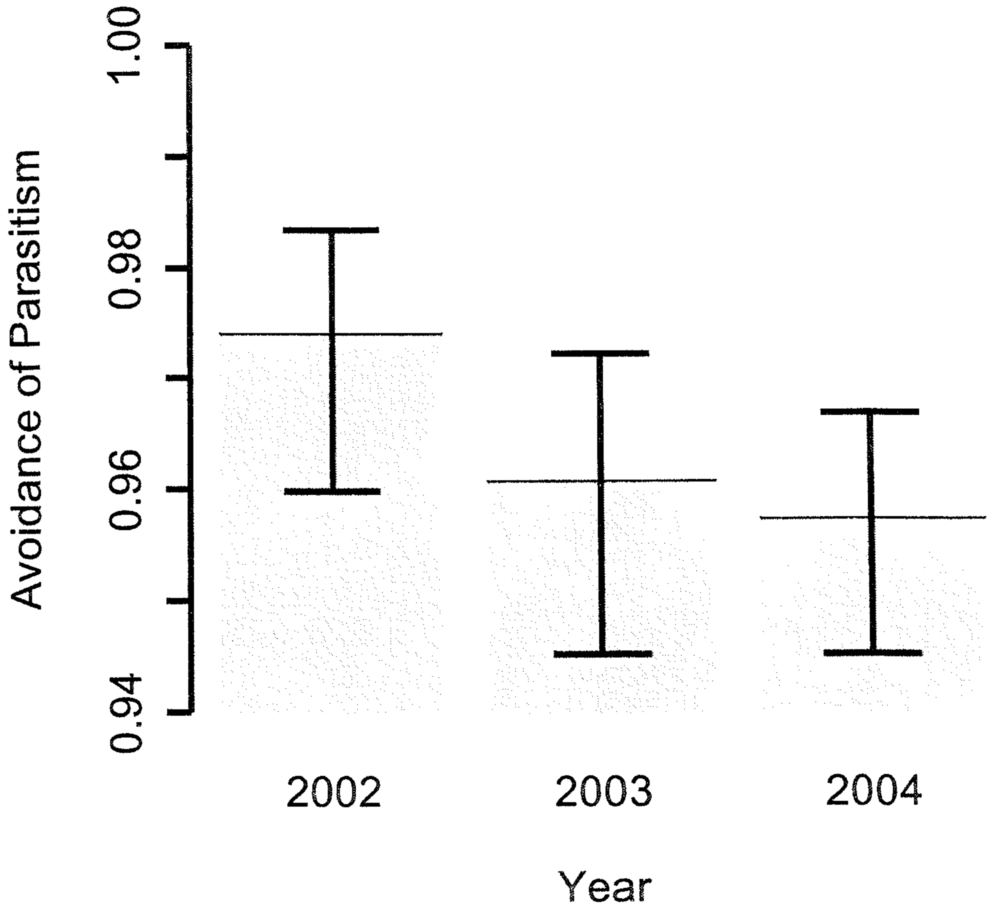

Figure 10. Daily probability of avoiding parasitism for 2002-2004. Error bars represent 95% CI.

APPENDIX I

Table 1. Daily, species-specific, nest survival estimates (DNS) for all nests that were found and monitored throughout the course of this study. Sample size represents number of nests monitored for the species.

2002

Species	DNS	Nests
Red-winged Blackbird (*Agelaius phoeniceus*)	0.943 (0.930-0.953)	119
Dickcissel (*Spiza americana*)	0.946 (0.865-0.980)	6
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	0.881 (0.747-0.948)	5
Mourning Dove (*Zenaida macroura*)	1.000 (NA)	1
Willow Flycatcher (*Empidonax traillii*)	1.000 (NA)	1
Eastern Kingbird (*Tyrannus savanna*)	1.000 (NA)	1

2003

Species	DNS	Nests
Red-winged Blackbird (*Agelaius phoeniceus*)	0.954 (0.945-0.962)	165
Dickcissel (*Spiza americana*)	0.923 (0.606-0.989)	1
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	0.933 (0.885-0.961)	15
American Coot (*Fulica Americana*)	0.918 (0.718-0.980)	2

2004

Species	DNS	Nests
Red-winged Blackbird (*Agelaius phoeniceus*)	0.938 (0.929-0.945)	308
Dickcissel (*Spiza americana*)	0.908 (0.780-0.965)	4
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	0.955 (0.928-0.972)	25
American Coot (*Fulica Americana*)	0.577 (0.098-0.945)	1
Sora (*Poranza carolina*)	0.951 (0.725-0.993)	1
Virginia Rail (*Rallus limicola*)	0.961 (0.857-0.990)	2
Common Grackle (*Quiscalus quiscula*)	1.000 (NA)	2
Mallard (*Anas platyrhynchos*)	0.888 (0.495-0.985)	1
Blue-winged Teal (*Anas discors*)	0.841 (0.393-0.977)	1

APPENDIX II

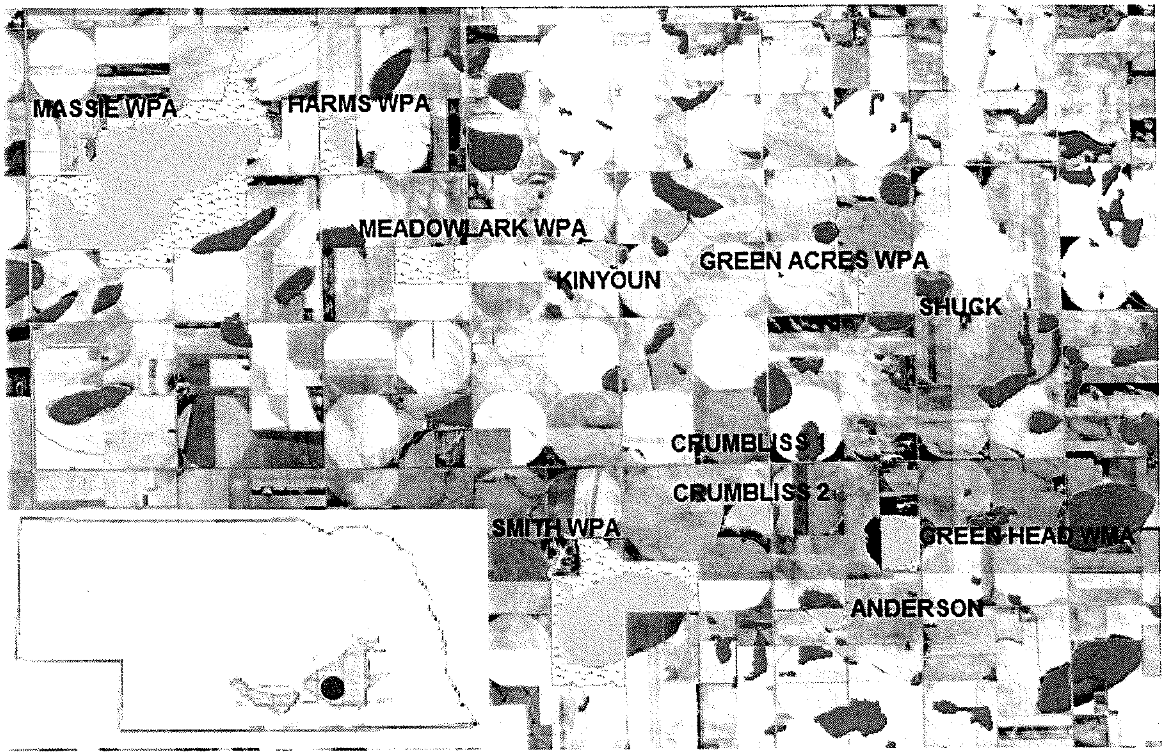

Figure 1. A map of my study area with study wetlands in blue and associated uplands in green pattern. Public wetlands are denoted by WPA or WMA, while private wetlands are labeled with last name of the land owner. Other wetlands not included in this study are shown in red. (Inset: Location of the Rainwater Basin within the state and the approximate location of my study are represented by a blue dot.

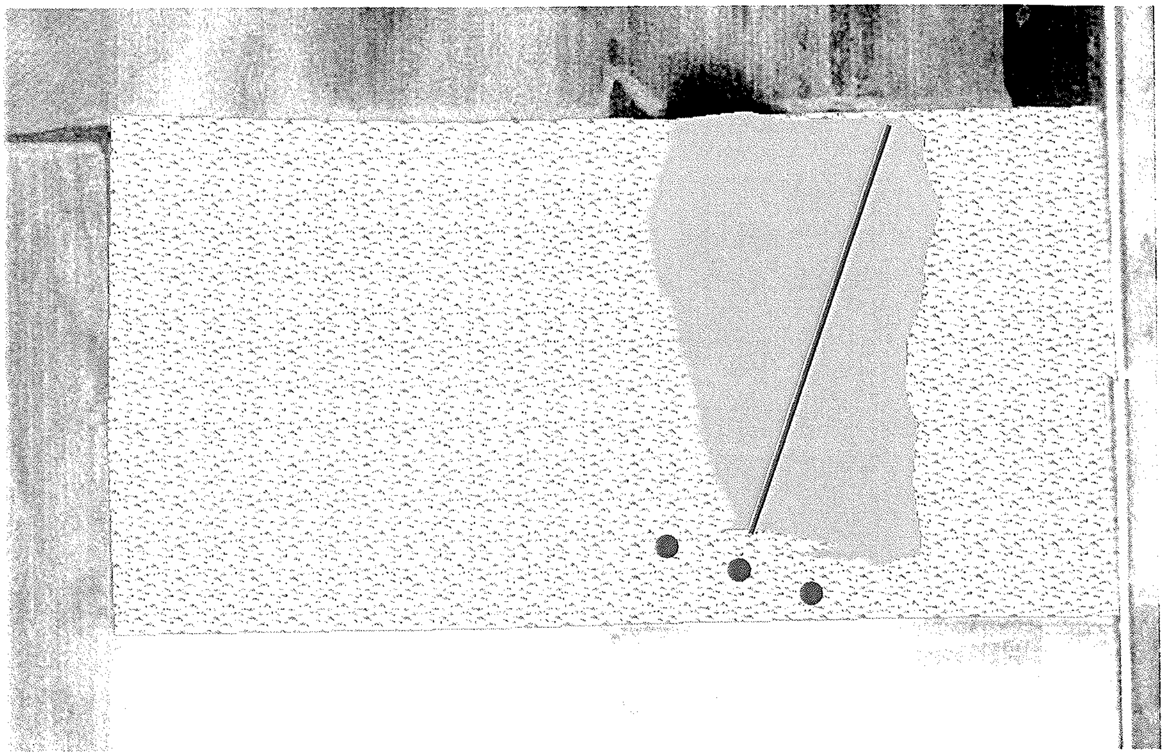

Figure 2. An example of a sampling transect in a wetland (red line) with upland track stations (red dots).

APPENDIX III.

The following is the R code used to modify the logit link function for the log-exposure analysis. Simply copy this into R before any analysis. When a binomial GLM model is fit reference the link function as “logexp”. Specific modifications to the code have been emboldened.

R code:

```
"make.link" <-
function (link)
{
   if (is.character(link) && length(grep("^power", link) > 0))
      return(eval(parse(text = link)))
   else if (!is.character(link) && !is.na(lambda <- as.numeric(link))) {
      linkfun <- function(mu) mu^lambda
      linkinv <- function(eta) pmax(.Machine$double.eps, eta^(1/lambda))
      mu.eta <- function(eta) pmax(.Machine$double.eps, (1/lambda) *
         eta^(1/lambda - 1))
      valideta <- function(eta) all(eta > 0)
   }
   else switch(link, logit = {
      linkfun <- function(mu) log(mu/(1 - mu))
      linkinv <- function(eta) {
         thresh <- -log(.Machine$double.eps)
         eta <- pmin(thresh, pmax(eta, -thresh))
```

```
      exp(eta)/(1 + exp(eta))
    }
    mu.eta <- function(eta) {
      thresh <- -log(.Machine$double.eps)
      res <- rep.int(.Machine$double.eps, length(eta))
      res[abs(eta) < thresh] <- (exp(eta)/(1 + exp(eta))^2)[abs(eta) <
        thresh]
      res
    }
    valideta <- function(eta) TRUE
  }, logexp = {
    linkfun <- function(mu) log(mu^(1/ed)/(1 - mu^(1/ed)))
    linkinv <- function(eta) {
      thresh <- -log(.Machine$double.eps)
      eta <- pmin(thresh, pmax(eta, -thresh))
      (exp(eta)/(1 + exp(eta)))^ed
    }
    mu.eta <- function(eta) {
      thresh <- -log(.Machine$double.eps)
      res <- rep.int(.Machine$double.eps, length(eta))
      res[abs(eta) < thresh] <- ((exp(eta)/(1 +
exp(eta))^2)*ed*(exp(eta)/(1+exp(eta)))^(ed-1))[abs(eta) <
        thresh]
```

```
        res
    }
    valideta <- function(eta) TRUE
  },probit = {
    linkfun <- function(mu) qnorm(mu)
    linkinv <- function(eta) {
        thresh <- -qnorm(.Machine$double.eps)
        eta <- pmin(thresh, pmax(eta, -thresh))
        pnorm(eta)
    }
    mu.eta <- function(eta) pmax(dnorm(eta), .Machine$double.eps)
    valideta <- function(eta) TRUE
  }, cloglog = {
    linkfun <- function(mu) log(-log(1 - mu))
    linkinv <- function(eta) pmax(.Machine$double.eps, pmin(1 -
        .Machine$double.eps, -expm1(-exp(eta))))
    mu.eta <- function(eta) {
        eta <- pmin(eta, 700)
        pmax(.Machine$double.eps, exp(eta) * exp(-exp(eta)))
    }
    valideta <- function(eta) TRUE
  }, identity = {
    linkfun <- function(mu) mu
```

```
    linkinv <- function(eta) eta
    mu.eta <- function(eta) rep.int(1, length(eta))
    valideta <- function(eta) TRUE
}, log = {
    linkfun <- function(mu) log(mu)
    linkinv <- function(eta) pmax(.Machine$double.eps, exp(eta))
    mu.eta <- function(eta) pmax(.Machine$double.eps, exp(eta))
    valideta <- function(eta) TRUE
}, sqrt = {
    linkfun <- function(mu) mu^0.5
    linkinv <- function(eta) eta^2
    mu.eta <- function(eta) 2 * eta
    valideta <- function(eta) all(eta > 0)
}, "1/mu^2" = {
    linkfun <- function(mu) 1/mu^2
    linkinv <- function(eta) 1/eta^0.5
    mu.eta <- function(eta) -1/(2 * eta^1.5)
    valideta <- function(eta) all(eta > 0)
}, inverse = {
    linkfun <- function(mu) 1/mu
    linkinv <- function(eta) 1/eta
    mu.eta <- function(eta) -1/(eta^2)
    valideta <- function(eta) all(eta != 0)
```

```
    }, stop(paste(link, "link not recognised")))
    list(linkfun = linkfun, linkinv = linkinv, mu.eta = mu.eta,
        valideta = valideta)
}
"binomial" <-
function (link = "logit")
{
    linktemp <- substitute(link)
    if (!is.character(linktemp)) {
        linktemp <- deparse(linktemp)
        if (linktemp == "link")
            linktemp <- eval(link)
    }
    if (any(linktemp == c("logit", "probit", "cloglog", "log","logexp")))
        stats <- make.link(linktemp)
    else stop(paste(linktemp, "link not available for binomial",
        "family, available links are \"logit\", ", "\"probit\", \"cloglog\" and \"log\""))
    variance <- function(mu) mu * (1 - mu)
    validmu <- function(mu) all(mu > 0) && all(mu < 1)
    dev.resids <- function(y, mu, wt) 2 * wt * (y * log(ifelse(y ==
        0, 1, y/mu)) + (1 - y) * log(ifelse(y == 1, 1, (1 - y)/(1 -
        mu))))
    aic <- function(y, n, mu, wt, dev) {
```

```
        m <- if (any(n > 1))
            n
        else wt
        -2 * sum(ifelse(m > 0, (wt/m), 0) * dbinom(round(m *
            y), round(m), mu, log = TRUE))
    }
    initialize <- expression({
        if (NCOL(y) == 1) {
            if (is.factor(y)) y <- y != levels(y)[1]
            n <- rep.int(1, nobs)
            if (any(y < 0 | y > 1)) stop("y values must be 0 <= y <= 1")
            mustart <- (weights * y + 0.5)/(weights + 1)
            m <- weights * y
            if (any(abs(m - round(m)) > 0.001)) warning("non-integer #successes in a
binomial glm!")
        } else if (NCOL(y) == 2) {
            if (any(abs(y - round(y)) > 0.001)) warning("non-integer counts in a binomial
glm!")
            n <- y[, 1] + y[, 2]
            y <- ifelse(n == 0, 0, y[, 1]/n)
            weights <- weights * n
            mustart <- (n * y + 0.5)/(n + 1)
        } else stop(paste("For the binomial family, y must be",
```

```
      "a vector of 0 and 1's or a 2 column", "matrix where col 1 is no. successes",
      "and col 2 is no. failures"))
  })
  structure(list(family = "binomial", link = linktemp, linkfun = stats$linkfun,
    linkinv = stats$linkinv, variance = variance, dev.resids = dev.resids,
    aic = aic, mu.eta = stats$mu.eta, initialize = initialize,
    validmu = validmu, valideta = stats$valideta), class = "family")
}
```