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Modeling Parental Provisioning by Red-winged Blackbirds in North Dakota

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ABSTRACT Male red-winged blackbirds (*Agelaius phoeniceus*) exhibit a difference in nest provisioning rates along an east-west gradient in North America. North Dakota is located in the center of North America and harbors a large population of breeding red-winged blackbirds (RWBL). This location provided an opportunity to compare provisioning rates in the central U.S. with those reported for the eastern and western populations. We placed video cameras at RWBL nests to record male and female feeding trips. Thirty-four nests were located on territories with original males and 30 were on territories where a replacement (floater) male had taken over a territory after we removed the original male by shooting or trapping. Original territory owners were more likely to feed young, and males were more likely to feed at nests with older chicks, at nests with more chicks, and later in the breeding season. Red-winged blackbird parental provisioning patterns in North Dakota appear to be similar to those observed in eastern North America.

KEY WORDS *Agelaius phoeniceus*, nestlings, North Dakota, parental care, provisioning, red-winged blackbird

The amount and quality of parental investment is important because it can contribute directly to the survival of offspring (Westneat and Sherman 1993). Most songbirds are monogamous, and both males and females contribute large amounts of parental care (Lack 1968). For a few species, however, breeding in highly productive habitats can allow one parent to gather sufficient resources to feed (Beletsky 1996). This condition, in concert with anisogamy, means that the benefits of male provisioning might be reduced. For these species, the amount of male provisioning may be variable. Polygyny is expected to arise when males can decrease parental provisioning with little cost and increase their reproductive success by attracting additional mates (Webster 1991).

Interest in male red-winged blackbird (RWBL; *Agelaius phoeniceus*) provisioning has been augmented by noticeable differences in provisioning rates along an east-west gradient that may be due to differences in habitat productivity, harem size, or breeding season length (Muldal et al. 1986, Beletsky 1996). For example, in Washington, only 6% of males fed nestlings, whereas 29–88% of males in the eastern United States feed nestlings (Searcy and Yasukawa 1995). However, Whittingham and Robertson (1994) found that 33% of the males in an Alberta population fed nestlings, and presented additional evidence that the east-west gradient in male provisioning rates may not be as strong as previously thought.

North Dakota lies between the eastern and western RWBL populations and thus, provides an opportunity to compare provisioning rates among these populations. Specifically, our objectives were to (1) document parental provisioning by RWBL for a population in North Dakota, (2) experimentally determine the role of breeding experience on male provisioning, and (3) examine the response of females to male assistance.

STUDY AREA

From 29 May to 29 June 2000–2001, we observed feeding contributions by male and female RWBL at 10 wetlands in Barnes County, North Dakota (46.93° N, 98.24° W), which was in the central portion of the Drift Plains Ecoregion (Bryce et al. 1998). This agricultural area contained a mix of row crops and Conservation Reserve Program (CRP) grassland interspersed with numerous temporary and seasonal wetlands. The Drift Plains Ecoregion hosted a large population of RWBL that breed in both wetland and upland habitats (Nelms et al. 1999). Our 10 study marshes contained a variety of wetland habitats including those covered by emergent vegetation, open water ringed by cattail (*Typha* sp.), and roadside ditches.

METHODS

To study the effects of breeding experience on male provisioning, we manipulated territory ownership on each of the study wetlands. As a polygynous species, male RWBL established exclusive territories and attempted to attract multiple females. Because the overall sex ratio for RWBL approached 50:50, this arrangement left a pool of floater males who regularly monitored territory ownership, looking for a chance to establish a territory in a vacant area. One difficulty with territory manipulations involving RWBL is that neighboring territory owners often annex the territories of removed males, preventing floaters from filling vacancies (Beletsky and Orians 1996). This complicated any effort to

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manipulate ownership of individual territories.

To circumvent this problem, while still controlling for variation between wetlands, we used a box trap with a live decoy bird and shooting (permit #MB019065-5) to permanently remove territory owners on a randomly selected half of each study wetland (Bray et al. 1975). Prior to removal, we captured all territorial males and fitted them with a United States Fish and Wildlife Service aluminum band (permit # 21672) and a unique combination of plastic color bands in order to track movements into vacated territories. The original territory owners remained in place on the other half of the wetland. We also captured and banded the replacement males on the manipulated portion of the wetland. The result of the manipulations was that half of the territory owners resembled the overall population (control), with a mix of experienced and new breeders. The other half (treatment) contained floaters that moved into the vacated territories. Most of these floater males probably never maintained a territory and had no breeding experience (Beletsky and Orians 1996). Removals occurred before most females had started to build nests. Throughout the experiment, we tracked active nests by searching for new nests every 6 days and checking on the status of known nests every 3 days.

Accurately observing parental provisioning in person can be difficult because real-time observations are time consuming, observer presence can alter feeding patterns, and feeding can be hard to observe at obscured nests. Therefore, we used small video cameras mounted on tripods and concealed with camouflage netting to record feeding activities at randomly selected nests containing nestlings. We were able to avoid recording at two nests on the same territory because most males were color-banded, and we made regular territory maps. We typically recorded at two nests each day. When possible, we selected one nest from a treatment area and one nest from a control area in order to collect data in treatment and control areas throughout the season. Recording did not take place when weather conditions would interfere with camcorder electronics.

To allow the blackbirds to adjust to the presence of the camera, we placed camouflage netting 1–3 m from the nest 12–24 hr before recording began. For each day of recording, we selected a 2-hr time block (the length of a videotape) at random from the first and second half of the day (AM and PM), with the stipulation that the two recording periods were at least 2.5 hr apart. At the designated recording time, we placed the video cameras under the pre-positioned camouflage netting and oriented towards the nest. The investigators left the area until after the 2-hr recording period was complete.

After videotaping was complete, we viewed tapes in a random order, and the observer did not know the location or identity of the nest. For each feeding visit, we recorded time of visit and sex of the provisioning parent. One advantage of videotapes over real-time observations is that nest visits without feedings can be verified. For purposes of analysis, we considered AM and PM recordings from the same day samples of the same experimental unit and averaged. In order to minimize the effects of camera setup, we did not use the first 15 min of each tape. In practice, the first female feeding typically occurred before the 15 min period had passed.

We considered male feeding as a binary response (yes/no), so some of the possible factors influencing the probability of male feeding were examined using logistic regression (Agresti 1996). We considered 6 *a priori* models ranging in complexity from a similar probability for all males to a dependence on treatment/control status, number of chicks, age of chicks, and Julian date (Table 1). The treatment/control factor loosely represented breeding experience; males in treatment areas were expected to have virtually no breeding experience, while control areas resembled the overall population containing a mix of experienced and inexperienced breeders.

The simplest model to describe male feeding probability assumed a constant feeding probability for all males. A second model, (T), assumed a difference based primarily on treatment/control status. Based on consistent reports that males only feed chicks older than 4 days, all 4 of the remaining models included nestling age as a factor. Support in previous studies for Julian date and number of chicks varied, so a combination of models including these factors were considered (Table 1).

We used odds ratios for determining associations between chick feeding (response) and predictor variables, which included treatment (original territory owners or replacement territory owners), nestling age, number of chicks and date. The odds ratio for a predictor variable was the relative amount by which the odds of the outcome increase (odds ratio >1.0) or decrease (odds ratio <1.0; Hosmer and Lemeshow 2000, Jacques et al. 2011). That is, multiplicative effects on the odds of a 1-unit increase in the response variable were associated with fixed levels of other predictor variables (Hosmer and Lemeshow 2000, Jacques et al. 2011).

We summarized the data for female feeding for each nest as the number of feeding trips/hour and used log-linear models (log link/ Poisson distribution) to relate feeding trips to male assistance (yes/no), number of chicks, and age of chicks (Agresti 1996). We considered 7 *a priori* models, differing by which potentially influential factors were included (Table 2). The first model, H, modeled the number of female feeding trips/hour as a log-linear function of male assistance. The remaining models considered effects of the number and age of chicks while including or excluding male assistance. Support for models that included male assistance (Table 2; models H, HA, HC and HAC) could indicate that females scaled back their feeding efforts when males were actively feeding. Conversely, males may have initiated feeding when female provisioning was not sufficient. Support for models excluding male assistance (Table 2; models A, C and AC) may have indicated that

females maintained feeding effort regardless of the level of male assistance. This implied that male feeding was in addition to female feeding and resulted in an increased overall level of provisioning.

We considered each of the candidate models to represent a competing hypothesis regarding the factors influencing parental provisioning in this population. Our overall goal was to estimate feeding-related parameters (Stoehr 1999); using a model with too few parameters would introduce statistical bias, and using too many parameters would unnecessarily increase the variance of our estimates. Therefore, we used a corrected Akaike's Information Criterion corrected for small sample size (AIC_c) to select a parsimonious model (or set of models) to make inferences about parental provisioning (Burnham and Anderson 2002). We performed statistical analyses using the LOGISTIC (males) and GENMOD (females) procedures in SAS v.8.0 (SAS Institute, Inc. 1999).

RESULTS

Across study years, we videotaped parental feeding for 256 hr at the nests of 64 different males. We did not identify individual females; however, the number of potential females and the time required to re-nest and incubate make it unlikely that any females were observed more than at a single nest. Nests varied in the number and age of chicks present (Table 3).

We recorded male provisioning at 15 nests located at 8 of the 10 study wetlands. Males provisioned nests with as few as 1 chick (26 June 2000, 3–5 days old) and with chicks as young as 0–2 days old (5 chicks, 29 June 2000). Average female provisioning rates (across all combinations of age and number of chicks) were similar in treatment (95% CI = 8.9–12.6 trips/hr) and control areas (95% CI = 8.4–11.5 trips/hr). Males in the control area made far fewer feeding trips than did females (95% CI = 1.8–3.9 trips/hr).

Four of the 6 models considered to describe the probability of male feeding had substantial support (Table 1). Model TA had 33% of the support, but none of the models had significant support over the others. An analysis of the odds ratios for each of the factors shows that 'treatment group' has the most dramatic effect; the estimated odds of an original territory owner feeding chicks are about 20 times the odds of a replacement owner feeding chicks (Table 4). Following with the concept of tapering effect sizes, the age of chicks may be the next important factor. Males were estimated to be about 2.8 times more likely to feed for each 3 days of growth. These models described smaller impacts for number of chicks and Julian date. For Julian date, however, the odds of male feeding increased 5% for each day that passed, a substantial increase over the course of the breeding season.

We would expect male feeding rates in the overall RWBL population in this region to be similar to the rates observed in the control side of our study. Rates for a particular circumstance can be determined based on the parameters given in Table 5. For example, under model TA these data would predict that 16.5% of the males would feed 0–2 day-old chicks and 59.8% would feed 6–8 day-old chicks (Fig. 1). We think these equations are more useful for comparing between populations than citing only the proportion of males in our population that fed nestlings.

Only two of the models considered to describe female feeding had substantial support (Table 2). Both models included number of chicks and age of chicks, confirming the expected influence of these factors on female feeding rates. Model AC gained almost twice as much support as model HAC (65% vs. 35%). The estimated number of feeding trips for females in any situation can be reconstructed with the parameters shown in Table 6.

Table 1. Summary of the evidence supporting each of 6 *a priori* logistic regression models considered to describe the probability of observing a male feeding at red-winged blackbird nests in Barnes County, North Dakota, USA, 2000–2001.

Model[a]	−2 Log Likelihood	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]
T A	46.93	3	52.55	0.00	0.33
T A D	45.86	4	53.24	0.69	0.24
T A C D	44.36	5	53.42	0.87	0.21
T	54.84	2	58.65	6.10	0.02
Constant	69.70	1	71.63	19.08	0.00

[a] T = Treatment (T) or Control (C), A = Nestling age, C = Number of nestlings, D = Date; [b] Number of parameters; [c] Akaike's Information Criterion for small sample size (Burnham and Anderson 2002); [d] Difference in AIC_c relative to minimum AIC_c; [e] Akaike weight (Burnham and Anderson 2002).

Table 2. Summary of the evidence supporting each of 7 *a priori* log-linear models considered to describe the number of female feeding trips/hr at red-winged blackbird nests in Barnes County, North Dakota, USA, 2000–2001.

Model[a]	LogLikelihood	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]
A C	902.80	3	−1799.96	0.00	0.65
H A C	903.05	4	−1798.72	1.24	0.35
H	884.73	2	−1765.65	34.31	0.00
A	888.19	2	−1772.57	27.39	0.00
C	896.58	2	−1789.35	10.61	0.00
H A	888.22	3	−1770.81	29.15	0.00
H C	896.84	3	−1788.05	11.91	0.00

[a] T = Treatment (T) or Control (C), A = Nestling age, C = Number of nestlings, D = Date; [b] Number of parameters; [c] Akaike's Information Criterion for small sample size (Burnham and Anderson 2002); [d] Difference in AIC_c relative to minimum AIC_c; [e] Akaike weight (Burnham and Anderson 2002).

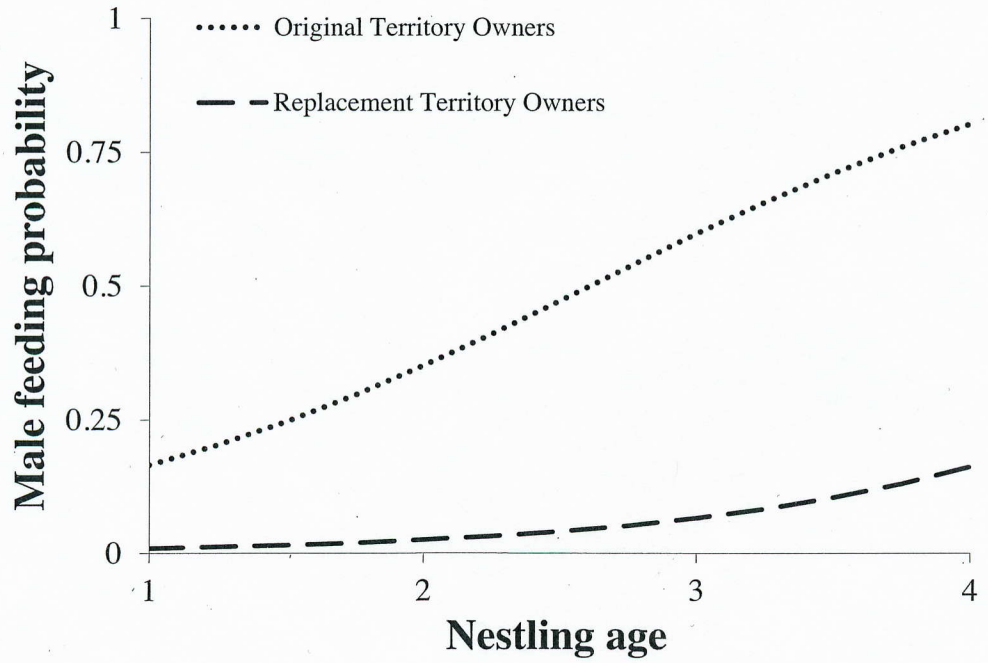

Figure 1. Functional form of logit linear model TA describing male red-winged blackbird (*Agelaius phoeniceus*) feeding probability for original and replacement territory owners as a function of nestling age in Barnes County, North Dakota, USA, 2000–2001.

DISCUSSION

Male RWBL in central North Dakota fed nestlings on a regular basis. While the data did not clearly arbitrate between some of the competing models, the importance of male breeding experience was clear. The importance of nestling age, number of chicks, and Julian date, factors predicted based on theory and previous studies, were probably real but less important than male breeding experience. The proportion of males in central North Dakota (98° W longitude) that fed nestlings was more similar to previously studied populations in eastern North America (74° W – 89° W) than populations in western North America (113° W – 123° W; Whittingham and Robertson 1994, Searcy and Yasukawa 1995).

Female provisioning rates (feeding trips/hr) were similar to those reported from other areas (Muldal et al. 1986, Teather 1992, Clark and Lee 1998). However, interpretation of these rates is difficult because the amount of food brought per trip may vary by sex and habitat (Whittingham and Robertson 1994). Variation in the amount of food delivered per trip adds variation to the data and could make it more difficult to estimate the effects of the factors of interest. Further, the number of feeding trips per hour does not reflect the changes we would expect based on the age and number of chicks in the nest. Building statistical models to describe how the number of feeding trips varies according to additional factors could help determine what influences the number of feeding trips, and will help facilitate comparisons between populations.

Table 3. Characteristics of 64 red-winged blackbird nests videotaped to study parental provisioning of nestlings in Barnes County, North Dakota, USA, 2000–2001.

Male Feeding						
Treatment Group	Nests Videotaped			Males Observed Feeding		
Original Territory Owners	34			14		
Replacement Territory Owners	30			1		
Chicks/Nest[a]						
Treatment Group	1	2	3	4	5	6
Original Territory Owners	6	7	11	8	1	1
Replacement Territory Owners	3	7	11	11	1	1
Age of Chicks (days)						
Treatment Group	0–2	3–5	6–8	9+		
Original Territory Owners	10	11	9	4		
Replacement Territory Owners	16	6	6	2		

[a] Nestlings/nest included red-winged blackbird and brown-headed cowbird chicks.

Our experiment to manipulate male breeding experience demonstrated that original territory owners are more likely to feed nestlings than males that replaced original owners following permanent removals. We observed only one male feeding nestlings in a treated (manipulated) area of the wetlands, where we assumed that males had no breeding experience. The estimated proportion of feeding males in control areas, however, indicated that some males without breeding experience may feed nestlings. Because 40–60% of adult RWBL die each year (Yasukawa and Searcy 1995), we would expect the maximum proportion of males that feed nestlings to be in the 40–60% range if first year breeders do not feed. Our data predicted situations where higher proportions of males may feed nestlings as have been observed in other populations (Searcy and Yasukawa 1995), suggesting that males without breeding experience may feed in some populations.

Table 4. Estimated odds ratios (and confidence intervals) for factors affecting the probability of observing a male feeding at red-winged blackbird nests for 4 competing models in Barnes County, North Dakota, USA, 2000–2001.

Model[a]	Factor			
	Treatment/Control	Age of Chicks	Number of Chicks	Julian Date
T A	21.15 (2.31, 193.96)	2.74 (1.26 , 5.95)	N/A	N/A
T A C	20.74 (2.26 , 190.26)	2.88 (1.28 , 6.47)	1.33 (0.70 , 2.54)	N/A
T A D	20.13 (2.14 , 188.95)	2.79 (1.26 , 6.18)	N/A	1.05 (0.96 , 1.15)
T A C D	18.74 (2.04 , 172.01)	2.99 (1.29 , 6.97)	1.52 (0.76 , 3.02)	1.07 (0.97 , 1.18)

[a] T = Treatment (T) or Control (C), A = Nestling age, C = Number of chicks, D = Date.

Table 5. Estimated parameters (and standard errors) for 4 logistic regression models describing the probability of observing a male feeding at red-winged blackbird nests in Barnes County, North Dakota, USA, 2000–2001.

Model[a]	Parameter				
	Intercept	Treatment / Control	Age of Chicks	Number of Chicks	Date
T A	–5.70 (1.53)	3.05 (1.13)	1.01 (0.39)	N/A	N/A
T A C	–6.75 (1.98)	3.03 (1.13)	1.06 (0.41)	0.29 (0.33)	N/A
T A D	–13.87 (8.36)	3.00 (1.14)	1.03 (0.41)	N/A	0.05 (0.05)
T A C D	–17.92 (9.05)	2.93 (1.13)	1.10 (0.43)	0.42 (0.35)	0.06 (0.05)

[a] T = Treatment (T) or Control (C), A = Nestling age, C = Number of chicks, D = Date.

Our results supported the hypothesis that females receiving male assistance provisioned at the same rate as females without male help. There was not sufficient evidence, however, to rule out the possibility that male RWBL feed when female provisioning was insufficient (Whittingham 1989).

Table 6. Estimated parameters (and standard errors) for 2 log-linear models describing the number of female feeding trips/hr red-winged blackbird nests in Barnes County, North Dakota, USA, 2000–2001.

Model [a]	Parameter			
	Intercept	Male Assistance	Age of Chicks	Number of Chicks
AC	1.51	N/A	0.14	0.18
	(0.15)		(0.04)	(0.03)
HAC	1.50	–0.07	0.15	0.18
	(0.15)	(0.10)	(0.04)	(0.03)

[a] T = Treatment (T) or Control (C), A = Nestling age, C = Number of chicks, D = Date.

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