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THE EFFECTS OF FOOD SUPPLEMENTATION ON EXTRATERRITORIAL BEHAVIOR IN FEMALE NORTHERN CARDINALS

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Abstract. We tested how food supplementation affects extraterritorial behavior in the socially monogamous Northern Cardinal (*Cardinalis cardinalis*). Assuming extraterritorial movements are energetically costly, we predicted that if these movements function for gaining extra-pair matings, females on supplemented territories would spend more time off territory, make more extraterritorial forays, and have larger home ranges in relation to territory size than those on unsupplemented territories. If extraterritorial movements function for foraging purposes, then supplemented females should spend less time off territory, make fewer forays, and have smaller home ranges than unsupplemented

females as a result of plentiful food on their home territories. We radio-tracked seven females during their fertile periods and found a trend for supplemented females to make more extraterritorial forays and spend more time off territory than unsupplemented females; however, there was no significant difference in home range sizes between treatment groups. Our findings provide some support for the extra-pair copulation function of extraterritorial movements in female Northern Cardinals.

Key words: *Cardinalis cardinalis*, *extra-pair copulation*, *home range*, *Northern Cardinal*, *radio-telemetry*.

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Efectos del Suplemento Alimenticio en el Comportamiento Extra-territorial de las Hembras de *Cardinalis cardinalis*

Resumen. En este estudio, investigamos los efectos del suplemento alimenticio en el comportamiento extra-territorial de *Cardinalis cardinalis*, una especie monógama y social. Debido a que los movimientos extra-territoriales que estas aves realizan implican un desgaste energético, predijimos que si estos viajes ayudan a las hembras a obtener apareamientos extra-pareja, entonces las hembras en territorios suplementados pasarían más tiempo fuera de su territorio, harían más excursiones extra-territoriales y tendrían áreas de hogar más grandes con relación al tamaño de su territorio que aquellas hembras de territorios no suplementados. Si los movimientos territoriales son más útiles para buscar comida, entonces las hembras de territorios suplementados con alimento deberían pasar menos tiempo fuera de su territorio, hacer menos excursiones para buscar alimento y tener áreas de hogar de menor tamaño que las hembras con territorios no suplementados, ya que tienen suficiente alimento en sus propios territorios. Rastreamos con transmisores siete hembras durante sus periodos fértiles y encontramos que las hembras de los territorios suplementados tienden a hacer más excursiones extra-territoriales y a pasar más tiempo fuera de su territorio que las hembras de territorios no suplementados. Sin embargo, no hubo una diferencia significativa en el tamaño de las áreas de hogar de las hembras de territorios suplementados y no suplementados. Nuestros resultados apoyan la idea de que los movimientos extra-territoriales de las hembras tienen que ver con la búsqueda de cópulas extra-pareja.

Females of some songbird species participate in extraterritorial forays during the fertile period, potentially in search of extra-pair copulations (EPCs) with neighboring males (Smiseth and Amundsen 1995, Neudorf et al. 1997, Mays and Ritchison 2004, Pedersen et al. 2006). Females may seek EPCs to enhance the genes of their offspring, lessen the costs of losing a mate, or to gain direct benefits (reviewed by Petrie and Kempenaers 1998). However, Westneat and Stewart (2003) recently questioned the role of females in the pursuit of EPCs because many studies reporting female extraterritorial forays provide only suggestive evidence that forays function for obtaining EPCs (but see Double and Cockburn 2000, Pedersen et al. 2006). Furthermore, a recent analysis by Arnqvist and Kirkpatrick (2005) questioned the benefits of EPCs to females. Extraterritorial forays are presumably energetically costly and may be risky if females are attacked by territorial females (Kinser 1973, Mays and Hopper 2004, Neudorf et al. 2008); thus, females should engage in them only if the benefits outweigh the costs. An alternative explanation for female extraterritorial behavior is foraging (Neudorf et al. 1997). We used food supplementation experiments to examine the function of extraterritorial behavior in female Northern Cardinals (*Cardinalis cardinalis*).

The Northern Cardinal is a sexually dimorphic songbird of the eastern United States and a year-round resident of eastern Texas (Halkin and Linville 1999). It is an ideal species on which to test the effects of supplementation on extraterritorial forays because it is socially monogamous with a moderate level of extra-pair paternity (16% of nests contained extra-pair young; Ritchison et al. 1994), and both males and females are known to move off territory (Merritt 1975). We monitored females with radio-telemetry to determine if they left their own territories during the fertile stage. If the purpose of forays is to gain EPCs, supplemented females should have more extraterritorial forays, a larger percentage of

time off territory, and larger home ranges in relation to territory size than unsupplemented females as a result of plentiful food to lessen the energetic demand of off-territory movements. If females use forays primarily for foraging, forays should occur less frequently among supplemented females because of the abundance of food on their territories.

METHODS

STUDY AREA AND SPECIES

The study was conducted during the 2005 and 2006 breeding seasons (March–July) at the Sam Houston State University Center for Biological Field Studies (CBFS), located northeast of Huntsville, Walker County, Texas. The CBFS encompasses approximately 100 ha that includes forested areas ranging from dense to sparse upper story and dense understory (Dent and Lutterschmidt 2001). The core area used for the study was approximately 18.8 ha and was an ideal location for studying Northern Cardinals because the population at the study site is dense (approximately 1.4 males per ha; Dow 1969) allowing opportunities for individuals to pursue extra-pair copulations.

Northern Cardinals were each banded with a USFWS band and a unique combination of three celluloid color bands sealed with acetone. Once individuals were banded, a male's territory was determined by observing song posts, where interactions with neighboring males occurred, and by playbacks of male song. Four to six points were flagged for each territory and then recorded with a GPS unit. The GPS points were then processed using GPS Pathfinder Office 2.90 (Trimble Navigation Limited, Westminster, Colorado) and imported into the GIS program ArcMap (ERSI, Redlands, California). A line was traced over the boundary points to create a polygon of the territory, and territory area was calculated using ArcMap.

FOOD SUPPLEMENTATION

Food supplementation of each territory began in early spring (March and April), when pairs were observed on their territories, and continued until the breeding attempt was complete (fledging). Each bird feeder was constructed from two 30 cm plant trays and wire mesh. The feeders were elevated approximately 180 cm off of the ground using 3.8 cm PVC pipe. Black oil sunflower seeds were provided ad libitum (Geis 1980). Two feeders were placed in each experimental (supplemental) territory, whereas territories without supplemented food were designated as control territories. The study area was divided so that control territories were not adjacent to those that were supplemented (i.e., at least one buffer territory between them). This reduced the possibility of unsupplemented individuals feeding on supplemented territories. The sides of the study site containing experimental and control territories were reversed each year.

RADIO-TELEMETRY

Female Northern Cardinals ($n = 9$) were radio-tagged either during their fertile or incubation periods using a figure-eight harness attachment method (Rappole and Tipton 1991). We tracked a total of nine female Northern Cardinals, of which seven were included in the statistical analysis (Table 1). Two of the females were omitted because they did not build nests during or after our tracking session, which indicated that they were not likely fertile at the time of tracking. A female's fertile period was defined as the time from the onset of nest building until her penultimate egg was laid (Neudorf et al. 1997). Three females were radio-tagged during nest building. We waited at least 24 hr after attaching a

TABLE 1. Territory size, home range size, time off territory, and foray rate for fertile female Northern Cardinals occupying territories supplemented with black oil sunflower seed and occupying unsupplemented territories at the Center for Biological Field Studies, Walker County, Texas, (March–July 2005 and 2006).

Treatment	Female number	Total time tracked (min)	Territory size (ha)	Home range size (ha)	% time off territory	Forays ^a per hour	Territories visited ^b
Supplemented (<i>n</i> = 3)	1	600	0.2	0.9	43	1.0	2
	2	465	0.3	0.9	61	1.0	2
	3	570	0.3	1.1	58	1.1	2
Unsupplemented (<i>n</i> = 4)	4	600	0.2	0.8	23	0.9	2
	5	600	0.5	1.0	43	0.9	1
	6	600	0.5	1.3	32	0.8	0
	7	600	0.9	1.5	25	0.7	1

^aForays refer to trips made by females off of their home territories.

^bRefers to total number of different known territories visited by females during forays.

radio-transmitter to a female to begin tracking. Four females were radio-tagged during incubation, and due to high predation rates, all four nests were depredated. We were able to radio-track the females whose nests were depredated once they began reneesting. Radio transmitters were BD-2 (1.4 g) transmitters (Holohil Inc., Woodlawn, Canada). Cardinals weigh 40–45 g; therefore, the transmitters were 3.1%–3.5% of their weight. Female movement was tracked throughout the fertile period using a TRX 1000 receiver (Wildlife Materials Inc., Carbondale, Illinois) and a hand-held three-element Yagi antenna. We attempted to track each female for a total of 10 hr (five 2-hr sessions) during the fertile period in the morning between 06:00 and 12:00 (CDT). Female locations were flagged every 15 min to map home-range size using a GPS unit. This was achieved by following a female at a distance (approximately 20 m) to prevent disturbances; flags were placed after she had left the area. Forays were defined as movements by the female outside of her territorial boundaries. Time off territory was calculated using the number of a female's location points that occurred outside her home territory boundaries. With maps prepared using ArcMap, we determined whether a female was off her home territory or on another male's territory by observing female location points with regards to the territory boundaries of her mate and other males respectively. Amount of time off the territory was compared between supplemented and unsupplemented females. Female home range size was determined using convex polygons.

STATISTICAL ANALYSIS

We used nonparametric statistics because our data were not normally distributed. We compared home range sizes, territory sizes, number of extraterritorial forays, and time spent off territory between supplemented and unsupplemented females using Mann-Whitney *U* tests. For the home range size comparison, we first calculated a ratio of home range size to territory size for each female. All means are reported \pm SE, and all statistical tests were two-tailed. We used SPSS (SPSS 2005) software for our analyses.

RESULTS

During the 2005 and 2006 breeding seasons, we mapped 20 Northern Cardinal territories (11 and nine, respectively). Of these, nine were supplemented, and 11 were unsupplemented. Supplemented and unsupplemented territories did not differ in size (Mann-Whitney *U*-test, *n* = 20, *P* = 0.3). Females (*n* = 7) were tracked during their fertile periods for a total of 67.3 hr (supplemented: 27.3 hr,

unsupplemented: 40 hr). On average, each supplemented female was tracked for 9.1 hr (range: 7.8–10 hr; Table 1), and each unsupplemented female was tracked for 10 hr. The mean number of forays per hour for supplemented females was 1.0 ± 0.01 , whereas unsupplemented females averaged 0.8 ± 0.1 forays per hour, and this difference approached significance (Mann-Whitney *U*-test, *P* = 0.06, *n* = 7; Table 1). Supplemented females spent more time off their territories than did unsupplemented females, and this difference approached significance (Mann-Whitney *U*-test, *P* = 0.06, *n* = 7; Table 1). Supplemented females had on average 19.6 ± 1.9 points off of their territories, accounting for 54% of the observation time (Table 1). The average number of points off territory for unsupplemented females was 12.5 ± 1.7 , or 31% of the total observation time. Both supplemented and unsupplemented females left their territories and visited other males' territories, but the number of different territories visited did not differ significantly between the two groups (Mann-Whitney *U*-test, *P* = 0.1, *n* = 7). Only one female, an unsupplemented female, did not visit another known male's territory during a foray (Table 1).

The average home range size for supplemented females (*n* = 3) was 1.0 ha and for unsupplemented females (*n* = 4) was 1.1 ha (Table 1). After determining the ratio of home range size to territory size, we found that supplemented females had slightly larger home ranges in relation to territory size than did unsupplemented females, but this difference was not significant (Mann-Whitney *U*-test, *P* = 0.1, *n* = 7).

DISCUSSION

Both supplemented and unsupplemented female Northern Cardinals participated in extraterritorial forays during the fertile period. Supplemented females made more extraterritorial forays and had a higher percentage of time off territory than unsupplemented females; both of these differences approached significance. The total number of known territories visited and home range size in relation to territory size did not differ between supplemented and unsupplemented females. Our findings provide some support for the idea that supplementation of food allowed females to spend more time off their territories, potentially in search of EPCs. In contrast to our study, Václav et al. (2003) found lower rates of extra-pair paternity on supplemented territories in House Sparrows (*Passer domesticus*) and attributed the result to increased nest attentiveness by females on supplemented territories. Supplemented Red-winged Blackbird (*Agelaius phoeniceus*) territories also had lower rates of extra-pair paternity, with supplemented

females showing a trend toward lower foray rates than unsupplemented females (Westneat 1994).

Our findings provide only indirect support for the EPC function of forays. No extra-pair copulations were observed during tracking sessions in our study, and we did not conduct paternity analysis. During extraterritorial forays, females would often move through dense foliage that prevented us from observing whether any copulation attempts were made. Although females of some species have been observed engaging in EPCs off territory (Black-capped Chickadees [*Poecile atricapillus*]; Smith 1988), for many species, EPCs are rarely seen (Neudorf et al. 1997, Pedersen et al. 2006). Furthermore, when female Northern Cardinals were observed off of their territories, their mates were often seen in close proximity to them. Male Northern Cardinals are known to guard their mates by maintaining contact nearly 75% of the time while the females are fertile (Ritchison et al. 1994). A similar study on Yellow-breasted Chats (*Icteria virens*) revealed that males tried to remain close to their females while they were off territory (Mays and Ritchison 2004).

Other possible motivations for female extraterritorial forays are foraging (Neudorf et al. 1997) and seeking nesting material (Poston 1997). Northern Cardinals are known to forage off of their territories (Halkin and Linville 1999). The foraging hypothesis predicts that females in low quality environments should have larger home ranges, more forays, and more time off territory than females in high quality environments (i.e., supplemented territories)—the opposite of what we found. However, the Northern Cardinal diet does not consist exclusively of seed; females may have been foraging for other food types such as berries, insects, or flower buds during forays. Although females were difficult to see while radio-tracking, none of the supplemented females were observed foraging while off territory; however, two out of four unsupplemented females were observed foraging while off territory. None of the females were observed gathering nesting material while off territory, but this remains a possible explanation for forays made during the nest building stage.

In conclusion, our study suggests that food supplementation increases female Northern Cardinal tendency to travel off territory. Future studies should incorporate paternity analyses with food supplementation and radio-tracking to determine the role of female extraterritorial behavior in the pursuit of EPCs.

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