starts (*Setophaga ruticilla*): A test of functional hypotheses. Z. Tierpsychol. 69:1169–1176.

McGREGOR, P. K. 1991. The singer and the song: On the receiving end of bird song. Biol. Rev. 66:57–81.

MORSE, D. H. 1966. The context of songs in the Yellow Warbler. Wilson Bull. 78:444–455.

MOUNTJOY, D. J., AND R. E. LEMON. 1990. Song as an attractant for male and female European Starlings, and the influence of song complexity on their response. Behav. Ecol. Sociobiol. 28:97–100.

PEEK, F. W. 1972. An experimental study of the territorial function of vocal and visual display in the male Red-winged Blackbird (*Agelaius phoeniceus*). Anim. Behav. 20:112–118.

SEARCY, W. A. 1992. Song playback to females. Pages 175–190 *in* Playback and studies of animal communication (P. K. McGregor, Ed.). Plenum Press, New York.

SPECTOR, D. A. 1991. The singing behaviour of Yellow Warblers. Behaviour 117:29–52.

SPECTOR, D. A. 1992. Wood-warbler song systems: A review of paruline singing behaviors. Curr. Ornithol. 9:199–238.

WEARY, D. M., R. E. LEMON, AND S. PERREAULT. 1992. Song repertoires do not hinder neighbor-stranger discrimination. Behav. Ecol. Sociobiol. 31:441–447.

Response of Male Brown-headed Cowbirds to Broadcast of Complete or Partial Flight Whistles

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The vocal repertoire of male Brown-headed Cowbirds (*Molothrus ater*) during the breeding season is rich and varied, and includes several different vocalizations. The best-known cowbird vocalization, the species-typical song, consists of several low-frequency introductory notes followed by a high-frequency whistle (Friedmann 1929). A second vocalization heard throughout the breeding season is the flight whistle (FW). Cowbird FWs consist of two or more syllables that are largely pure tones, although some FWs may contain extensive frequency sweeps (Rothstein and Fleischer 1987, Rothstein et al. 1988). For example, the FW given by male cowbirds in our study population consists of two parts (Fig. 1). The first half is a single syllable of relatively pure tone, although it has rapid frequency sweeps at its beginning and end. The second half of the FW contains two syllables that always accompany each other in the order shown in Figure 1. The first of these syllables is brief and has an overall rise in frequency, while the second begins with a gradual frequency descent that ends as a pure tone over the last half of the syllable.

Most males have a single stereotyped FW, and most males in a given area share the same FW, producing FW dialects (Rothstein and Fleischer 1987). FWs are used in a variety of contexts: they are given in response to female vocalizations; they act as alarm calls; and they are produced during copulatory attempts (Rothstein et al. 1988, Dufty and McChrystal 1992). However, the most frequent behavior associated with flight whistles is, as the name suggests, flight. Cowbirds will give FWs when they are about to take flight, during the flight itself, and when landing (Friedmann 1929, Rothstein et al. 1988). Furthermore, all or only part of a FW may be produced (Rothstein and Fleischer 1987, Dufty pers. obs.). For example, male cowbirds near Boise, Idaho may perform only the first half, only the second half, or the full FW. Full FWs usually are presented in the sequence shown in Figure 1, but it is not uncommon for the two-syllable second half to be emitted first, followed by the first half (hereafter termed full FW [reversed]).

While working with cowbirds in upstate New York and Boise, one of us (A.M.D.) noted that, when a male cowbird flying into an area produced part of a FW, it often was answered with the remaining part by a male already in that area. The newcomer typically would alter his flight path to approach the resident, and additional social interactions frequently followed such vocal interplay.

Male cowbirds have breeding home ranges of up to 30 ha or more in size (Darley 1982, Dufty 1982a, Rothstein et al. 1984). Ranges are not defended in a way that provides exclusive use of an area for any given male (Dufty 1982b, Rothstein et al. 1986, Yokel 1989). Thus, several males may occupy overlapping

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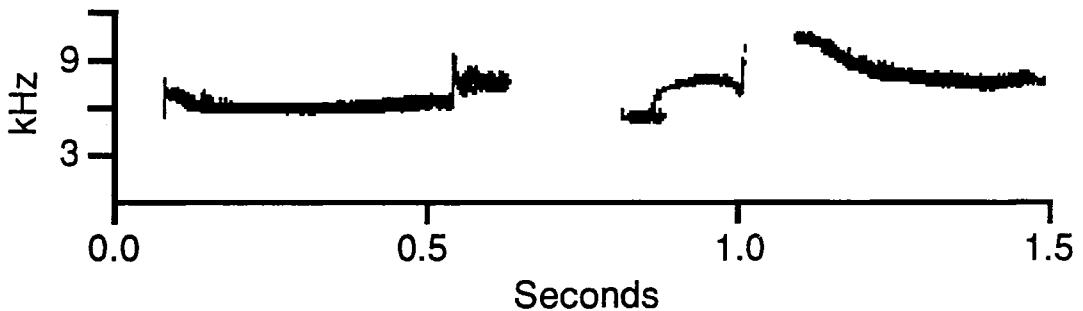
Fig. 1.   Audiospectrogram of Boise-type flight whistle produced by male Brown-headed Cowbirds in study population. First syllable (continuous trace) constitutes first half of FW, while second and third syllables, which are always given together, constitute second half of FW (redrawn from Dufty and McChrystal 1992).

areas. Males make long flights within their ranges to search for and/or guard females. They also fly to feeding sites that may not be part of, or even adjacent to, their breeding ranges (e.g. Rothstein et al. 1984). Thus, it may be many minutes between visits to any given area of a male's breeding range, and it is unlikely that males can monitor the movements and activities of conspecific males that also are active in an area. A ritualized vocal exchange, initiated upon the arrival of a male, could facilitate social interactions among males that might otherwise be unaware of each other's presence.

We broadcasted tape recordings of the first half, second half, or full FW to male cowbirds, and recorded their vocal and behavioral responses. We tested the hypothesis that perched male cowbirds respond to partial FWs by producing the missing section. This hypothesis was based on previous field observations, and led us to predict that the initial FW response of a male cowbird would not match the section of the FW we broadcast. That is, if we broadcast the first half of the FW, the predicted vocal response was the second half; conversely, if the second half was broadcast, the predicted vocal response was the first half. In the case of broadcast of the full FW, we predicted that the test birds would avoid matching the last part of the FW they heard (i.e. they would produce the first half of the FW). Furthermore, based on the work of Rothstein et al. (1988), we predicted that male cowbirds would approach the playback apparatus in response to broadcast of the FWs.

Methods.—The study was conducted in 1990 in and around the city of Boise. Cowbirds were located in city parks, in a riparian corridor running along the Boise River, and in wooded areas along streams that feed into the river. Males were unmarked, but most testing locations were separated by several kilometers to avoid multiple testing of the same bird. In three cases test sites were only about 200 to 400 m apart. In these cases, the direction of movements of the males when not being tested convinced us that we were testing different birds.

The playback apparatus consisted of the playback tape (Sony HF90, Type I, normal bias), a Marantz PMD221 portable tape recorder, a Realistic 40-watt equalizer/booster, a 12-volt battery power supply, and a Realistic woofer/tweeter speaker mounted on a 2-m pole. A male cowbird mount in a normal perching position was also attached to the top of the pole.

Eight high-quality, full flight whistles were recorded from a single free-living male cowbird, and these were used to construct each of the three FW playback tapes. One tape consisted of full FWs, one contained only the first half of each FW, and the remaining tape included only the second half of each FW. Playback tapes were 190 s long, contained 17 vocalizations each, were matched for amplitude, and consisted of one vocalization approximately every 10 s. Broadcast of a Song Sparrow (*Melospiza melodia*) song served as a control.

Playbacks were conducted between 14 May and 18 June, during the middle of the cowbird breeding season. A playback session began as soon as an appropriate perched male cowbird was encountered. Each session consisted of the broadcast of one of the four playback tapes (first half of the FW, second half of the FW, full FW, or Song Sparrow [*Melospiza melodia*] song), during which time we noted the test male's vocal and behavioral responses. Four presentations (one presentation of each of the four tapes) were made at each of 15 locations. At least three days were allowed between successive presentations at the same sight. We do not know if the same male was tested with all four tapes at any given location. The order of presentations was randomized for each location.

Sample sizes vary because only results from solitary males are included. Cowbirds already engaged in social interactions do not respond to playbacks (Dufty 1982b, Rothstein et al. 1988) and, in some instances, males that we initially thought were alone turned out to be with a female or another male; these cases were eliminated from consideration. All males were in sight and within hearing range of the playbacks at the beginning of each test, all treatment groups averaging

between 40 and 45 m (Kruskal-Wallis ANOVA, $H = 0.21$, 3 df, $P < 0.95$).

Each session was tape recorded using a second Marantz recorder. This allowed us to provide a running commentary during the playbacks and to verify vocal responses for some birds. We analyzed only the first FW given by males in response to each playback, because subsequent vocalizations may not represent independent events. No distinction was made between partial and complete FW responses. That is, males responding with full FWs were credited with whichever part of the FW they produced first. Thus, males that produced the "normal" full FW (i.e. first half followed by the second half) were considered to have given the first-half FW as their initial response. Similarly, males that produced the full FW [reversed] (i.e. second half followed by first half) were considered to have given the second half FW as their initial response.

Although limiting our analysis of vocal responses to the first FW produced is justified on statistical grounds, it eliminates many other FWs given during the playback sessions that could provide additional insight into cowbird behavior. Consequently, we determined the total number of FWs given by each male that responded, calculated the percentage of his total responses that consisted of each FW category (i.e. first-half FW, second-half FW, full FW, and full FW [reversed]), and averaged the results for all males that responded to a particular playback type.

We also recorded additional activities of test male cowbirds during playbacks (i.e. whether they approached playback apparatus, number of flights, delay to first flight, time spent in sight, and closest approach to playback apparatus).

Results.—The number of flights by males did not differ among the four groups ($H = 3.87$, 3 df, $P < 0.3$). Males tested with the control Song Sparrow playback averaged fewer flights (1.5 ± SD of 1.2) than did males tested with any of the three experimental playbacks (first half of FW, 2.6 ± 2.3; second half of FW, 2.1 ± 1.3; full FW, 3.1 ± 2.7). Flights made during the Song Sparrow playback typically consisted of only one or two movements that took the male out of sight. Conversely, there was a large amount of variance in the responses of males in the experimental groups, reflecting the fact that some males sat and watched the cowbird model or made a single flight towards it, while other males made several passes over the model.

There also was no significant difference in the time from the onset of playback to first flight among the four groups of birds ($H = 3.80$, 3 df, $P < 0.3$). Solitary male cowbirds in the control group did not spend very long in any one place ($\bar{x} = 36.1 ± 48.7$ s). They often vocalized for a few moments and then flew off. Test birds took twice as long, on average, to make their first flight, but there was a great deal of variance (first half of FW, 72.0 ± 69.2 s; second half of FW,

66.6 ± 59.4 s; full FW, 73.4 ± 66.5 s); some birds flew toward the model almost immediately, while others appeared to watch the model for a considerable time before making their first flight.

As predicted, significantly more males approached the playback apparatus when cowbird whistles were broadcast (regardless of FW type) than when Song Sparrow songs were broadcast (Table 1). There was no significant difference in the tendency to approach among males in the three experimental groups ($G_{adj} = 0.32$, 2 df, $P < 0.9$). Furthermore, of those males that did approach the playback apparatus, males exposed to FWs approached significantly closer than did the control males (first half of FW, 12.6 ± 8.2 m; second half of FW, 13.0 ± 12.3 m; full FW, 15.8 ± 12.6 m; Song Sparrow song, 49.0 ± 7.9 m; $H = 8.41$, 3 df, $P < 0.05$). Here, again, there was no difference among the experimental groups ($H = 0.40$, 2 df, $P < 0.9$).

Another indicator of a response to FWs is the amount of time birds spend in sight during the 190-s playbacks. Male cowbirds exposed to Song Sparrow songs tended to spend only a short time in the area, while the males exposed to the first-half, second-half, or full FW remained in sight for a significantly longer period of time (first half of FW, 177.0 ± 40.0 s; second half of FW, 190.0 ± 0.0 s; full FW, 162.0 ± 45.0 s; Song Sparrow song, 75.5 ± 70.0 s; $H = 24.22$, 3 df, $P < 0.001$).

Most males in each of the experimental groups gave FWs in response to playbacks (Table 1). However, most control males also gave FWs during the playback period, usually when they flew off. As a result, there was no significant difference among the groups in the tendency to give FWs during playbacks (Table 1). This demonstrates how frequently FW vocalizations are used by male cowbirds.

An examination of the type of FW given by male cowbirds that responded to the playbacks (Table 1) reveals that males exposed to the second half of the FW or to the full FW tended to give the first half of the FW in response, as predicted. However, control males that gave FWs also tended to produce the first half, so the responses of males in the two experimental groups, while supporting our predictions, are in and of themselves perhaps not surprising. The critical response, then, is that of males exposed to the first half of the FW. Unlike males in the other groups, we predicted that these birds would emit the second half of the FW. Indeed, these males responded in the expected manner, with 12 of 14 producing the second half of the FW, rendering a highly significant effect overall (Table 1).

The mean total number of FW responses of any type was similar for all four playback types (first half of FW, 4.29 ± 4.08; second half of FW, 3.83 ± 4.02; full FW, 3.33 ± 1.94; Song Sparrow, 2.38 ± 1.06; $H = 0.67$, 3 df, $P < 0.80$). Figure 2 shows the percent of total vocal responses that consisted of partial FWs,

TABLE 1. Number of male Brown-headed Cowbirds that (1) approached model, (2) gave FWs, and (3) gave first- or second-half FW as their initial vocalization during playback of partial or complete cowbird FWs or Song Sparrow songs.

	Approach[a]		Flight whistles[b]		FW response[c]	
					First-half FW	Second-half FW
Playback type	Yes	No	Yes	No		
First-half FW	13	1	14	1	2	12
Second-half FW	8	1	6	3	6	0
Full FW	12	2	9	3	8	1
Song Sparrow	3	12	8	7	6	2

[a] $G_{adj} = 22.80$, 3 df, $P < 0.001$.
[b] $G_{adj} = 6.47$, 3 df, $P < 0.1$.
[c] $G_{adj} = 21.52$, 3 df, $P < 0.001$.

full FWs, or full FWs [reversed]. The results are similar to those using only the first vocal response; first-half FWs and full FWs (which have the first half FW as initial component) together comprise 72.3 and 74.4% of the responses during playback of the second half of the FW and playback of the full FW, respectively. This is consistent with our predictions but, as seen above, responses during playback of the control vocalization also strongly favored first-half FWs and full FWs (70.9%). Thus, the critical responses, once again, are those given to the first half of the FW. In this case, first-half FWs and full FWs accounted for only 22.7% of the responses, with the remaining vocalizations consisting of second-half FWs and full FWs [reversed]. The percentages used to produce Figure 2 were arcsine-transformed and compared, and the results support the observation that the total responses that are first-half FWs/full FWs differ among the four playback types ($H = 10.91$, 3 df, $P < 0.02$). Comparisons among the four playback types indicate that first-half FWs/full FWs were given significantly less to playbacks of first-half FWs than to full FWs (nonparametric Tukey-type test for multiple comparisons [Zar 1984], $Q = 2.878$, $P < 0.05$). A similar finding, albeit not significant statistically ($Q \approx 0.1$), occurs when responses to broadcast of first-half and second-half FWs are compared ($Q = 2.383$). No other comparisons approached significance.

Discussion.—Males of several passerine species that possess large song repertoires and sing with eventual variety are known to produce predictable vocal responses during interactions with conspecifics. For example, many territorial males match the song types of rivals (either neighbors or nonterritorial intruders) or respond at a stereotyped time interval during agonistic encounters (e.g. Hinde 1958, Kroodsma 1971, Lemon 1974, Smith and Norman 1979, Krebs et al. 1981, McGregor et al. 1992). This behavior may serve to direct responses to the bird that is being matched (J.-C. Brémond, cited *in* Armstrong 1973), a task that otherwise would be difficult to accomplish in a clamorous acoustic environment. Matching may indicate dominance relationships (Kroodsma 1979), and the

degree of matching may alert the receiver to changes in the motivational state of the singer (McGregor et al. 1992).

The above investigations describe matching behavior, and cowbirds in our study avoided matching the playback. Matching behavior requires that there be a pool of several different variants of the vocalization from which the birds may choose. Cowbirds do have song repertoires made up of several different song types, and these are shared throughout local populations (Dufty 1985). Therefore, male cowbirds could, conceivably, match song types during aggressive interactions; however, thus far no such relationship has been found between song type and context (West et al. 1981).

Birds possessing a single exemplar of a particular vocalization cannot signal a specific recipient, for the obvious reason that all birds produce the same sound. Most cowbirds have but a single flight whistle, but these contain two or more syllables that can be produced separately (Rothstein and Fleischer 1987). Cowbirds in our study used their two-part FWs antiphonally. That is, in response to the broadcast of one part of the FW, the recipient males tended to
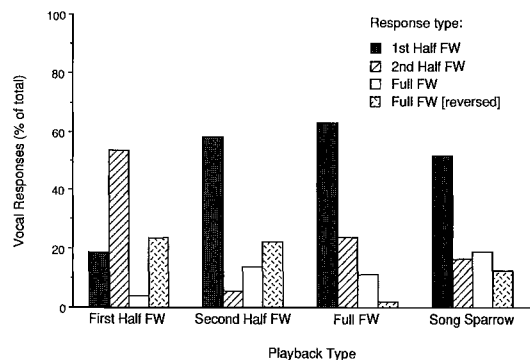

Fig. 2. Percent of all flight whistle responses during playbacks that were first-half FWs, second-half FWs, full FWs, or full FWs [reversed].

produce the missing part, regardless of which section was absent. This occurred both for the initial FW response, and for the overall pattern of responses during playbacks. Capp (1992) found similar results in Bobolinks (*Dolichonyx oryzivorus*), where males avoid song matching, using their two-song repertoires.

This kind of vocal avoidance may be functionally equivalent to song matching. Indeed, the same effect could be generated if cowbirds matched, rather than avoided, the FW section we broadcast. However, it is doubtful that FW matching would provide the same power, in terms of designating a recipient, as FW avoidance, because males typically produce the first half of the FW much more frequently than the second (Dufty pers. obs.; see also Table 1 and Fig. 2 for FWs produced during the control [Song Sparrow] playbacks). In other words, a male whose first FW syllable was matched would have difficulty determining whether he was receiving a specific reply, or simply hearing an unrelated vocalization from another male. In birds with larger repertoires, avoidance of matching is unlikely to be of functional value in directing vocal responses to particular recipients because of the large number of responses that would be necessary to distinguish such active avoidance from chance nonmatching replies (Whitney 1991).

One difficulty with our study is that the experimental design does not meet all of the criteria recommended by Kroodsma (1989). Thus, it remains to verify the external validity of the results, which requires expansion of the data set using flight whistles of additional cowbirds.

In summary, our results suggest that male cowbirds interact in a leader-follower manner, using a nonsong vocalization. We suggest that males give part or all of a FW when they traverse their large home ranges, or when they land at a new location in order to announce their presence and to canvass for conspecifics in the area. "Follower" responses not only denote the presence of a conspecific male, but may designate a particular individual, the "leader," as the recipient of the answering FW syllable. Whether this behavior is related to the expression of dominance in Brown-headed Cowbirds must await further investigation.

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LITERATURE CITED

ARMSTRONG, E. A. 1973. A study of bird song. Academic Press, New York.

CAPP, M. S. 1992. Tests of the function of the song repertoire in Bobolinks. Condor 94:468–479.

DARLEY, J. A. 1982. Territoriality and mating behav-

ior of the male Brown-headed Cowbird. Condor 84:15–21.

DUFTY, A. M., JR. 1982a. Movements and activities of radio-tracked Brown-headed Cowbirds. Auk 99:316–327.

DUFTY, A. M., JR. 1982b. Response of Brown-headed Cowbirds to simulated conspecific intruders. Anim. Behav. 30:1043–1052.

DUFTY, A. M., JR. 1985. Song sharing in the Brown-headed Cowbird (*Molothrus ater*). Z. Tierpsychol. 69:177–190.

DUFTY, A. M., JR., AND R. MCCHRYSTAL. 1992. Vocalizations and copulatory attempts in free-living Brown-headed Cowbirds. J. Field Ornithol. 63: 16–25.

FRIEDMANN, H. 1929. The cowbirds: A study in the biology of social parasitism. C. C. Thomas, Springfield, Illinois.

HINDE, R. A. 1958. Alternative motor patterns in Chaffinch song. Anim. Behav. 6:211–218.

KREBS, J. R., R. ASHCROFT, AND K. VAN ORSDOL. 1981. Song matching in the Great Tit, *Parus major* L. Anim. Behav. 29:918–923.

KROODSMA, D. E. 1971. Song variations and singing behavior in the Rufous-sided Towhee, *Pipilo erythrophthalmus oregonus*. Condor 73:303–308.

KROODSMA, D. E. 1979. Vocal dueling among male Marsh Wrens: Evidence for ritualized expressions of dominance/subordinance. Auk 96:506–515.

KROODSMA, D. E. 1989. Suggested experimental designs for song playbacks. Anim. Behav. 37:600–609.

LEMON, R. E. 1974. Song dialects, song matching and species recognition by Cardinals *Richmondena cardinalis*. Ibis 116:545–548.

MCGREGOR, P. K., T. DABELSTEEN, M. SHEPHERD, AND S. B. PEDERSEN. 1992. The signal value of matched singing in Great Tits: Evidence from interactive playback experiments. Anim. Behav. 43:987–998.

ROTHSTEIN, S. I., AND R. C. FLEISCHER. 1987. Vocal dialects and the possible relation to honest status signalling in the Brown-headed Cowbird. Condor 89:1–23.

ROTHSTEIN, S. I., J. VERNER, AND E. STEVENS. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77–88.

ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1986. Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free-living Brown-headed Cowbirds. Curr. Ornithol. 3:127–185.

ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1988. The agonistic and sexual functions of vocalizations of male Brown-headed Cowbirds, *Molothrus ater*. Anim. Behav. 36:73–86.

SMITH, D. G., AND D. O. NORMAN. 1979. "Leader-

follower" singing in Red-winged Blackbirds. Condor 81:83–84.

WEST, M. J., A. P. KING, AND D. H. EASTZER. 1981. Validating the female bioassay of cowbird song: Relating differences in song potency to mating success. Anim. Behav. 29:490–501.

WHITNEY, C. L. 1991. Avoidance of song matching in the Wood Thrush: A field experiment. Wilson Bull. 103:96–101.

YOKEL, D. A. 1989. Intrasexual aggression and the mating behavior of Brown-headed Cowbirds: Their relation to population densities and sex ratios. Condor 91:43–51.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Extrapair Paternity and Intraspecific Brood Parasitism in Eastern Bluebirds Revealed by DNA Fingerprinting

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Traditionally, mating systems have been classified on the basis of observed social relationships between males and females, but parentage of offspring may not reflect observed social bonds. Copulations between nonmates (extrapair copulations) are common in many monogamous birds (reviewed in Ford 1983, McKinney et al. 1984, Westneat et al. 1990), and recent genetic studies have shown that extrapair copulations can lead to extrapair fertilizations (e.g. Westneat 1987, Sherman and Morton 1988, Bollinger and Gavin 1991). In some monogamous species there is no evidence of extrapair paternity (e.g. Willow Warblers, *Phylloscopus sibilatrix*; Gyllensten et al. 1990), but in others as many as 40% of nestlings may be fathered by extrapair males (Tree Swallows, *Tachycineta bicolor*; Lifjeld et al. 1993).

Several factors are thought to influence the likelihood of extrapair copulations and extrapair paternity in birds. A high density of breeding individuals promotes extrapair copulations in colonial species (Møller 1985), and can also affect extrapair paternity in dispersed species (Gowaty and Bridges 1991a). Low breeding synchrony should encourage extrapair copulations by enabling mated males to guard their mates while they are fertile, and to pursue copulations with other females when their mates are not fertile (Birkhead and Biggins 1987, Westneat et al. 1990). In several species, younger males suffer more extrapair paternity than older males (Westneat 1987, Morton et al. 1990, Gowaty and Bridges 1991b).

Male birds protect their paternity primarily through mate guarding or frequent copulations with their mate (Birkhead and Lessells 1988). Males guard their mates through constant surveillance (Mumme et al. 1983,

Birkhead et al. 1987) and close following (Møller 1987, Birkhead and Lessells 1988) of females during the females' fertile periods.

Eastern Bluebirds (*Sialia sialis*) are secondary cavity nesters, which readily breed in nest boxes. They are socially monogamous, with extensive biparental care (Pinkowski 1978, Meek 1991). Male Eastern Bluebirds guard their mates (Gowaty et al. 1989, Meek and Robertson 1994), and allozyme electrophoresis has detected extrapair paternity in populations in South Carolina (Gowaty and Karlin 1984) and Arkansas (Karlin et al. 1990). Eastern Bluebirds and Tree Swallows compete aggressively for nest cavities in areas where the two species co-occur (Hersey 1933, Kuerzi 1941, Rustad 1972), and Meek and Robertson (1993) found evidence of a trade-off between mate guarding and territory defense in an Ontario population of Eastern Bluebirds. Competition between Eastern Bluebirds and Tree Swallows is more intense on bluebird territories containing multiple nest boxes than territories with a single nest box, with the consequence that male Eastern Bluebirds on multiple-box territories guard their mates significantly less than males on single-box territories (Meek and Robertson 1994).

We assessed the level of extrapair paternity in an Ontario population of Eastern Bluebirds. We examined the relationship between mate guarding and paternity by looking at the correlation between mate guarding and paternity for individual males, and by comparing paternity on territories with one nest box with territories having multiple nest boxes. We also assessed whether male or female age, first or second brood, or the breeding stage of the nearest neighbor was associated with extrapair paternity in our study.

Methods.—We studied a population of Eastern Bluebirds nesting in boxes in the vicinity of Chaffeys Locks, Ontario, Canada (44°34'N, 76°19'W) in the summers

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