

Do male Hooded Warblers guard their mates when their paternity is most at risk?

Bradley C. Fedy,¹ D. Ryan Norris,² and Bridget J. M. Stutchbury

Department of Biology, York University, 4700 Keele St., Toronto, Ontario, M3J 1P3, Canada

Received 23 October 2001; accepted 28 January 2002

ABSTRACT. Males of socially monogamous species may benefit from using behavioral tactics to ensure their paternity of the young produced by their social mates. We tested whether male Hooded Warblers (*Wilsonia citrina*) use mate guarding and high song output in an attempt to prevent extra-pair copulations (EPC) by their mates. In this species, most EPC intrusions occur when females produce conspicuous chip vocalizations. Using radiotelemetry, we tracked the male response to female chipping throughout her fertile and non-fertile periods. Our results show that males do not intensively guard their mates by closely associating with them or by increasing their song rate. Mate guarding was not influenced by male age or their own EPC behavior. Female influence on fertilizations and male pursuit of EPC may render mate guarding an ineffective strategy for ensuring paternity in Hooded Warblers.

SINOPSIS. ¿Vigilan los machos de *Wilsonia citrina* a su pareja cuando esta en mayor riesgo su paternidad?

Los machos de especie sociales monógamas pudieran beneficiarse en el uso de tácticas de conductas para asegurar la paternidad de los pichones que produce su pareja. Pusimos a prueba si los machos de *Wilsonia citrina* utilizaban la vigilancia cercana de la hembra y un incremento en las canciones para tratar de prevenir la copulación de su parejas con otros machos. En esta especie las copulaciones fuera de la pareja ocurren cuando la hembra produce una vocalización muy particular. Usando radiotelegrafía pudimos seguir a machos en respuesta a la vocalización particular de las hembras durante sus períodos fértiles e infértiles. Nuestros resultados demuestran que los machos no vigilan intensivamente a su pareja ya sea, pasando más tiempo asociada a ésta o incrementando su tasa de canto. La vigilancia de la pareja no fue influenciada para la edad del macho o por su propia conducta de copular con otras hembras. La influencia de la hembra en la fecundación y la persecución del macho para prevenir la copulación de su pareja con otros individuos pudiera ser una estrategia inefectiva para asegurar la paternidad en este tipo de ave.

Key words: EPC, female vocalizations, mate guarding, radiotelemetry, *Wilsonia citrina*

In species where extra-pair fertilizations (EPF) are known to occur, males face the threat of cuckoldry and loss of reproductive success. To protect their paternity, one option males have is to guard their mate during her fertile period (Møller and Birkhead 1991). Mate guarding can reduce the chances of other males gaining access to their mate, as well as prevent their female from initiating extra-pair copulations (EPC; Beecher and Beecher 1979; Westneat 1994; Kempnaers et al. 1995; Dickinson 1997; Chuang-Dobbs et al. 2001). Much of the evidence for mate guarding highlights the find-

ing that males consort with their mates more intensely in the fertile period than in the non-fertile period (e.g., Møller 1985; Sheldon 1994; Westneat 1994; Johnsen and Lifjeld 1995; Riley et al. 1995). However, females in most species are fertile for extended periods of time (Birkhead 1998). Following females closely may be costly by reducing the amount of time males can spend foraging or seeking EPC (Birkhead and Møller 1992). Mate guarding in certain circumstances may be an ineffective strategy for males to protect their paternity, especially if females exert considerable control over EPF (Lifjeld et al. 1994; Kempnaers et al. 1995; Stutchbury and Neudorf 1997).

We used radiotelemetry to examine mate guarding of Hooded Warblers (*Wilsonia citrina*), a socially monogamous Neotropical-Nearctic migrant that breeds in forests throughout the eastern United States (Evans-Ogden and Stutchbury 1994). Hooded Warblers have high

¹ Corresponding author. Current address: Department of Forest Sciences, Forest Sciences Centre, University of British Columbia, 3041-2424 Main Mall, Vancouver, British Columbia, V6T 1Z4 Canada. Email: <bfedy@interchange.ubc.ca>

² Current address: Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

rates of EPF (35% of broods, 27% of nestlings; Stutchbury et al. 1997), and both males and females actively leave their territories to seek EPC (Neudorf et al. 1997; Stutchbury 1998). When their social mates are fertile, males will chase intruding conspecific males off their territories (Stutchbury and Neudorf 1997; Stutchbury 1998), suggesting males invest time and energy protecting their paternity.

Female Hooded Warblers give "chip" calls often throughout their fertile and non-fertile periods (Stutchbury and Neudorf 1997). This species is especially interesting with respect to mate guarding because radiotelemetry has revealed that 78% of EPC attempts by neighboring males occur while females are chipping in the fertile period (Stutchbury 1998). Hence, males face the greatest risk of cuckoldry when their mates are chipping and fertile. Mate guarding is costly for males, and they should concentrate their efforts while the risks of EPF are greatest (Birkhead 1998). Given this, we expect male Hooded Warblers to guard their mates most intensely while the females are chipping in the fertile period.

We tested two predictions from the mate guarding hypothesis (Møller and Birkhead 1991): that males will associate closely with fertile females when they are chipping, and that males will join chipping females quicker and remain closer to them during the fertile period than in the non-fertile. Furthermore, Møller (1991) suggested that high song output during the female's fertile stage could function as a paternity guard by intimidating neighboring males poised to make an EPC attempt. Therefore, we also tested a third prediction that males will increase their song output while their females are fertile. In addition, we tested the prediction that males will increase song output specifically when females are chipping. We also tested several factors which have been shown to influence the intensity of mate guarding in birds. We examined whether male age affects mate guarding intensity, since in other species younger males may guard more intensely than older males to compensate for their higher risk of cuckoldry (Wagner et al. 1996). Mate guarding may also be costly in reducing the amount of time males can spend pursuing EPC (Westneat et al. 1990; Chuang-Dobbs et al. 2001). Therefore, we examine the extra-pair foray behavior of males to test our fifth prediction that

a negative correlation will exist between the extra-pair foray rate of males and the level of their mate guarding behavior.

METHODS

Our study was conducted from May–July 1999–2000 in Crawford County, northwest Pennsylvania (41°46'N, 79°56'W). Pairs were located in small forest fragments surrounded by roads, agricultural land, and residential land. Territories always occurred within a single forest fragment (based on >80% time spent singing), and any movements outside the fragment were considered "forays" to other fragments (Norris and Stutchbury 2001). Although fragments contained only one mated pair, forays for extra-pair matings were as common as EPC forays in high density, continuous forest (Norris and Stutchbury 2001). Microsatellite parentage analysis revealed that 21% of young were extra-pair (13/61) and 27% of nests (7/26) contained at least one extra-pair offspring in isolated fragments (B. Stutchbury et al., unpubl. data).

Male Hooded Warblers were caught in mist nets using playbacks and fitted with a 0.67-g radio transmitter (Holohil Systems Ltd., Woodlawn, Ontario, Canada). Transmitters were attached using a figure-eight loop harness made of lightweight cotton embroidery floss. The loops of the harness were fit over the bird's legs so the transmitter rested on the synsacrum and the 14-cm whip antenna extended along the bird's tail feathers. See Rappole and Tipton (1991) for details on harness construction. Transmitters do not affect the physical condition, locomotion, feeding rates (Neudorf and Pitcher 1997) or reproductive success (Neudorf et al. 1997) in Hooded Warblers. Fertile and non-fertile periods were determined by frequent nest checks (at least every second day). We defined the fertile period as five days before laying the first egg until the penultimate egg was laid (Neudorf et al. 1997). The incubation and nestling stages were considered the non-fertile period.

Males were tracked ($N = 11$) from the ground between 06:00 and 12:00 using handheld Yagi antenna (10.5 h per male on average). Tracking sessions were 2 h long and were separated by a minimum of 24 h. Researchers moved quietly and maintained a minimum distance of 30 m between themselves and the focal

Table 1. Male movements and song rates in response to chipping by their mate in the fertile and non-fertile period.

	Fertile	SE	Non-fertile	SE	z^a	P
Distance						
Initial distance (m)	27.1	3.5	29.5	5.3	-0.41	0.68
Closest approach (m)	20.6	4.1	16.0	4.9	-0.89	0.37
Maximum distance moved (m)	6.5	2.1	13.5	2.6	-2.09	0.04
Time						
Time of first move (s)	38	6	62	18	-0.89	0.37
% of time less than 10 m	31	6	40	9	-0.71	0.48
Song						
Song rate for each period (#/min)	4.5	0.5	4.1	0.5	-1.51	0.13
Song rate during chip bouts (#/min)	1.0	0.3	2.1	0.9	-0.87	0.39

^a Wilcoxon paired-samples test ($N = 11$ males).

birds to ensure they did not influence the bird's movements. Male response to "chipping" by their mates was recorded by measuring five variables: (1) initial distance between the male and female at the beginning of the chipping bout, (2) closest approach to female while chipping, (3) time to male's first movement from start of chipping bout, (4) proportion of time spent less than 10 m from the female, and (5) measures of song rate before, during, and after the chipping bout. Furthermore, the maximum distance moved was calculated by subtracting the closest approach from the initial distance to determine the maximum movement of the male bird towards his mate during a chipping bout.

Song rate was calculated as the number of songs per minute. Female chipping bouts were considered over when more than a minute passed between two chips.

Data were pooled for the fertile and non-fertile periods, and averages were calculated for each individual during the different periods. Data were not normally distributed so we used nonparametric tests. Data were analyzed with SPSS, and means (\pm SE) are presented.

RESULTS

Male behavior during the fertile period.

Contrary to our first prediction, males did not associate closely with fertile females when they were chipping (Table 1). The average closest approach was 20.5 m, and males spent only 31% of their time less than 10 m from the

female. Males also did not respond quickly to the onset of female chipping bouts, taking an average of 38 s before they moved for the first time. Female chipping bouts in the fertile period were 128 ± 19 s in duration. Males did not necessarily move toward the female when they began chipping, and the maximum distance moved indicates that on average males only moved 6.5 m toward their chipping female.

Male movements in fertile versus non-fertile period. If males mate guard in response to female chips, then males should approach females more closely, approach females quicker in response to chipping, and remain in closer proximity to females during chipping bouts in their mate's fertile than in their non-fertile stage. Contrary to these predictions, male behavior toward females did not vary between the fertile and non-fertile stages. There was no significant difference in closest approach, the time to first movement, or percent time less than 10 m from the female during the chipping bouts between the fertile and non-fertile period (Table 1). Contrary to expectations, maximum distance moved toward the female was significantly lower in the fertile period (6.5 m) than in the non-fertile period (13.5 m; $z = -2.09$, $P = 0.04$). The initial distance to the female did not differ between the fertile and non-fertile periods (Table 1), hence the lack of difference in maximum distance moved was not due to males remaining closer to their mates.

Male singing behavior. Male song rate

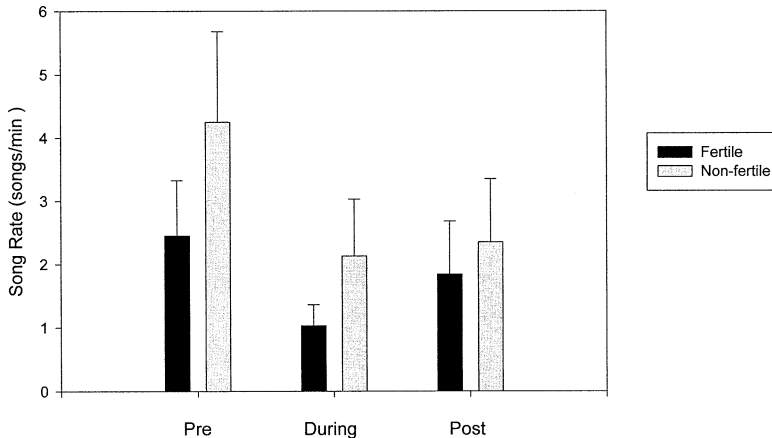


Fig. 1. Male song rate before, during, and after female Hooded Warbler chipping bouts ($N = 11$ males).

did not differ between the fertile (4.52 ± 0.53) and non-fertile (4.09 ± 0.50) periods ($z = -1.51$, $P = 0.13$). Male song rate was influenced by the onset of female chipping bouts in the opposite direction predicted from Møller's (1991) hypothesis. Male song rate was 2.5 songs/min prior to chipping bouts, but decreased to 1.0 songs/min during the chipping bout, with a subsequent increase following the female chipping (Fig. 1). The difference was close to significant (Friedman ANOVA, $\chi^2 = 5.4$, $P = 0.067$). Interestingly, males reduced song rate during chipping bouts even when females were not fertile (Friedman ANOVA, $\chi^2 = 6.2$, $P = 0.05$). Post hoc, non-parametric tests revealed that the significant difference existed only between song rates before and during the chipping bout.

Male age. The age of the resident males did not account for any difference in male behavior during the fertile period in closest approach (second-year males $N = 5$, after second-year males $N = 6$; $U = 11.0$, $P = 0.47$), the percent of time during the chipping bout that the male spent less than 10 m to his mate ($U = 8.5$, $P = 0.23$), or the maximum distance moved ($U = 8.5$, $P = 0.23$).

Foray behavior of males. Males may also differ in their time allocation between pursuing EPC and mate guarding, representing alternative strategies to siring young. The foray rate of males was not correlated with their closest approach to their own mate ($r_s = -0.09$, $P = 0.79$, $N = 11$), percent time less than 10 m to

chipping female ($r_s = -0.11$, $P = 0.75$, $N = 11$), or the maximum distance moved ($r_s = -0.10$, $P = 0.76$, $N = 11$). The percent of time males spent off territory also did not account for a significant amount of variation during the fertile period in any of the three variables above ($N = 11$ for all variables: closest approach $r_s = -0.05$, $P = 0.89$; percent time less than 10 m $r_s = -0.14$, $P = 0.68$; maximum distance moved $r_s = 0.18$, $P = 0.60$).

DISCUSSION

Male Hooded Warblers did not associate closely with their fertile mates during chipping bouts despite the high frequency of EPC and EPF (Norris and Stutchbury 2001; Norris, Stutchbury, Tuttle and Gonsar, unpubl. data) and the increased chance of male intrusion during female vocalization (Stutchbury 1998). Males did not approach their chipping mates more quickly or remain in closer proximity to them during the fertile than the non-fertile period. Furthermore, our four measures of mate guarding behavior did not vary with an individual's age, foray rate, or percent time spent pursuing EPC. All of our results suggest that males do not intensively use mate guarding as a strategy to ensure their paternity.

Although males may not systematically guard their mates, they will opportunistically break up EPC attempts when they are detected. However, Stutchbury (1998) found that males making EPC forays were detected by the territory

owners in only 20% of forays. This suggests that it is difficult for males to detect intruders on their territory and provides further evidence that mate guarding, by close association with the female, is not a prevalent strategy in male Hooded Warblers. We cannot know if males were guarding while their females were silent because females, like males, cannot be systematically monitored in this forested habitat without the use of radiotelemetry. However, 78% of all male intrusions during the fertile period occur while a female is chipping (Stutchbury 1998). Therefore, for mate guarding to be effective against EPC attempts it must occur during female chipping bouts in the fertile period and all of our data suggests that it does not. Other studies using continuous radio-tracking on this population have detailed accounts of males' foray behavior and use of edge habitat (Norris et al. 2000; Norris and Stutchbury 2001) outside of and during female chipping bouts.

Our study suggests that males do not elevate song output as a form of mate guarding because we found that males do not sing more when females chip and do not sing more when females are fertile. Males actually sang less during chipping bouts, not more, and the pattern was similar when females were fertile and non-fertile. This decrease in song rate during the chipping bouts is contrary to our prediction based on Møller's (1991) hypothesis that increased song rate during the fertile period could act as a form of mate guarding. It is possible that the observed decrease in male song rate during the chipping bouts exists to allow the male to increase his vigilance in an attempt to detect potential intruders. However, this explanation seems unlikely given the lack of movement toward chipping females by the resident male. Furthermore, the pattern of decreased song rate was similar between the fertile and non-fertile periods.

Why don't male Hooded Warblers closely guard their fertile mates, especially when females are chipping? Male Hooded Warblers may gain greater reproductive success by focusing their time and energy into obtaining EPF rather than guarding their mates. One of the main costs of mate guarding could be the time lost for pursuing EPC attempts with other females. Males who closely guard their females would presumably have less time available for

pursuit of EPC on other territories (Johnsen and Lifjeld 1995; Chuang-Dobbs et al. 2001). For most species the time investment in EPC forays has not been measured, making it difficult to test this hypothesis (Stutchbury and Neudorf 1997). In isolated fragments, male Hooded Warblers make long (30 min) forays (Norris and Stutchbury 2001), but females rarely leave their fragments and do not make frequent forays (Norris and Stutchbury, 2002). How much risk, in terms of cuckoldry, does a male assume by leaving his mate and territory for 30 min when she is fertile? The background level of EPF is 21% of offspring in this habitat, but the extent of the tradeoff depends on both the intrusion rate onto the territory and whether or not the female will mate with the intruder. Mate guarding is thought to be costly to males in other ways as well: increased energetic costs, decreased time for feeding (Komdeur 2001), increased risk of injury in fighting intruding males (Birkhead and Møller 1992), and less predator vigilance (Westneat 1994).

The mate guarding behavior of male Hooded Warblers may also be influenced by the habitat they breed in. Most data on the intensity of mate guarding in birds is derived from open habitat and/or colonial nest species (Birkhead and Møller 1992). Little information exists for species that use forest during their life history (Samson 1976; Wasserman 1980), and almost no quantitative studies have been conducted on non-colonial species that use dense forest throughout the breeding season (but see Chuang-Dobbs et al. 2001). These ecological factors may influence mate guarding and make it too costly to pursue as a primary form of paternity assurance.

Another important constraint on mate guarding in Hooded Warblers is female mate choice. In other species, mate guarding has been shown to be an ineffective paternity guard because females pursue EPC (Morton 1987; Morton et al. 1990; Kempanaers et al. 1995; Riley et al. 1995; Wagner et al. 1996). Female Hooded Warblers show the potential to influence EPC by refusal of copulation attempts and seeking EPC themselves on neighboring territories. Female Hooded Warblers have a high frequency of EPF (Stutchbury et al. 1997) and leave their territories only during their fertile period (Neudorf et al. 1997), strongly suggesting that females are pursuing EPC off territory.

The actual paternity of the young likely results from the dynamics of female and male extra-pair mating tactics and male-male competition. Given the importance of female influence on fertilization and male pursuit of EPC, males would not necessarily gain an increased confidence of paternity by closely mate guarding. Thus, on balance, the costs of mate guarding would seem to outweigh the potential benefits.

ACKNOWLEDGMENTS

We thank Mike Stone for field assistance. Kristine Johnson, Peter Dunn and two anonymous reviewers provided useful comments on the manuscript. Research support to DRN was provided by an Ontario Graduate Scholarship, Kenneth G. Molson Graduate Fellowship, and the Society of Canadian Ornithologists' Taverner Award. BJMS was funded by a research grant from the Natural Sciences and Engineering Research Council of Canada and a Premier's Research Excellence Award. We thank the many landowners in Crawford and Eric Counties who gave us permission to work in their woodlots.

LITERATURE CITED

- BEECHER, M. D., AND I. M. BEECHER. 1979. Sociobiology of Bank Swallows: reproductive strategy of the male. *Science* 205: 1282–1285.
- BIRKHEAD, T. R., AND A. P. MØLLER. 1992. Sperm competition in birds: evolutionary causes and consequences. Academic Press, London.
- . 1998. Sperm competition in birds: mechanisms and function. In: Sperm competition and sexual selection (T. R. Birkhead, and A. P. Møller, eds.), pp. 579–622. Academic Press, London.
- CHUANG-DOBBS, H. C., M. S. WEBSTER, AND R. T. HOLMES. 2001. The effectiveness of mate guarding by male Black-throated Blue Warblers. *Behavioral Ecology* 12: 541–546.
- DICKINSON, J. L. 1997. Male detention affects extra-pair copulation frequency and pair behavior in Western Bluebirds. *Animal Behaviour* 53: 561–571.
- EVANS-OGDEN, L. J., AND B. J. STUTCHBURY. 1994. Hooded Warbler (*Wilsonia citrina*). In: The birds of North America (A. Poole, and F. Gill, eds.), no. 110. Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, D.C.
- JOHNSON, A., AND J. T. LIJFELD. 1995. Unattractive males guard their mates more closely: an experiment with Bluethroats (Aves, Turdidae: *Luscinia s. svecica*). *Ethology* 101: 200–212.
- KEMPENAERS, B., G. R. VARHEYEN, AND A. A. DHONDT. 1995. Mate guarding and copulation behaviour in monogamous and polygamous Blue Tits: do males follow a best-of-a-bad-job strategy? *Behavioral Ecology and Sociobiology* 36: 33–42.
- KOMDEUR, J. 2001. Mate guarding in the Seychelles Warbler is energetically costly and adjusted to paternity risk. *Proceedings of the Royal Society of London B* 268: 2103–2111.
- LIJFELD, J. T., P. O. DUNN, AND D. F. WESTNEAT. 1994. Sexual selection by sperm competition in birds: male-male competition or female choice? *Journal of Avian Biology* 25: 244–250.
- MØLLER, A. P. 1985. Mixed reproductive strategy and mate guarding in a semi-colonial passerine, the Swallow *Hirundo rustica*. *Behavioral Ecology and Sociobiology* 17: 401–408.
- . 1991. Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *American Naturalist* 138: 994–1014.
- , AND T. R. BIRKHEAD. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour* 118: 170–186.
- MORTON, E. S. 1987. Variation in mate guarding intensity by male Purple Martins. *Behaviour* 101: 211–224.
- , L. FORMAN, AND M. BRAUN. 1990. Extra-pair fertilizations and the evolution of colonial nesting in Purple Martins. *Auk* 107: 275–283.
- NEUDORF, D. L., AND T. E. PITCHER. 1997. Radio transmitters do not affect nestling feeding rates by female Hooded Warblers. *Journal of Field Ornithology* 68: 64–68.
- , B. J. M. STUTCHBURY, AND W. H. PIPER. 1997. Covert extraterritorial behavior of female Hooded Warblers. *Behavioral Ecology* 8: 595–600.
- NORRIS, D. R., AND B. J. M. STUTCHBURY. 2001. Extraterritorial movements of a forest songbird in a fragmented landscape. *Conservation Biology* 15: 729–736.
- , AND ———. 2002. Sexual differences in the gap-crossing ability of a forest songbird in a fragmented landscape revealed through radio-tracking. *Auk* 119: 528–532.
- , ———, AND T. E. PITCHER. 2000. The spatial response of male Hooded Warblers to edges in isolated fragments. *Condor* 102: 595–600.
- RAPPOLE, J. H., AND A. P. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62: 335–337.
- RILEY, H. T., D. M. BRYANT, R. E. CARTER, AND D. T. PARKIN. 1995. Extra-pair fertilizations and paternity defence in House Martins, *Delichon urbica*. *Animal Behaviour* 49: 495–509.
- SAMSON, F. B. 1976. Territory, breeding density, and fall departure in Cassin's Finch. *Auk* 93: 477–497.
- SHELDON, B. C. 1994. Timing and use of paternity guards by male Chaffinches. *Behaviour* 129: 79–97.
- STUTCHBURY, B. J. M. 1998. Extra-pair mating effort of male Hooded Warblers (*Wilsonia citrina*). *Animal Behaviour* 55: 553–561.
- , W. H. PIPER, D. L. NEUDORF, S. A. TAROF, J. M. RHYMER, G. FULLER, AND R. C. FLEISCHER. 1997. Correlates of extra-pair fertilization success in Hooded Warblers. *Behavioral Ecology and Sociobiology* 40: 119–126.

- , and D. L. NEUDORF. 1997. Female control, breeding synchrony, and the evolution of extra-pair mating systems. *Ornithological Monographs* 49: 103–121.
- WAGNER, R. H., D. S. MALCOLM, AND E. S. MORTON. 1996. Condition-dependent control of paternity by female Purple Martins: implications for coloniality. *Behavioral Ecology and Sociobiology* 38: 379–389.
- WASSERMAN, F. E. 1980. Territorial behavior in a pair of White-throated Sparrows. *Wilson Bulletin* 92: 74–87.
- WESTNEAT, D. F. 1994. To guard mates or go forage: conflicting demands affect the paternity of male Red-winged Blackbirds. *American Naturalist* 144: 343–354.
- , P. W. SHERMAN, AND M. L. MORTON. 1990. The ecology and evolution of extra-pair copulations in birds. *Current Ornithology* 7: 331–369.