

Mating Behavior of Reed Buntings (*Emberiza schoeniclus*) in Captivity

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ABSTRACT.—We studied sexual pair behavior and cuckoldry of nine female and five male Reed Buntings (*Emberiza schoeniclus*) in a large outdoor aviary. Three males established small territories and paired with females. We observed 23 copulation attempts with identified partners during a period of approximately 6 weeks, 10 between social mates, 12 between unpaired females and paired males (extrapair for males), and one between a paired female and a paired male which was not the social mate (extrapair for both). Both males and females initiated copulation attempts which, in most cases, were preceded by precopulatory displays. No forced copulations were observed and females appeared to have an active role in mating behavior. Received 2 October 2006. Accepted 15 December 2006.

Paternity analyses have revealed the majority of socially monogamous birds are genetically promiscuous (e.g., Birkhead and Møller 1992, Westneat and Stewart 2003). Surprisingly little is known about the actual mating behavior in contrast to a flood of genetic data. Detailed knowledge of events that lead to copulations is crucial for deciding whether extrapair behavior is male or female-driven, or both (Westneat and Stewart 2003). Observations of extrapair copulations in the field are scarce and studies of birds in captivity may yield more data on this behavior. The rate of extrapair paternity (EPP) in the Reed Bunting (*Emberiza schoeniclus*) is one of the highest reported in socially monogamous birds (Westneat and Stewart 2003). It ranges from 30 to 55% of the young (Dixon 1993, Buchanan 2001, Kleven and Lifjeld 2005, Bouwman et al. 2006; EN, unpubl. data). However, observations of extrapair copulations (EPCs) in this species are rare (Bouwman et al. 2006); to our knowledge there are no published data on which partner initiates copulations. Marthin-

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sen et al. (2005) observed intrusions of extra-pair males into female territories. That suggests that males intend to initiate EPCs, but it is not known how the female reacts to these intrusions and whether she intrudes into extra-pair male territories (Kleven et al. 2006). The objective of our study is to provide detailed descriptions of copulatory behavior in the Reed Bunting with social mates as well as with extra-pair partners. We investigated this behavior in a large outdoor aviary where males and females had access to different mating partners.

METHODS

Fourteen Reed Buntings (9 females, 5 males) were studied in captivity from mid-June to late July 2005 at the Konrad Lorenz Institute in Vienna, Austria. They had been caught one and one-half year before observations started. The color-ringed birds were kept together with 10 Bearded Tits (*Panurus biarmicus*) in an outdoor aviary. The aviary was 78.8 m² in area and consisted of 14 interconnected rectangular compartments (3 × 1.88 m). The maximal height was 3.20 m. Each compartment contained pots with sedges and dead reed stems, willow (*Salix* spp.) branches, and bamboo (*Phyllostachys aurea*). Pine (*Pinus* spp.) twigs were attached to the walls because they have been demonstrated to be used as nest sites by captive Reed Buntings (Giebing 1995). All nests except one were built in small wicker baskets, 5 cm in diameter, mounted with wire on reed stems or pine twigs at a height of 0.5–1.8 m. Sufficient nesting material (dog and horse hair, dried grass) was placed in each compartment. We provided *ad libitum* mealworms, ant pupae, crickets, and soft food with various seeds, insects, and mussels. Territory sizes ranged from one to six compartments and each territory had at least one feeding place. The entire aviary was divided between territorial males and there were no neutral or common feeding grounds. Three of the five males were paired.

Pairs or individuals were observed for 1–3 hrs (all pairs in 40 hrs total) between 0800 and 1800 hrs CET. Either the male's social mate or a female in the territorial neighborhood was fertile during observation. We ascertained social pairs by mate guarding and the male's participation in incubation or feed-

ing of young. We recorded the distance between pair members every 2 min similar to Marthinsen et al. (2005) to investigate mate guarding. The male followed his mate in close proximity, more or less constantly, in this period. We defined the time a male spent within 3 m of the mate as time spent mate guarding. Mate guarding was clearly distinguishable from periods without mate guarding when males showed little interest in their mates. Unpaired females were not mate-guarded or relegated to one territory. We scored copulations of these females with paired males as EPCs for males. We classified copulation attempts as male or female initiated when we were able to observe precopulatory behavior. We scored copulation attempts as female initiated if the female approached the male first or showed a soliciting display. All other cases were classified as male initiated.

OBSERVATIONS

Males sang and defended their established territories and, after pair formation, females started building nests. Twenty-five of 28 broods failed due to predation. We could not ascertain the type of predators responsible but the most likely candidates were mice (*Mus musculus*, *Apodemus* spp.), snakes (Colubridae), and weasels (*Mustela* spp.). We assume they gained access to nests through small gaps and holes in the aviary. Only 11 chicks fledged from the three successful nests from May to July.

Three of the five males in the aviary mate guarded their females 36 to 100% of the observed time (8 observation sessions). The earliest mate guarding observed was 7 days before egg-laying. Mate guarding did not occur after the day the second egg of the clutch was laid.

Copulation attempts ($n = 25$) occurred between day 4 of the pre-egg-laying phase and day 2 after the first egg. All but one occurred on the ground. We observed 17 successful and eight failed copulation attempts (Table 1) within 9–11 different pairs. Only three of these pairs were social pairs (10 copulation attempts). Six females and 3–5 males were involved in all attempts; in two cases male identity could not be ascertained. Within pairs, unsuccessful attempts failed because females rejected males. EPCs of paired males with un-

TABLE 1. Copulation attempts of captive Reed Buntings (within-pair [WP], extrapair [EP], with unidentified males [?]).

	Failed	Successful	Initiation by male	Initiation by female	Initiation unknown
WP	2	8	1	3	6
EP paired males - unpaired females	3	9	3	4	5
EP paired males - paired females	1				1
? Unidentified males - unpaired females	2		1	1	

paired females failed because females rejected males ($n = 2$) or the attempt was interrupted by the social female ($n = 1$). We observed one unsuccessful EPC attempt between a paired male and a paired female, which were not social partners. It failed, because an unidentified male interfered. The two additional unsuccessful copulation attempts with unpaired females and unidentified males failed because females rejected the attempts.

We were able to observe the behavior preceding copulations in only 13 of 25 mating attempts. Copulations occurred on two of these 13 occasions without any preceding displays. In all other cases precopulatory behavior consisted of more or less complex interactions between males and females. Our observations showed that both males and females initiated copulation attempts (Table 1). Males showed a complex precopulatory courtship display (the 'fluffed-run' [Andrew 1957]) in 77% (10/13) of the cases. The fluffed run occurred in open spaces on the ground when males made a series of swift runs towards or in a circle around the female with a more or less vertical, sometimes erect body, bent legs, ruffled feathers on rump and head, the bill occasionally lowered, trailed wings, and a spread and drooped tail. Before mounting, males approached females from behind and hovered over them, standing with flapping wings, looking down, and then attempted to copulate. The bodies of the females during copulation were horizontal, the tails erect, so that cloacae could come in contact. The males flew some distance (0.5–1.5 m) after copulating for approximately 3–4 sec. Males started the fluffed run either before females were approaching them (4/10) or when females were already nearby (6/10). Females approached singing males three times. On two of these occasions, males ceased singing and started the fluffed run; in one case the male continued

to sing at low volume during the fluffed run. These were the only observations where male song preceded a mating attempt. Males performing a fluffed run were attacked by neighboring males at least three times. In one copulation attempt a female displayed a fluffed run in reaction to the mate's fluffed run.

We found high plasticity in female behavior connected to copulations. Both paired and unpaired females approached displaying or non-displaying males (8/13) to initiate copulations (Table 1). On two occasions, females rejected copulation attempts by a bill forward gesture towards the males, which already hovered over them. In one case the rejected male was the social partner. One unpaired female gave the female soliciting display (Andrew 1957) twice when a male was nearby. In this display, the female crouched with her body in a horizontal posture and the bill, head, and tail were raised while she rapidly quivered her raised wings. We did not observe a female performing this soliciting display in reaction to the male's courtship run.

We observed male post-copulatory behavior on one occasion when a male became prostrate on the ground with the bill pointing upwards. When the male gave this display, the female mounted, and the male disengaged himself by walking forward.

DISCUSSION

Mating was often initiated with displays described by Andrew (1957). Copulations occurred on only two occasions without any preceding displays. Precopulatory interactions were a complex behavioral chain consisting of male and female displays to demonstrate the inclination to copulate. Reed Bunting males, in contrast to three other Emberizinae species (Andrew 1957), often displayed with an erect head. In this position their black badge, which extends from their submoustachial white

stripe to the upper breast, was clearly visible. Badge color was correlated with fertilization success in a Dutch population (Bouwman et al. 2006). The fluffed run could have developed to present the male's plumage features provided that females choose between males. One male sang during his fluffed run on one occasion, indicating that song might also be an indicator of male quality as shown by Bouwman et al. (2006).

We observed a male post-copulatory behavior which had only been reported once for the Reed Bunting (Andrew 1957), but which is common in the Yellow-breasted Bunting (*Emberiza aureola*). This was the prone-display ('head-up-lie-flat') (Masatomi and Kobayashi 1982) which resembles the female's soliciting display. The female reaction to the male prone-display was mounting in the Reed Bunting as well as in the Yellow-breasted Bunting. Male post-copulatory and reversed sexual displays have been described for other Emberizinae species (Andrew 1957) and are known in passerine and non-passerine species (e.g., Lorenz 1941, Nero 1982). The function of this display is enigmatic in the Reed Bunting as it is in other species. It possibly may have a role in pair bond maintenance or signaling a successful copulation (Johnson et al. 2000).

Males spent a considerable amount of time mate guarding and ceased guarding after the second egg was laid as reported by Marthinsen et al. (2005). The frequency of copulation attempts was probably influenced by the specific situations in the aviary. Thirteen of 25 copulation attempts were extrapair for males and we observed only one paired female copulating with an extrapair male. Our results are probably not directly applicable to field conditions due to the female biased sex ratio and good mate guarding conditions in the aviary. However, our observations reveal that females actively engage in sexual behavior and we are not convinced that females behave completely different in the field. No copulation appeared to be forced by the male. In both within-pair and extrapair copulation attempts, females could show their willingness for copulation by approaching the male and were able to reject copulations. It seems doubtful that females have a passive role in cuckoldry as proposed by Marthinsen et al. (2005). We expect that

female Reed Buntings are able to selectively accept and reject EPCs in the field.

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LITERATURE CITED

- ANDREW, R. J. 1957. The aggressive and courtship behaviour of certain Emberizines. *Behaviour* 10: 255–308.
- BIRKHEAD, T. R. AND A. P. MØLLER. 1992. Sperm competition in birds: evolutionary causes and consequences. Academic Press, New York, USA.
- BOUWMAN, K. M., R. E. VAN DIJK, J. J. WIJENGA, AND J. KOMDEUR. 2006. Older male Reed Buntings are more successful at gaining extrapair fertilizations. *Animal Behaviour* 73:15–17.
- BUCHANAN, G. 2001. Mate choice in Reed Buntings (*Emberiza schoeniclus*). Dissertation. University of Sunderland, Sunderland, United Kingdom.
- DIXON, A. 1993. Parental investment inversely related to degree in extrapair paternity in the Reed Bunting (*Emberiza schoeniclus*). Dissertation. University of Leicester, Leicester, United Kingdom.
- GIEBING, M. 1995. Die Rohrammer (*Emberiza schoeniclus*) in Menschenobhut. *Die Voliere* 18:52–54.
- JOHNSON, K. P., F. MCKINNEY, R. WILSON, AND D. SORENSON. 2000. The evolution of postcopulatory displays in dabbling ducks (Anatini): a phylogenetic perspective. *Animal Behaviour* 59:953–963.
- KLEVEN, O. AND J. T. LIFJELD. 2005. No evidence for increased offspring heterozygosity from extrapair mating in the Reed Bunting (*Emberiza schoeniclus*). *Behavioral Ecology* 16:561–565.
- KLEVEN, O., G. MARTHINSEN, AND J. T. LIFJELD. 2006. Male extraterritorial forays, age and paternity in the socially monogamous Reed Bunting (*Emberiza schoeniclus*). *Journal of Ornithology* 147:468–473.
- LORENZ, K. 1941. Vergleichende Bewegungsstudien an Anatiden. *Journal für Ornithologie* 89:19–29.
- MARTHINSEN, G., O. KLEVEN, E. BRENNAN, AND J. T. LIFJELD. 2005. Part-time mate guarding affects paternity in male Reed Buntings (*Emberiza schoeniclus*). *Ethology* 111:1–13.
- MASATOMI, H. AND S. KOBAYASHI. 1982. Mating behaviour of the Yellow-breasted Bunting *Emberiza aureola*. *Journal of the Yamashina Institute for Ornithology* 14:306–324.
- NERO, R. W. 1982. Post-copulatory display in the Lark Bunting and other species. *Wilson Bulletin* 94: 585–590.
- WESTNEAT, D. F. AND I. R. K. STEWART. 2003. Extrapair paternity in birds: causes, correlates, and conflict. *Annual Review of Ecology, Evolution and Systematics* 34:365–396.