

Extra-pair copulation and extra-range movements in Flammulated Owls

Richard T. Reynolds, Rocky Mountain Forest and Range Experiment Station, 222 South 22nd Street, Laramie, WY 82070, USA.

Brian D. Linkhart, 2051 West Caley Avenue, Littleton, CO 80123, USA.

We report an extra-pair copulation (EPC) in the Flammulated Owl *Otus flammeolus*, the first in strigiforms, and document 21 cases of extra-range movements (ERMs) in this species. Extra-range movements occurred throughout nesting with both sexes participating: males anytime during nesting and females only after their young fledged. Males appear to make ERMs to gain EPCs and later to evaluate resources and the status of males in other areas, whereas females may be assessing the success of nests in adjacent ranges to judge the quality of potential future mates.

Recent studies have shown that extra-pair copulations (EPCs) in many birds are frequent in spite of a variety of mate-guarding strategies. McKinney et al. (1984) and Ford (1983) together list 115 birds in 30 families in which EPCs have been reported. No strigiforms appear on these lists. Ford (1983) discussed the adaptive significance of EPCs and associated extra-range movements (ERMs) of males holding "Type A" territories. Møller (1987) reviewed three main hypotheses regarding intrusions by individuals into the territories of others (the territorial establishment hypothesis (Howard 1920, Morse 1976), the non-territorial holder hypothesis (Kacelnik and Krebs 1983), and the sperm competition hypothesis (Hinde 1956, Ford 1983)) and discussed the predictions of each according to, among others, the timing of intrusions (daily, seasonal) and the intruder's sex. We report an EPC in the Flammulated Owl *Otus flammeolus* and document 21 cases of ERMs in this species, some of which were intrusions that are not directly predicted by either of the hypotheses.

The breeding biology of Flammulated Owls was studied in Colorado, U.S.A., from 1980–88 (Linkhart 1984, Reynolds and Linkhart 1987a, 1987b). This insectivorous and migratory owl is a dispersed nester in which males are the sole defenders of territories and the sole foragers from prior to egg-laying until shortly before the young fledge. Females remain close to the nest before laying and brood in the nest cavity until a few nights before fledging. Because males regularly forage as far as 200 m from the female during courtship feeding, the

Flammulated Owl is a "non-guarding" species (Birkhead et al. 1987). Although polygyny occurs in some strigiforms, especially in species that feed on small mammals and whose breeding dispersal is nomadic (Korpimäki 1988), there is no evidence of polygamy in the Flammulated Owl.

In spring, male Flammulated Owls returned to their traditional nesting home ranges before most females arrived. Returning females typically paired with their previous year's male unless he did not return. New females settling into our area sought unpaired males by moving in a more or less random route, announcing their presence and soliciting food from males by begging continuously. Copulation was first observed 11 days before laying of the first egg, and pairs copulated at a mean rate of 0.8 times per hour (range = 0.4–1.4 copulations h⁻¹, n=4 pairs, 17.5 h of total observation during the copulatory period). Each year eggs were laid over two weeks (29 May – 14 June) and clutches consisted of 1–3 eggs ($\bar{x}$ =2.7 eggs, n=11) (Reynolds and Linkhart 1987b). The mean nearest-neighbor distance between nests was 506 m (SD=215.5, range = 195–1030 m, n=24) and the mean home range estimate from telemetry was 14.1 ha (SD=5.0, range = 8.5–24.0 ha, n=7) (Linkhart 1984). Radio-telemetry indicated that Flammulated Owls preferred to forage in old-growth forests of ponderosa pine *Pinus ponderosa* mixed with Douglas-fir *Pseudotsuga menziesii* (Linkhart 1984).

Owls were banded with U.S. Fish and Wildlife Service leg bands that were visible on released owls with a flashlight. Females were easily captured throughout nesting, whereas only males associated with nests or nestlings could be captured and banded (Reynolds and Linkhart 1984).

Extra-pair copulation

On 6 June 1981 at 2130 hours (MDT) we captured and banded a female Flammulated Owl in the home range of male A12. During the course of the night (2130–0330 hours) we followed the female from this range, where she was being fed by the A12 male, on a 1260 m circuitous route that took her to the edge of three other male

ranges and eventually back to A12. Throughout this trip the female begged loudly and was approached and, at least in one case, fed by males in the ranges she visited.

Because females are typically paired with males by the third week of May, we assumed that this female was a late arrival to our area. However, when captured she weighed 74.0 g (15 g above mean post-breeding female mass) suggesting that courtship feeding had been in progress (Reynolds and Linkhart 1987b). Alternatively, because the A12 male occupied a relatively small patch of old-growth ponderosa pine-Douglas-fir, and each of the three males she visited were in large contiguous stands of old-growth, it was possible that the female was attempting to locate an unpaired male in more suitable habitat.

At 2300 hours on 11 June, we again found the female (she was the only female banded on the study area at this time) in home range A12. She continually begged for food, and between 2400–0240 hours the A12 male fed her 10 moths and copulated with her three times. Each time the male approached the female he gave the “location call” (Reynolds and Linkhart 1987b). At 0102 hours the male approached from the center of his territory (upslope and to the south) and gave location calls from several meters south of the female. The female responded by leaning toward him into a horizontal position rocking from side to side. The male flew in and copulated with her. At 0211 hours we heard location calls of a male to the northwest of the begging female, and discovered a male in a quaking aspen *Populus tremuloides* sapling 10 m west of the female. Almost immediately we heard location calls of the A12 male to the south. When the A12 male flew in and copulated with the female the intruder dropped from his perch into shrubbery. At 0213 hours the A12 male departed to the south. Two minutes later, the intruder silently approached the female and copulated with her. At 0224 hours we again observed the intruder perched quietly 10 m from the female. At 0225 hours the intruder flew to and mounted the female. Both owls subsequently fell off their perch. Eight min later the intruder attempted another copulation and again both owls fell from the perch before cloacal contact. At 0238 hours the intruder successfully copulated with the female with no preliminary vocalizations. The A12 male returned at 0247 hours, gave location calls, and copulated with the female. The intruder was no longer visible.

On the night of 16 June 1981, the female was in the approximate center of A12’s range and was being fed by him. In spite of an intensive search, the nest of this pair was not found and we concluded that the owl’s nest had probably failed.

Extra-range movements

During the eight years of the study we observed 21 cases of resident males or females moving beyond their normal range limits (typically > 200 m from their nests, Linkhart 1984). Of these ERMs, three occurred during the egg-laying period, five during incubation, seven during the nestling stage, and five after the young had fledged (Tab. 1). In 19 of the ERMs the owls intruded into the home range (14 of these to the nest) of another pair, while two ERMs involved owls exploring 200–400 m from their ranges but not into the ranges of others.

Tab. 1. Extra-range movements by sex and stage of nesting in Flammulated Owls.

	Egg laying		Incubation		Nestling			Fledgling		
	M	F	M	F	M	F	Un ^b	M	F	Un ^b
Intruder visited nest	1	–	4	–	4	–	3 ^c	–	2	–
visited home range	1	–	1	–	–	–	–	1	–	2
Exploring ^a	1	–	1	–	–	–	–	–	–	–
Intruder known to be paired	–	–	3	–	2	–	–	–	2	–
Total extra-range movements	3		6		6			5		

^aextra-range movement that did not intrude on another home range.

^bsex unknown.

^ctwo owls (probably a pair) intruded simultaneously.

The identity, sex, and reproductive status of the participants in seven of these movements were known as each of the seven had a radio-transmitter. The sex of two non radio-tagged males was determined by the behaviour of one during the EPC described above, and another in interactions with a resident female who had lost her clutch (see below). Home ranges and sex of three additional males were known because we had followed two from their ranges and determined the third on the basis of its voice prior to, and from the direction of, its intrusion. Four additional intruders were judged to be males by the aggressive behavior directed at them by resident males. Finally, the sex and home range of five intruders were unknown (Tab. 1).

Five ERM’s involved males and two involved females that were radiotagged and known to be nesting. In one case, both members of a radio-tagged pair made an ERM; the male during the nestling period and the female shortly after her young had fledged. Another radio-tagged male intruded to nests in two adjacent territories during the incubation period. Only three (15%) ERMs, all by males, occurred during the egg-laying period, and in only one of these were interactions of the intruder with a resident female observed (see EPC above). However, because the egg-laying period is about 10 days shorter than the incubation, nestling, and fledgling periods, and fewer pairs were under observation during this early period, the frequency of ERMs during egg-laying may be higher than our data suggest. All intruding males and females were silent and furtive. In several cases, resident males monitored the intruder’s movements by staying close, giving territorial calls, or chasing. Intrusions to nests lasted 2–30 min. and intruders of both sexes typically perched within 3–5 m of the residents nest and quietly observed their activities.

In general, males made more ERMs in the early half of nesting, and females more in the latter half. This is

expected if males are seeking EPCs when females are fertile. Intrusion by males after the egg-laying period may reflect the possibility of gaining EPCs with late-arriving females or with females laying replacement clutches. In fact, we observed a begging female who had lost her clutch two weeks earlier being fed by her mate and a second male. ERMs by males later in nesting may function in the evaluation and comparison of nest sites and home ranges and to determine the status of neighboring males (Nolan 1978, Buitron 1983). Although we reported earlier (Reynolds and Linkhart 1987a) that males, once they are established in suitable habitat, do not change home ranges in subsequent years, two recent observations suggest that they may abandon a home range or shift their ranges into new areas. One of these involved the A12 male, whose range contained only several ha of the preferred foraging habitat, and who was known to have successfully nested only in 1984, 85, and 86. In the spring of 1987 this male and his mate of two years moved to an adjacent range that was entirely old-growth ponderosa pine and Douglas-fir and whose prior occupants fledged young in six of the seven previous years. The second involved a male who expanded his 1984 range the next spring into an adjacent range when its prior occupant did not return. The male achieved this expansion by regularly day-roosting within 15 m of the traditional nest of the prior occupant.

Females, probably because of their incubation and brooding duties, do not make ERMs until after fledging. We suggest that females visit nests in adjacent ranges to assess the nesting experience of neighboring males, and by so doing are hedging the bet that their mates may not return the next year. Reynolds and Linkhart (1987a) demonstrated that experienced Flammulated Owls fledged more young, and proposed that this was related to the male's previous experience with the spatial and temporal variation in food resources, with flight lanes to and from nests, and with the defense of his territory. When a female's previous male did not return in spring, she typically abandoned her home range and paired with an experienced male in an adjacent range. Six of seven experienced females whose mates did not return paired with males on an adjacent range and both observed ERMs by radio-tagged females were to nests in adjacent ranges. Furthermore, in 10 cases in which females paired with different males, only two did so with males whose histories were unknown to us.

Each of the radio-tagged females that made ERMs had fledged three young, the maximum brood size observed in our study. The history of one of these females was unknown and she was not found nesting the following year. The other, however, made her ERM the year in which she first paired with a male who had nested on his home range the two previous years. The year after the ERM she moved to a new home range when her mate did not return. On the new range she paired with a male who had nested successfully there only the year

before, and she subsequently fledged two owlets the first year and three the next.

Although ERMs by male Flammulated Owls are similar to those of males of other species with Type A territories (Ford 1983 and references therein), females appear unique in that those who successfully nested participated in ERMs. There are few data from other species with dispersed nests, but females of some are known not to make ERMs (Black-billed Magpie *Pica pica*, Buitron 1983), while others temporarily leave their territories after failing at their initial nesting attempt (Prairie Warblers *Dendroica discolor*, Nolan 1978), or visit nesting territories of neighboring males but only during pair formation (Sparrowhawk *Accipiter nisus*, Newton 1986, p. 152), and for still others only the non-breeding female helpers at nests make ERMs (Florida Scrub Jay *Aphelocoma coerulescens*, Woolfenden and Fitzpatrick 1984). To the three hypotheses accounting for territorial intrusions discussed by Møller (1987), we suggest a fourth - the assessment of potential mates and/or surrounding habitat.

Acknowledgements - We thank J. Jeansen for help with field work. T. A. Gavin, G. D. Hayward, R. L. Knight, J. S. Marks, A. P. Møller and R. A. Ryder commented on earlier drafts.

References

- Birkhead, T. R., Atkin, L. and Møller, A. P. 1987. Copulation behaviour of birds. - *Behaviour* 101: 101-138.
- Buitron, D. 1983. Extra-pair courtship in Black-billed Magpies. - *Anim. Behav.* 31: 211-220.
- Ford, N. L. 1983. Variations in mate fidelity in monogamous birds. - *Current Orn.* 1: 329-356.
- Hinde, R. A. 1956. The biological significance of territories in birds. - *Ibis* 98:340-369.
- Howard, H. E. 1920. Territory in bird life. - John Murray, London.
- Kacelnik, A., and Krebs, J. R. 1983. The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. - *Behaviour* 83:287-309.
- Korpimäki, E. 1988. Factors promoting polygyny in European birds of prey - a hypothesis. - *Oecologia (Berl.)* 77:278-285.
- Linkhart, B. D. 1984. Range, activity, and habitat use by nesting Flammulated Owls in a Colorado ponderosa pine forest. M.S. Thesis, Colorado State Univ., Fort Collins.
- McKinney, F., Cheng, K. M. and Bruggers, D. J. 1984. Sperm competition in apparently monogamous birds. - In: R. L. Smith (ed.). *Sperm competition and the evolution of animal mating systems*. Acad. Press, New York, pp. 523-545.
- Møller, A. P. 1987. Intruders and defenders on avian breeding territories: the effect of sperm competition. - *Oikos* 48: 47-54.
- Morse, D. H. 1976. Hostile encounters among spruce-wood warblers (*Dendroica*, *Parulidae*). - *Anim. Behav.* 24: 764-771.
- Newton, I. 1986. The Sparrowhawk. - Poyser, Staffordshire, England.
- Nolan, Jr., V. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. - *Orn. Monogr.* 26: 1-595.
- Reynolds, R. T. and Linkhart, B. D. 1984. Methods and materials for capturing and monitoring Flammulated Owls. - *Great Basin Natur.* 44: 49-51.
- and Linkhart, B. D. 1987a. Fidelity to territory and mate in

Flammulated Owls. – In: Nero, R. W., Clark, R. J., Knapton, R. J. and Hamre, R. H. (eds.). Biology and conservation of northern forest owls: Symposium proceedings. USDA For. Serv. Gen. Tech. Rept. RM-142, Fort Collins, Colorado, pp. 234–238.
– and Linkhart, B. D. 1987b. The nesting biology of Flammulated Owls in Colorado. – In: Nero, R. W., Clark, R. J.,

Knapton, R. J. and Hamre, R. H. (eds.). Biology and conservation of northern forest owls: Symposium proceedings. USDA For. Serv. Gen. Tech. Rept. RM-142, Fort Collins, Colorado, pp. 239–248.
Woolfenden, G. E. and Fitzpatrick, J. W. 1984. The Florida Scrub Jay; demography of a cooperative-breeding bird. – Princeton Univ. Press, Princeton, New Jersey.

*A suggested antipredator function for snow-roosting behaviour in the Black Grouse *Tetrao tetrix**

Arto Marjakangas, Dept of Zoology, Univ. of Oulu, Linnanmaa, SF-90570 Oulu, Finland

Several studies suggest that grouse conserve heat in cold winter weather by snow-roosting. However, Black Grouse frequently snow-roost even in mild weather when it may not be necessary for energetic reasons, and in moist snow when there is the risk of being imprisoned after freezing of the snow. Thus, snow roosting may also have other important functions for Black Grouse, such as the avoidance of predators.

Both Eurasian and North American grouse (Tetraoninae) commonly roost in snow in winter. The snow roost is a cavity dug by the bird in deep snow, with about 5–15 cm snow above, and used for one resting period (e.g. Porkert 1969, Sulkava 1969, Godfrey 1970, Braun and Schmidt 1971, Watson 1972, Höglund 1980, Marjakangas 1986, Back et al. 1987).

Two hypotheses have been proposed to explain the primary function of snow-roosting behaviour. Many authors stress the importance of snow roosting for conserving energy during cold winter nights (e.g. Kuzmina 1961, Gullion 1970, Braun and Schmidt 1971, Höglund 1980). This view is based on the well-known thermo-insulative capacity of powdery snow. In contrast, Bergesrud and Gratson (1988) and Mossop (1988) argue that snow roosting principally serves as a means of avoiding predators, particularly raptors. There are examples of grouse surviving cold while roosting in conifers (Bergesrud and Gratson 1988). According to this view, the warm microclimate of the snow roost is an extra advantage.

If snow roosting has important antipredator significance, birds should not change their roosting tactic markedly in response to changes in weather conditions. However, there are few detailed data on roosting behaviour of grouse in relation to weather (Höglund 1980).

The purpose of this paper is to document that Black Grouse *Tetrao tetrix* frequently snow roost during weather conditions when it may not be necessary for energetic reasons.

The data were collected at three study sites in west-central Finland (64 and 65°N) during winter in 1977–1982 and 1988. Black Grouse are dark in color, highly gregarious, mostly arboreal when feeding, and dwell in relatively open habitats in winter, and so are rather easy to observe. Birds were watched in the morning from a blind through binoculars or a spotting scope at one winter feeding station supplied with oats at each study site. They were engaged in feeding only for a period of a few hours in the morning and spent the rest of the day roosting (Marjakangas 1986). If they went out of view, they were cautiously followed in an attempt to observe them settling for the night. Roosting was confirmed by watching Black Grouse leaving their roosting sites spontaneously in the morning or by flushing them. Air temperature, wind velocity, and suitability of snow for roosting were recorded continuously and/or instantaneously. During field work, ambient temperatures ranged from –34 to +3°C.

Goshawks *Accipiter gentilis* were often observed attempting to catch Black Grouse at the study sites, and carcasses of Black Grouse killed by Goshawks were sometimes found. Eagle Owl *Bubo bubo* and red fox *Vulpes vulpes* were other potential predators of Black Grouse observed. No Black Grouse were found to have been killed while snow-roosting.

There was readily penetrable top snow for roosting during 137 field days. Using –3°C as a lower limit for mild weather, observations of Black Grouse leaving snow roosts were made on 42 out of 111 days below –3°C and 13 out of 26 days at or above –3°C ($\chi^2 = 0.84$,