

Short communication

Extra-pair copulation and intraspecific nest intrusions in the Northern Goshawk *Accipiter gentilis*

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Detailed descriptions of the behaviour of individual birds engaged in extra-pair copulations (EPCs) are comparatively rare. This might be due to the fact that EPCs occur infrequently and/or that EPC-seeking males and females usually behave in a secretive manner (Birkhead & Møller 1992a). Even in birds of prey, often observed intensively in the field, detailed reports of EPCs are scarce (e.g. Birkhead & Lessells 1988, McGrady 1991, Sodhi 1991, Negro *et al.* 1992, Arroyo 1999). Observational data are important, however, as they can shed light on aspects of sperm competition (e.g. age and status of intruders, timing of EPC events, behaviour of the sexes), which may pass unnoticed in quantitative DNA-profiling studies.

The Northern Goshawk *Accipiter gentilis* is a socially monogamous, territorial raptor (Squires & Reynolds 1997, Rutz *et al.* in press) with a distinct division of sex roles during the breeding season. Males provision their mates and, later, their offspring with prey, whereas females incubate the eggs, care for the young and defend the nesting territory (Squires & Reynolds 1997). During the males' foraging trips, their mates remain unattended at the nest-sites, where they might either seek EPCs or become victim to forced copulation attempts by intruders. The latter case, however, is unlikely in the Goshawk, as females are about a third heavier than males (Squires & Reynolds 1997) and are therefore capable of fighting off unwanted copulation partners.

Male birds may reduce the risk of cuckoldry by two main strategies: (i) they can guard their mates by close following; or (ii) copulate with them at a high rate during the fertile period (Birkhead & Møller 1992a). Male Goshawks cannot follow their partners closely while hunting. They can, however, attempt to maximize the time spent near the nest, and hence their mates, when the probability of fertilization is high (i.e. close to and during egg-laying). This strategy is known as 'mate attendance' (Birkhead & Møller 1992a). Both mate attendance and frequent copulations have been recorded in the Goshawk (Holstein 1942, Møller 1987).

So far, only genetic evidence has existed for the occurrence of EPCs in the Goshawk (Gavin *et al.* 1998). In this paper the first observation of an EPC in this species is described, and nine cases of intraspecific nest intrusions are reported. Radiotracking data on the spatio-temporal organization and the behaviour of males of three breeding pairs were used to address predictions from the mate-attendance and frequent-mating hypotheses (Birkhead & Møller 1992a).

MATERIALS AND METHODS

All observations were made during a radiotracking study, conducted in the city of Hamburg (53°34'N, 9°59'E), Germany, in 1997–99 (Rutz 2003a). In each year, a single male Northern Goshawk was trapped near its nest, instrumented with a tail-mounted radio-transmitter (Biotrack Ltd, Dorset, UK; Kenward 1987) and subsequently monitored throughout the breeding season. Nest-sites of the pairs were located in a public park in the city centre (1997, this pair is henceforth referred to as Pair 1), in hospital grounds (1998, Pair 2) and in a large urban cemetery (1999, Pair 3). Birds were aged, and individually identified, using moulted primaries, which were found at the nest-sites (for method, see Bijlsma 1997: Male 1 in 1997, 4 years old; Male 2 in 1998, 3 years; Male 3 in 1999, ≥ 5 years). All three males had been paired to their partners in the two seasons preceding the respective year of data collection, suggesting that pair-bonds were well established. All pairs raised offspring in the year in which observations were made (three, three and four juveniles, respectively). For a detailed description of nest-sites, breeding individuals and diet composition of the pairs, see Rutz (2003a, 2003b, 2004).

Radio locations were made with an M-57 receiver (Mariner Radar Ltd, Suffolk, UK) and a three-element hand-held Yagi antenna. Goshawks were followed continuously by bicycle during half- or full-day tracking sessions (due to logistical constraints, focal observations could not be carried out at nest-sites to check for EPCs when the resident males were away). Sessions were conducted during the week and on weekends in an attempt to control for varying levels of human disturbance. Fixes were recorded every 10 min by homing-in on the tagged animal or by cross-triangulation (Kenward 1987). Additional fixes were taken opportunistically whenever possible. Goshawks in the city of Hamburg are used to the presence of humans (see Rutz 2003a, 2003b). The remarkable tameness of the birds and the infrastructure of the urban breeding habitat facilitated close monitoring. During 858 h of continuous radiotracking, 4791 standard locations were recorded, 52% based on direct observations.

The fraction of observation time that males spent within 50 m of the nest tree was used as a measure of their mate attendance efforts because: (i) direct observations, moulted feathers and faecal droppings indicated that the

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principal roost sites of all three females were situated within this area; and (ii) results were believed to be comparable with data collected by Holstein (1942) (analysed by Møller 1987) by observing untagged Goshawks from hides near their nests.

A copulation event was recorded if it was either witnessed or if copulation calls were heard (see Møller 1987). It cannot be ruled out that the sample of copulations inferred from calls (25% of a total of $n = 97$ copulations) included additional EPCs. To characterize seasonal and diurnal patterns of vocal activity, bouts of two main Goshawk call types were counted when tagged males were at their respective nest-sites: (i) the guttural, chattering 'kek-kek-kek ...'; and (ii) the plaintive, wailing 'whee-oo ... whee-oo ...' (see Penteriani 2001, and literature therein). A call bout was defined as a series of 'kek' or 'whee-oo' calls separated by a gap of at least 2 s from the next vocalization of the same individual. As it can be difficult to distinguish between male and female vocalizations under field conditions, all call bouts of a session were pooled to obtain a measure of 'overall' vocal activity at a particular nest-site. Copulation calls (see above) were excluded from this data set.

Only a strange male Goshawk appearing within 250 m of the nest was considered to be an intruder and potential EPC partner, i.e. Goshawks showing territorial displays outside the inner nesting area were excluded. In all cases of intraspecific interaction, resident breeding males could be identified by their radiotags. None of the resident females was colour-ringed, and no rings were observed on any of the intruding birds. Intruders could be sexed readily by their size (Squires & Reynolds 1997). Birds could sometimes be aged on the basis of plumage pattern and colour (Cramp & Simmons 1980). The start of egg-laying was calculated by backdating from nestling wing length when ringed (Kenward *et al.* 1993, Bijlsma 1997), and all data were arranged so that the first egg of a clutch was laid on day '0'.

RESULTS

Field observations

On 27 February 1997, an EPC was observed in the nesting territory of Pair 1. It occurred 29 days before the estimated start of egg-laying (Fig. 1a). At 14:40 h an unknown adult male Goshawk landed about 250 m from the nest. The resident male was not visible at that moment, but the radiosignal indicated that it was perched within 50 m of the stranger. Five minutes later the intruder flew toward the resident female, which was perched on an exposed side branch in the upper third of a Larch *Larix* sp. c. 310 m from the nest. On arrival of the male, the female consensually adopted a copulation posture, whereupon the male mounted her, and copulated for at least 5 s; this probably involved cloacal contact. The resident male then appeared between the trees and landed 2 m from the copulating pair. It observed the action but made no attempts to inter-

fere. There were no vocalizations before the copulation occurred (e.g. no solicitation calls from the female). However, during mating both individuals gave typical copulation calls, whereas the resident male remained silent throughout. Only seconds after the copulation, all three individuals flew off and left in different directions. The female flew towards the nest, the resident male landed on a nearby tree where it stayed for the next 4 min and the intruder started soaring and sky-dancing over the nesting territory, gradually drifting away. There was no apparent change in the behaviour of the resident male after the EPC incident. In particular, it showed no aggressive behaviour toward its mate and continued feeding it throughout the breeding cycle.

There were also indications that Male 1 regularly interacted with another (unpaired) female. On 27 February (day -29) at 16:36 h, it was observed to give series of 'kek-kek-kek' calls in a small park, about 2 km away from its nest-site. No other birds were seen. On 12 April 1997 (day 15) at 15:29 h, however, the male was sky-dancing with an immature female over the same park. Fifteen minutes later it came out of a potential nest stand in the park, which contained an old nest of the Common Buzzard *Buteo buteo*. Male 1 was found in this nest stand again twice on 21 April (day 24; 14:40 and 19:00 h), and was located another nine times in the park area throughout the observation period. There was no Goshawk breeding attempt in the park concerned in 1997 or later.

Nine further cases of intraspecific nest intrusion on to two of the three closely monitored nesting sites were observed (Pair 1: seven intrusions; Pair 2: two intrusions; see also Fig. 1a). All intruding birds were males, of which one was adult, one probably adult, one immature and six were of unknown age. Nest intrusions occurred throughout the breeding cycle (days -26 to 64) and did not appear to be more common during the females' presumed fertile period (see Fig. 1a). Seven intrusions occurred in the morning between 07:41 and 11:52 h. In five cases, the resident male attacked the intruder, and in three of these instances the territory holder circled above the nest stand after driving away the intruder.

Radiotracking data

Radiotracking data revealed a peak in the presence of Male 1 in the inner nesting area just before egg-laying (about 80% of daylight hours; Fig. 1a,i). The duration of its daily mate attendance dropped markedly during completion of the clutch (to about 50%), but increased again after day 20. Patterns for Male 2 were similar but more variable. For Male 3, only data from day 50 onwards were available. No consistent daily mate attendance patterns were found (Fig. 1b,i). However, Male 2 spent more time in the vicinity of the nest in the early mornings in the pre-laying and egg-laying periods than afterwards. On average, it was close to the nest for 50 min from 07:00 to 08:00 h ($n = 7$ days).

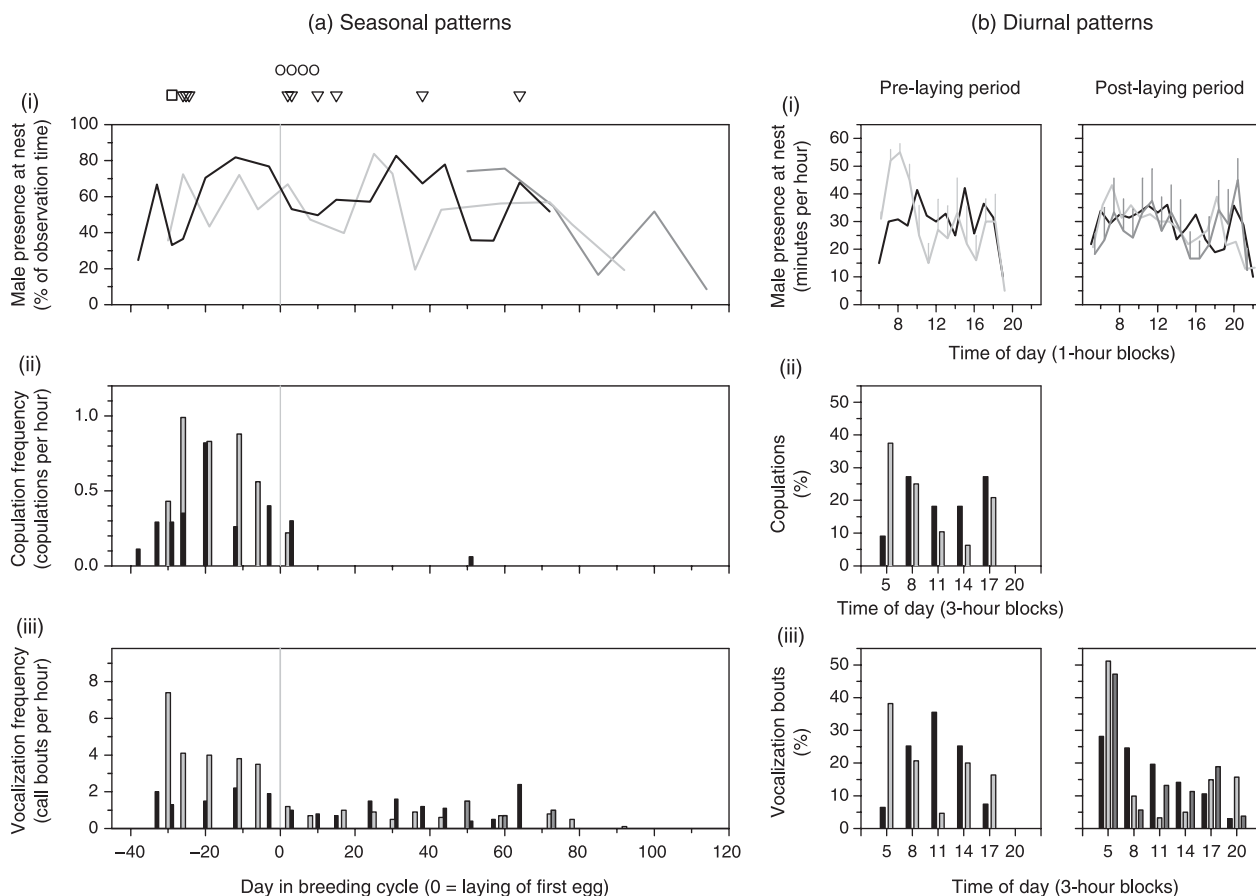


Figure 1. Seasonal (a) and diurnal (b) patterns of male mate attendance (i), copulatory behaviour (ii) and vocal activity (iii) in three breeding pairs of Northern Goshawks in the city of Hamburg, Germany (Male 1/Pair 1: black; Male 2/Pair 2: light grey; Male 3/Pair 3: dark grey). In (a), day '0' is the day on which the first egg of a clutch was laid; oval symbols above the top panel represent estimated laying dates. The extra-pair copulation, which was observed in Pair 1, is indicated with a square, and intraspecific nest intrusions at all three breeding sites are shown as triangles. In (b), data are shown separately for the pre-laying period (left-hand panels) and the post-laying period (right; includes days of laying). In (bi), values are means and standard errors, and in (bi)–(biii), axes labels mark the beginning of a time block. In all parts of the figure, only data from full-day tracking sessions (when Goshawks were continuously radio-monitored from dawn to dusk) were included. For definitions and further methodological details, see text.

Copulation frequency increased to about one copulation per hour in the pre-laying period and fell towards zero in the laying period in two pairs (but note the copulation observed in Pair 1 on day 51; Fig. 1a,ii). Copulations were distributed fairly evenly throughout daylight hours (Fig. 1b,ii). In Pair 2, vocal activity was high before onset of egg-laying and dropped markedly thereafter; a similar but less clear pattern was found in Pair 1. Calling activity was about one call bout per hour throughout the entire post-laying period (Fig. 1a,iii). Daily vocalization patterns were inconsistent among pairs, except perhaps for a tendency for early morning calling in the post-laying period (Fig. 1b,iii).

DISCUSSION

This is the first description of an EPC in free-ranging Northern Goshawks. Two cases of polygamy were

observed in the course of an extensive population monitoring study in The Netherlands (Bijlsma 1993). Both trios failed to raise young. In 1998 and 1999, possible polygamous breeding attempts (both unsuccessful) were recorded at a nesting site in the Hamburg study area. It is well known that Goshawks in captivity will mate with different partners in rapid succession. Gavin *et al.* (1998) collected blood samples from 39 complete Goshawk families and found that only one out of 77 nestlings was sired by an extra-pair male. The low frequency of extra-pair young in the Goshawk is consistent with results from other raptor species (see McGrady 1991, Warkentin *et al.* 1994, Korpimäki *et al.* 1996, Negro *et al.* 1996).

The EPC described in this paper occurred about 4 weeks before the female of the pair laid the first egg. In most bird species the female's fertile period starts about 10 days before the first egg of a clutch is fertilized (Birkhead &

Møller 1992b), so it is unlikely that the observed EPC resulted in a fertilization. Data from other studies confirm that it may be difficult for males accurately to assess the time of ovulation of potential mating partners (e.g. Mineau & Cooke 1979, Sodhi 1991). However, a paired male should have a better knowledge of its mate's fertility status than an intruder. This might explain the passive behaviour of the paired male Goshawk in the reported case (but note that it attacked intruders on other occasions). Goshawks are capable of killing conspecifics in escalating fights, and it therefore pays for them to avoid unnecessary conflicts. Similarly passive behaviour during an EPC event has been reported for the Merlin *Falco columbarius* (Sodhi 1991).

Radiotracking data suggested that Male 1 showed mate attendance just before the beginning of egg-laying. This finding agrees with observations from another study on Goshawks (Holstein 1942, Møller 1987). A second peak around day 30 (incubation period) was present in two tagged males (Males 1 and 2; Fig. 1a,i), and it was also found in Holstein's data set (see FIG. 3 in Møller 1987). Møller attributed it to two pairs copulating again during the mid-incubation period. In the present study, the peak was probably due to changes in the males' hunting behaviour: both tagged individuals started preying upon nestling birds (mainly European Starlings *Sturnus vulgaris*) in the nest stand during that time, which could explain the comparatively large amount of time spent in the nest vicinity. One male (Male 2) seemed to maximize the time it spent near its mate in the early morning hours in the pre-laying and egg-laying periods (Fig. 1b,i), but the peak in presence was considerably later than that reported by Møller (1987). Various degrees of mate attendance have been documented in other raptor species (e.g. Birkhead & Lessells 1988, Simmons 1990, McGrady 1991, Korpimäki *et al.* 1996, Mougeot 2000).

Copulation frequency showed a unimodal distribution with a peak just before the first egg was laid, supporting the hypothesis that frequent copulating is a means of male paternity assurance in this species (see also Møller 1987; for other raptor species, see, for example, Birkhead & Lessells 1988, Mougeot 2000). Within-pair copulation frequency was somewhat lower than previously reported (see Møller 1987), which is not surprising as some copulation calls might have been missed (wearing of headphones; see Methods). A second peak in copulation frequency around day -40, as described by Møller (1987), was not found.

Intraspecific nest intrusions have been reported for a number of raptor species (e.g. Birkhead & Lessells 1988, McGrady 1991, Mougeot 2000). In most cases the intentions of the intruder remain unclear, and it cannot be decided whether the bird was actively seeking EPC opportunities or just happened to cross another nesting territory during a foraging trip. Interestingly, all intruding Goshawks in the present study were males. This contrasts with the Eurasian Sparrowhawk *Accipiter nisus*, in which female intrusions are relatively frequent; here, females rather than

males seem to be searching for EPC opportunities by visiting other breeding pairs (McGrady 1991).

Recent comparative studies have shown a positive relationship between the frequency of extra-pair fertilizations (EPFs) and breeding density within, but not across, bird species (Westneat & Sherman 1997, Møller & Ninni 1998). Northern Goshawks breed at higher densities in urban environments than in most natural or rural settings (reviewed in Rutz *et al.* in press). One might therefore expect comparatively higher EPF frequencies in urban populations. However, considerable loss of genetic variability during the foundation of urban populations could reduce EPF frequency, as the potential genetic benefits for females engaging in EPCs would be low (Petrie *et al.* 1998). At least in the Hamburg population, comparatively small natal dispersal distances (as estimated from ring-recoveries; C. Rutz unpubl. data) and a first case of possible inbreeding depression (Rutz *et al.* 2004) suggest that the population has gone through a bottleneck during its foundation. This leads to the interesting prediction that EPF frequencies should be similar in the two habitats despite marked differences in breeding densities. A test of this hypothesis could help to understand the factors that determine the degree of sperm competition in birds.

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