Paternity assurance in two species of colonially breeding falcon: the kestrel *Falco tinnunculus* and the red-footed falcon *Falco vespertinus*

Rottraut Ille[1], Herbert Hoi[2], Frank Grinschgl[3] & Richard Zink[2]

[1]Landstrasser Gürtel 11/12, A-1030 Vienna, Austria.
[2]Konrad Lorenz-Institute for Comparative Ethology, Savoyenstr. 1a, A-1160 Vienna, Austria. e-mail: H.Hoi@klivv.oeaw.ac.at
[3] Schulg. 63, A-1180 Vienna, Austria.

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Abstract. Mate-guarding and frequent within-pair copulations are the two main paternity guards of male birds. Some species of birds of prey depend on large foraging areas due to the availability and dispersion of their food, and males supply their females with food from mating until early chick rearing. Furthermore, birds of prey often must prevent their nests from take-overs by nest-guarding. Therefore, males cannot prevent extra pair copulations only by mate-guarding. In this study we examine different parameters determining the two paternity assurance tactics for a kestrel *Falco tinnunculus* colony, which are usually solitary breeding and a similar sized colony of red-footed falcon *Falco vespertinus,* a colonial species. Kestrel pairs spent more time together near the nest than red-footed falcons and female red-footed falcons were off the nest alone for longer time than female kestrels. Kestrels also showed higher copulation frequency and duration than red-footed falcons. Female kestrels spent more time with nest-guarding than female red-footed falcons and agonistic interactions between kestrels were much more frequent than between red-footed falcons. Our results therefore suggest that the colonially breeding red-footed falcon shows less behavioural adaptation to protect paternity and less intraspecific competition, as it is known for other typically colonial species. However, copulation frequency of red-footed falcons is still higher than in most "mate-guarding" species and therefore can be used to protect paternity as well.
Key words: paternity assurance, sexual strategies, *Falco tinnunculus*, *Falco vespertinus.*

Resumen. *Confianza de paternidad en dos especies de rapaces coloniales: el cernícalo vulgar* Falco tinnunculus *y el cernícalo patirrojo* Falco vespertinus. La guarda de la pareja y las cópulas intra-pareja frecuentes son las dos estrategias principales de guarda de paternidad en los machos de las aves. Algunas especies de aves rapaces dependen de grandes áreas de aprovisiona-miento debido a la disponibilidad y dispersión de su comida, y los machos proporcionan alimento a sus hembras desde la cópula hasta las primeras fases de la cría. Además, las aves rapaces deben a menudo prevenir que sus nidos sean usurpados mediante la guarda del nido. Por consiguiente, los machos no pueden prevenir las cópulas extra-pareja solamente mediante la guarda de su hembra. En este estudio examinamos diferentes parámetros que determinan las dos tácticas de confianza de paternidad en una colonia del cernícalo vulgar *Falco tinnunculus*, cuya cría normalmente es solitaria y una colonia de tamaño similar del cernícalo patirrojo *Falco vespertinus*, una especie colonial. Las parejas del cernícalo vulgar pasaron más tiempo juntos cerca del nido que los patirrojos y las hembras de los patirrojos pasaron más tiempo solas lejos del nido que las hembras del cernícalo vulgar. Los cernícalos vulgares también mostraron una frecuencia de cópula más alta y de mayor duración que los patirrojos. Los cernícalos vulgares hembra emplearon más tiempo en la guarda del nido que las hembras de patirrojo y las interacciones agonísticas entre los cernícalos vulgares fueron mucho más frecuentes que entre los patirrojos. Nuestros resultados sugieren por consi-guiente que el cernícalo colonial muestra menos adaptaciones conductuales para proteger su paternidad y menos competencia intraespecífica, como ocurre en otras especies típicamente coloniales. Sin embargo, la frecuencia de cópula de los patirrojos es todavía más alta que en la mayoría las especies que guardan a la hembra y por consiguiente podría usarse también para proteger la paternidad.

Introduction

Mate-guarding and frequent within-pair copulations are considered to be the two main paternity guards of male birds (Birkhead & Møller, 1992, 1998; Mougeot, 2000). Mate-guarding is the only strategy for directly preventing extra-pair fertilisation and is often found in passerines (Birkhead & Møller, 1992; Pinxten & Eens, 1997). Some bird species have to guard their nests to avoid intra- or interspecific takeovers and depend on large foraging areas due to the availability and dispersion of their food. In this case one pair member has to guard the nest during the foraging trip of the other. As a consequence, males cannot prevent extra-pair copulations of their mates by guarding them.

Such a situation is frequent in birds of prey (Mougeot, 2000). Korpimäki et al. (1996) found that male kestrels *Falco tinnunculus* spend only 40% of their time near their female during their fertile period. Whenever males of a species have to trade between mate-guarding and other behaviours e.g. nest-guarding (Negro et al., 1992; Lifjeld et al., 1994; Schleicher et al., 1997), alternative strategies may evolve. For instance, birds of prey show extremely high within-pair copulation rates, which can be seen as an alternative strategy for paternity assurance (Birkhead & Møller, 1992; Holthuijzen, 1992; Korpimäki et al., 1996). Males supply their females with food from mating until early chick rearing. Therefore, their initial effort as well as the risk of extra-pair fertilisations due to this behaviour is increased, especially when prey abundance is low (Mougeot, 2000). This is in contrast to the prediction that males with heavy initial investment should assure paternity even more (van Rhijn, 1984). High within-pair copulation rate is often also the only possibility to increase paternity assurance for colonial bird species, since male-male competition increases to a level that makes efficient mate-guarding impossible (Birkhead & Møller, 1992; Schleicher et al., 1997). However, bird species that exclusively breed in colonies, sometimes do not show any adaptation in terms of paternity assurance and in spite of that show low or no extra-pair fertilisations (e.g. Wittenberger & Hunt, 1985; Catry & Furness, 1997).

In this study we examine some of the key parameters which may influence the possibility to perform one of the two paternity strategies for two raptor species varying in their degree of sociality: the kestrel which usually breeds solitarily (Glutz von Blotzheim et al., 1971; Zink, 1998) and the red-footed falcon *Falco vespertinus*, a primarily colonially breeding species preferring high breeding densities (Glutz von Blotzheim et. al., 1971). Here we examine both species in a colonial situation, and investigate whether there are differences in the way they can cope with high breeding density in terms of copulation behaviour and behaviours related to mate- and nest-guarding. If the risk of loosing paternity is density dependent we would predict a better adaptation in terms of paternity assurance tactics for the colonial species (red-footed falcon).

Material and Methods

Study area and study species

Kestrels were investigated during the breeding season 1997 in Fuchsnbigl, Austria (48º12' N, 16º45' E). The study area was dominated by intensively cultured crop fields. About twenty-nine pairs of kestrels have been breeding there in a colony since 1980, using nest boxes placed about 20 m apart. Fourteen pairs were included in the following analyses. The earliest breeding birds arrived at the beginning of March. The red-footed falcons were investigated in a colony of 24 breeding pairs at a distance of about 40 km from the kestrel colony during the breeding season 2001 South West of Rusovce, Slovakia (48º03' N, 17º07' E). Their breeding habitat was similar, characterised by large crop fields but also fields of lucerne, rape and pea. Lucerne fields were cut at the end of May for the first time. Falcons were breeding in wind breaks dominated by robinia *Robinia pseudacacia*, ailanthus *Ailanthus sp.*, ash-tree *Fraxinus excelsior*, maple *Acer sp.*, elder *Sambucus niger* and hawthorn *Crataegus sp.*, bordered by small grass stripes. Wind breaks had lengths of 260 m to 1560 m. The first red-footed falcons arrived at their breeding habitat on 30 April. We observed eighteen pairs, three of which occupied a nest only for several days but then disappeared.

Observations

For both species, observations took place between 10:00 h and 19:00 h and were conducted at a minimum distance of 20 m from a car. Behaviour was recorded during 30 min protocols. We recorded the time pair members spent near the nest (<20 m) as a measure for mate-guarding in 1-minute-intervals, copulation frequency and duration, time of nest- guarding being the time and distance males and females spent near the nest (<20 m), time the nest was unguarded and aggressive interactions (any kind of attacks against other conspecifics). Kestrels were individually colour ringed, red-footed falcons were not because we wanted to keep the disturbance low for one of the last bigger populations of this species in Central Europe. However the clear sex difference, individual feather characteristics like moult gaps and individual variation in colour were used to discriminate between individuals. Furthermore two observers were simultaneously following one breeding pair to avoid miss-identifications.

For the Red-footed falcon observations started from arrival of males until laying of the last egg (including approximately 15 days). For each pair in average 8.1±0.4 (ranging from 6 to 10) protocols (one protocol per day) were done and 196 copulations have been recorded during that period. For the kestrel observations from 12 days prior to laying until laying of the last egg were used (including approximately 16 days). For each pair in average 7.7±0.5 (ranging from 3 to 11) protocols (one protocol per day) were done and 234 copulations have been recorded during that period.

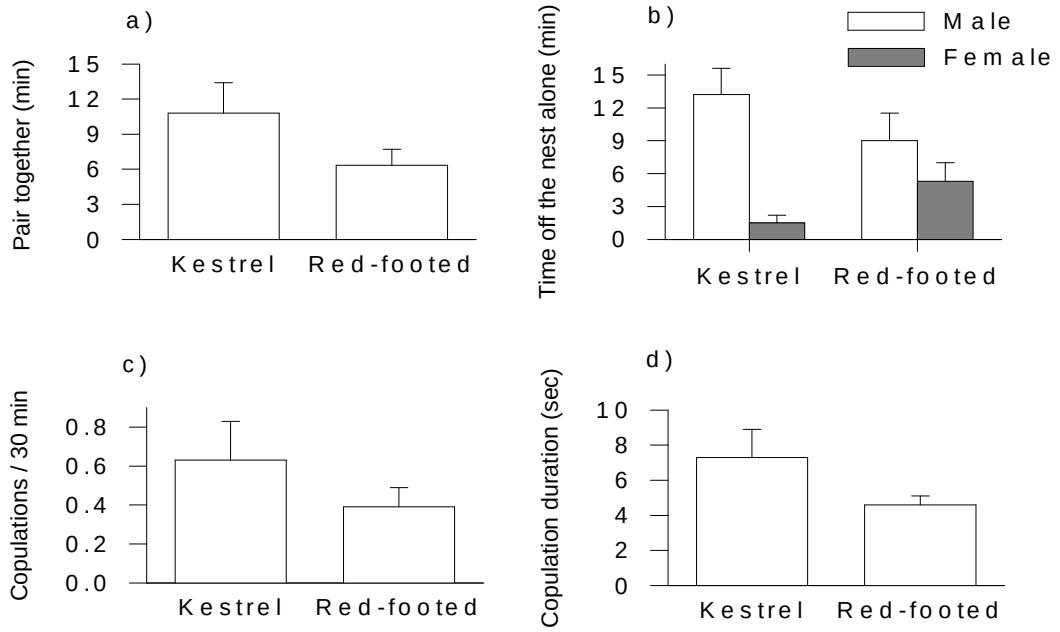

Figure 1. Parameters reflecting mate-guarding: a) average (SE) time in minutes pair members spent together near the nest and, b) average (SE) time in minutes pair members spent unguarded off the nest; and frequent within-pair copulations: c) average (SE) within-pair copulation rate per 30 minutes and, d) average (SE) copulation duration (seconds) as paternity guards for kestrel and red-footed falcon.

Statistics

Only parametric tests were used since data were normally distributed. Means±SE are given throughout.

Results

Paternity guards

Kestrel pairs spent significantly more time together near the nest than pairs of Red-footed falcons (Student's *t*-test: t=2.28, n1=14, n2=12, p=0.041) (fig. 1a). Average copulation frequency was not significantly different but tended to be higher for kestrels (t=-1.58, n1= 14, n2= 12, p=0.137) (fig. 1c). We found no correlation between copulation frequency and distance between red-footed falcon nests (r=-0.15, n=12, p=0.430). Copulation duration was significantly longer for kestrels (t=-5.05, n1=14, n2=12, p=0.002) (fig. 1d). The amount of time females spent away from the nest while males guarded the nest is very small for both species but seems to be higher for red-footed falcon females (t=2.2, n1=14, n2=12, p=0.044) (fig. 1b). In contrast, the time males have been out alone while the female is guarding the nest is higher but does not significantly differ between the species (t=-1.68, n1=14, n2=12, p=0.121) (fig. 1b). As a consequence, the time females are unguarded by their males (which is almost the half of the time during the fertile period: for kestrels on average 49%±7.6, and for red-footed falcons 41%±4.1) does not differ between the species (t=-0.99, n1=14, n2=12, p=0.341).

Nest guarding

Kestrels used nest boxes for breeding and distances between occupied nest boxes were about 20 m. Red-footed falcons occupied old nests of rooks (75%) and magpies (25%). Average distance between occupied nests was 23.8 m, varying between 2 and 558 m. Male kestrels but not male red-footed falcons spent less time near the nest than their female partners (kestrels: t=3.82, n=14, p=0.001; red-footed falcon: t=-0.83, n= 12, p=0.418; fig. 2), but there was no difference between males of the two species (t=0.36, n1= 14, n2 = 12, p=0.726) (fig. 2). However, kestrel females spent more time near the nest than females of red-footed falcons (t=-2.91, n1=14, n2=12, p=0.014). Male red-footed falcons (average distance to the nest: 2.6 m±0.84) were in general closer to the nest than male kestrels (average distance to the nest: 18.2 m±2.9; t=-18.96, n1=14, n2=12, p=0.001) and the same was observed for females (female kestrels: 10.4±2.5 m; female red-footed falcons: 1.3±0.38 m; t=-23.52, n1=14, n2=12, p=0.001). The time nests were unguarded did not differ between kestrels (17.2% of time; 5.2 min±1.55) and red-footed falcons (19.6% of time; 5.87 min±1.9) (t=0.37, n1=14, n2=12, p=0.719).

Agonistic behaviour

Agonistic interactions among kestrels of the colony were significantly more frequent than between individuals of the red-footed falcon colony (t=-34.93, n1=14, n2=12; p=0.001) (fig. 3). In red-footed falcons the few agonistic interactions were observed only between males.

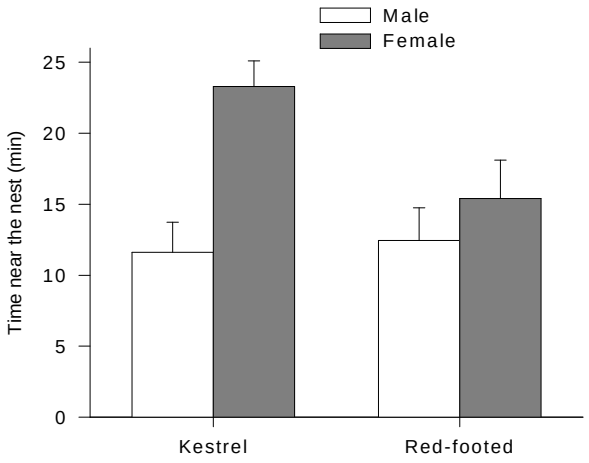

Figure 2. Average (SE) time pair members spent near the nest for male and female kestrels and red-footed falcons.

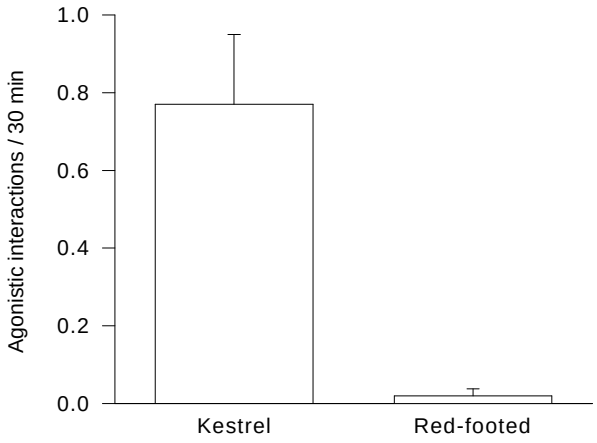

Figure 3. Average (SE) rate of intraspecific agonistic interactions (30 minutes) for kestrels and red-footed falcons.

Discussion

Regarding paternity guards our results suggest that the species with the regular colonial breeding situation (red-footed falcon) is the one, which shows less pair bond behaviour during the fertile period. This is indicated by the fact that red-footed falcon pairs spent less time together and their females spent more time off the nest without their partner. Within-pair copulation rate was lower and copulation duration shorter than for the normally solitarily breeding kestrel. Furthermore, there was no relation between red-footed falcon nest distance and copulation frequency. This suggests that male red-footed falcons as many other typically colonial species show less behavioural adaptation to protect paternity (Birkhead & Møller, 1992). In contrast kestrels, which are normally solitary breeders, invest more into paternity assurance in terms of within-pair copulation frequency. Comparisons with other kestrel populations showed that within-pair copulation frequency in fact increases with breeding density (Zink, 1998). Zink (1998) could further demonstrate that this happens mainly during the peak fertile period (few days around egg-laying), supporting its function as a paternity guard and contradicts the territorial signalling hypothesis which suggests that copulation rates should increase with breeding density mainly during the pre-fertile period (Negro & Grande, 2001). However, within-pair copulation frequency in red-footed falcons is still higher than in most "mate-guarding" species which hence does not necessarily contradict a paternity assurance function.

Alternatively, females may trade copulations for benefits like food, nest material or protection from other males (Birkhead & Møller, 1992) as observed in the American kestrel *Falco sparverius* (Villaroel et al., 1998). However, food transfer of red-footed falcons and kestrels are not obviously linked to copulation events (unpublished data). In fact in the red-footed falcon prey transfer was only once observed prior to a copulation attempt. Green & Krebs (1995) found similar results for ospreys.

The time partners spent together near the nest is rather low and the time females are left unguarded by their partners is high for both species although slightly higher for the kestrel. Consequently, there would be enough time for females of both species to perform extra-pair copulations which means that for both species male mate-guarding cannot be an efficient paternity assurance tactic (Birkhead & Møller, 1992). That partner proximity is not important for paternity assurance is also supported by Zink (1998) who did not find a relationship between breeding density and mate guarding in kestrels. In typical "mate-guarding" species pair partners spend together much more time, e.g. magpies *Pica pica* about 95 % of their time (Birkhead, 1982) or starlings *Sturnus vulgaris* 100% of their time (Pinxten et al., 1987). A common explanation for the lack of mate-guarding is that males have to trade with other behaviours (Lifjeld et al., 1994; Schleicher et al., 1997) f. i., nest-guarding (Schleicher et al., 1993). If there is high competition for nest sites, which is more likely in a colonial breeding situation, investment in nest-guarding may be higher and hence prevent efficient guarding of the partner, in particular when foraging sites are away from the colony (Birkhead & Møller, 1992). Zink (1998) in fact showed for the kestrel that the need for nest-guarding very much depends on breeding density. Solitary breeding birds spent more time off the nest. We found no difference in time red-footed falcons and kestrels spent with nest-guarding in the colonial situation. However, in kestrels females spent more time near the nest than their males whereas in red-footed falcons both sexes spent equal time near the nest.

Intraspecific competition seems in general lower in the colonial red-footed falcon than the kestrel. In fact aggression was almost non-existent for red-footed falcons (fig.3) although their nest distances were in general much shorter (for 50 % of the pairs inter-nest distance was less than 13 m). This may indicate that sperm competition is heavier for colonial kestrels.

The questions arise why investment in protection of paternity is low in many colonial bird species and why, in spite of that, they are still genetically monogamous

(Catry & Furness, 1997; Danchin & Wagner, 1997). One explanation could be that extra-pair paternity has not or less frequently evolved in non-passerines (for what ever reason) and many strictly colonial birds are non-passerines (Siegel-Causey & Kharitonov, 1990). In fact colonial breeding passerines sometimes show very high rates of extra-pair paternity (Riley et al., 1995; Pinxten & Eens, 1997; Alves & Bryant, 1998). This phylogenetic explanation holds for falcons because for some falcon species extra-pair paternity has been shown but rates are rather low for all of them (Korpimäki et al., 1996: 7% of kestrel nests; Swatschek et al., 1993: Eleonora's Falcon *Falco eleonorae*: no cases of extra-pair paternity; Negro et al., 1996: Lesser kestrel *Falco naumanni* 3.4%; Villarroel et al., 1998: American kestrel *Falco sparverius* 3.5%). Alternatively, the fitness pay-off of extra-pair behaviour may not be beneficial in a colonial situation and therefore extra-pair behaviour may not be selected for. Another possibility is that mate fidelity is a precondition of coloniality and only species with a genetically monogamous system do evolve to strictly colonial species. So determine the real extent of extra-pair paternity of red-footed falcons, colonial kestrels and other colonial or semi-colonial birds of prey would be necessary to evaluate the importance of sperm competition in relation to the breeding situation (density).

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