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Defence behaviour of Red-footed Falcons *Falco vespertinus* in the breeding period and the effects of disturbance on breeding success

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Near the village Melenci (Voivodina, northern Serbia) there were 22 Red-footed Falcon *Falco vespertinus* nests in 1991 in which offspring had been successfully brought up. The contents of four nests were checked daily from the start of incubation until the fledglings left the nests. Breeding success did not differ between the group of 4 nests disturbed by inspections and the remaining 18. Despite the fact that the ratio of parent bird presence (both, only female, only male) and absence differed in the comparison of the four nests, Red-footed Falcon parents were usually found in the close surroundings, i.e. they attended their nest. The attendance of the birds to the nests differed between the sexes during incubation as well as hatching and the nestling period, which fact can be interpreted as a difference between the roles of females and males. In 59% of the cases it was the female, while in 41% it was the male bird that was sitting on the eggs. At the time of hatching it was mostly the female (female 86%, male 14%) that was present in the nest, while after hatching it was only the female. Later on the adult birds usually took off from the branch supporting the nest, from neighbouring trees, or from abandoned Rook *Corvus frugilegus* nests, rather than from the nest itself. Females participated more times in the defence of the nest than males, yet the ratios of the studied types of behaviour (alarm, repellence, attack) did not differ between the sexes. However, significant difference appeared to be present between four nests when the distribution frequency of the three behaviour types was looked at. The distribution of the reaction types of the parent birds to disturbance was significantly different in the periods of incubation, hatching and nestling, respectively. As nesting proceeded and parental investment grew, the number of repellences and attacks increased proportionally.

1. Introduction

Studies on passerine birds shown minimal or no effect of nest-visiting by humans on nesting (Göttmark 1992, O'Grady et al. 1996, Mayer-Gross et al. 1997), while other few studies (Bart 1977, Lenington 1979, Major 1990) have clearly shown negative effects of research activity. Tryjanowski and Kuźniak (1999) found differences in breeding success with respect to the number of visits to a nest.

Smaller birds of prey are less sensitive to dis-

turbances than the larger species (Newton 1979). Red-footed Falcons *Falco vespertinus* are small (Brown & Amadon 1968, Weick 1980), but, since their nesting biology and behaviour is little known (Osmolovskaya 1939, Horváth 1955, 1956, 1963, 1964, 1975, Glutz et al. 1971, Cramp & Simmons 1980), information is sparse on how they react to the daily checking of the nests (i.e. disturbances). The studies by Osmolovskaya (1939) and Horváth (1964) allow to conclude that Red-footed Falcons do not abandon their nest but disturbances may lead to a decrease in their breeding success.

In most raptorial species the nest is attended by adults from 90–100% of the day during the incubation period and in the first few days after hatching (Rowe 1947, Rettig 1978, Stinson et al. 1988). Red-footed Falcon females and males participate at equal rates in egg incubation (Horváth 1955, 1963), therefore it is likely that the role of sexes in attending the nest is similar. According to Horváth (1975) females "worry" much more for the brood than males and it occurs more frequently that they return to the nest. According to Cramp and Simmons (1980) our knowledge about the role of sexes in parental care and nesting is still limited.

Information on the division of nest defence between the sexes in raptors is scarce (Mueller & Meyer 1985, Tolonen & Korpimäki 1995). Diurnal raptors can exhibit three strategies of nest defence: principally by the female, by both sexes, or principally by the male (Mueller & Meyer 1985, Andersson & Wiklund 1987). Aspects such as the sexual differences in defence behaviour among raptors with reversed sexual dimorphism has not yet been studied in detail (Wiklund & Stigh 1983, Andersson & Wiklund 1987, Wiklund 1990a). However, it is important to note that the relationship between the body size and agility of male as well as female birds is inverse (Andersson & Norberg 1981). There is no great difference between the size of Red-footed Falcon females and males (Glutz et al. 1971, Cramp & Simmons 1980); the male can reach 89–90% of the female's body weight (Cade 1982).

The aim of this study was, to examine: 1) whether the daily disturbance of nests has an effect on breeding success, 2) whether the ratio of presence (both, female, male) and absence of parent birds is different among the nests and in various phases of nesting, 3) which one of the parent birds (male or female) flies off the nest during incubation, at the time of hatching and after hatching, 4) how the parent birds react the intruder in different phases of nesting.

2. Study Area

In Voivodina (northern Serbia, Yugoslavia) approximately 5 km north-east from the village Melenci (DR44 according to a 10 × 10 km scale grid map of the UTM system) a Black Locust *Robinia pseudoacacia* forest stretched along the road leading to Bašaid, from the Kikinda Channel to the pull-off. On the right of the road there was a thin row of trees, while on the left there was a 3 km long forest stripe of 15–25 m width. A dirt road separated the forest from the lands. The majority of trees were Black Locust-trees, but scattered specimens of Ash *Fraxinus* spp., Maple *Acer* spp., Elm *Ulmus* spp., Plum *Prunus* spp., Walnut *Juglans* spp., Pagoda *Sophora* spp., Poplar *Populus* spp. and Mulberry *Morus* spp. were also present. A loose colony of Rooks *Corvus frugilegus* stretched almost all along the forest stripe (Lukač & Lukač 1990) where 27 Red-footed Falcon pairs had nested in 1991 (Purger 1996, 1997). Four nests (A, B, C, D) were selected randomly for the purposes of our study, which were more than 100 m apart from each other. The most important characteristics of the selected nests and their surroundings were as follows:

Nest A: situated on a Black Locust-tree at a height of 8.2 m (measured from the surface of ground to the rim of the nest; from 3 eggs 3 nestlings hatched, 2 fledged), 20 m away from the road. An empty nest was present 1.5 m higher on the same tree. Within a range of 10 m, 23 abandoned Rook nests were counted. In one of them, approximately 8 m from the observed nest, also Red-footed Falcons nested.

Nest B: situated only 6 m from the road, on a young Black Locust-tree with dense foliage, at a height of 6.3 m (from 4 eggs 3 nestlings hatched, 2 fledged). Two empty Rook nests were found within a 10 m range. A pair of Kestrels *Falco tinnunculus* nested in a Rook nest at 16 m from the observed nest.

Nest C: situated 8 m from the road, on a Black

Locust-tree at a height of 8.5 m (from 5 eggs 4 nestlings hatched, 2 fledged). A bare, totally dried Poplar stood 4 m further away, with 7 Rook nests. In one of these, at about 6 m from nest C, also Red-footed Falcons nested. Twelve empty Rook nests were counted within a 10 m range.

Nest D: situated in the middle of the forest stripe, at a height of 7.2 m, also on a Black Locust-tree (from 4 eggs 3 nestlings hatched, 2 fledged). Yet another 3 nests, 2 m, 3.5 m, and 4.5 m above the observed one, were situated on the same tree. Rooks nested in the lowermost one, just like in a nest on the neighbouring tree, at about 6 m from nest D. A total of 8 empty Rook nests were found within a 10 m range.

3. Methods

Observations took place from 22 June to 2 August 1991. All four nests were checked every day. At each occasion, selected nests were approached by car on the dirt road, between 16:30 and 18:30. The investigations occurred at the same time when food remains were collected (see Purger 1998). Red-Footed Falcon parents generally stay around the nest, because the majority of their diet is insects which they obtain in the surroundings of the nest (e. g. Horváth 1955, 1964, Keve & Szijj 1957, Haraszthy et al. 1994). On the contrary, species feeding on mammals or birds require more time for hunting and the availability of prey animals also varies, therefore the parent birds need to stay away from the nest for longer periods (e. g. Korpimäki et al. 1990, Tolonen & Korpimäki 1995, Wiebe et al. 2000). For the above reasons and in order to prevent habituation it was considered unnecessary to extend the investigations onto other parts of day. While my colleague climbed the trees, I was making notes about the presence and behaviour of the parent birds. We spent a maximum of 15 min. at each nest, so as to disturb the birds with our presence for as short a period as possible.

The four nests (A, B, C and D) were given their designations based on the sequence of hatching occurring in them. Since the time nestlings stayed in the nests was not the same, the number of observations also varied. The last fledglings had left the nests by 23 July (nest A), by 30 July (nest B), by 29 July (nest C), and by 3 August (nest D). Accordingly, the number of observations were 31 at nest A, 38 at nest B, 37 at nest C, and 42 at nest D. Twenty-five percent of the 148 observations occurred during the end of the incubation period, 11% at hatching, while 64% during the period between hatching and leaving the nest.

In order to test whether daily inspection (disturbance) affected breeding success, we monitored nestling numbers in the rest of the nests in the colony, too. Out of the 27 pairs (Purger 1996), 22 completed successfully their nesting in 1991 (Purger 1997), from which 4 pairs were exposed to repeated disturbance.

When approaching the selected nests, we firstly aimed at observing which of the parent birds were present in the close surroundings. Incubating birds often stay still until a human climbs as close as 1 m from the nest (Osmolovskaya 1939), therefore our next step was to determine whether the bird sitting on the nest was a male or a female. During the estimation of the number of breeding pairs in 1990 (Purger 1996), preliminary observations (Martin & Bateson 1986) were also made. We noticed that during inspections we could differentiate an alarming, a repelling and an attacking phase in the nest defence behaviour of the birds, although the parent birds did not always get to attacking. While nest inspection proceeded, I was observing, using binoculars, the nest defending behaviour of the birds present on the spot from a distance of 10–15 m, and was taking notes. As regards observations and notes I followed Lehner (1979). In the nest defence behaviour of Red-footed Falcon parents several manifestation forms of alarm, repellence and attack were observed: (1) alarm: the bird lands on a branch of the nest tree or a neighbouring one and frequently calls, flies from branch to branch and calls loudly, circles above canopy; (2) repellence: the bird circles at the height of the nest and frequently calls, circles and occasionally glides quietly; (3) attack: the bird circles and occasionally makes fast attacking glides with calls, flies figures of eight with fast glides, hovers - makes an attacking glide - hovers, occasionally circles. However, from the point of view of our present analysis, importance was attributed only to determining which behavioural level (alarm, repellence, attack) the parent bird(s) reached in defence of their nest, within the

time of observation.

For statistical analysis we used Statistica for Windows (Statsoft 1994). Results are presented as mean ± standard deviation. The t-test for comparing the means were two-tailed. In χ^2 tests, contingency tables were used. A minimum probability level of $P < 0.05$ was accepted for all the statistics.

4. Results

Breeding success did not differ significantly ($t = 0.67$, $df = 20$, $P > 0.05$) between the 4 nests subject to disturbance (2.0 ± 0.0 fledgling per nest) and the remaining 18 nests (2.3 ± 1.0 fledgling per nest).

Red-footed Falcon parents were usually near the nests when the nests were being inspected (Table 1). The ratios of parent bird presence (both parents present, only female present, only male present, both parents absent) during inspections differed significantly at the four nests ($\chi^2 = 37.48$, $df = 9$, $P < 0.001$) (Table 1). The ratio of parent bird presence differed significantly ($\chi^2 = 14.81$, $df = 6$, $P < 0.05$) during the incubation, hatching and nestling periods (Fig. 1). During the incubation and nestling periods, usually both parents were present, while in the hatching period only the female was near the nest in 44% of the cases. While at least one parent bird was found to be present at the nest at each occasion throughout the incubation phase, neither of the parent birds were near the nest in 6% of the cases during the hatching period, and in 10% of the cases in the nestling period (Fig. 1).

In the incubation period the four nests were visited 37 times, out of which there were only 3 occasions when neither of the adult birds was sitting in the nest incubating. Thus, in 92% of the cases either the female (59%) or the male (41%) bird was found sitting on the eggs ($\chi^2 = 1.09$, $df = 1$, $P > 0.05$). The hatching period encompassed a total of 16 days in all the four nests studied, during which time only two cases with no adult bird in the nest were recorded. In 86% of the cases it was the female, in 14% it was the male that flew off the nest ($\chi^2 = 7.21$, $df = 1$, $P < 0.01$). In the first few days following hatching only females were found to stay in the nest. At nest A, after the young had hatched, it was observed that the male (on 5 and 6 July) and the female (on 7 and 9 July) flew out from the abandoned Rook nest above the nest observed. We checked the contents of this "empty" nest six times, to find Spade-foot Toad *Pelobates fuscus* in it in two cases (6 and 10 July). On 9 July it was observed at nest D, too, that the Red-footed Falcon female took off from the abandoned Rook nest above its nest.

The role of the female and the male in attending the nest can be regarded as similar (Fig. 2), since the frequencies of alarm, repellence and attack did not differ significantly between the sexes ($\chi^2 = 1.15$, $df = 2$, $P > 0.05$). However, significant difference appeared to be present between A, B, C and D nests (Table 2) when the distribution frequency of the three behaviour types was looked at ($\chi^2 = 21.23$, $df = 6$, $P < 0.001$). The distribution of reaction types of the parent birds to disturbance (Fig. 3) was significantly different between the

Table 1. The ratios of parent bird presence at the four nests (A, B, C, D) during inspections.

Nest	Female+Male		Female		Male		Without birds		Total
	n	%	n	%	n	%	n	%	n
A	26	83.9	5	16.1	0	0	0	0	31
B	18	47.4	8	21.0	3	7.9	9	23.7	38
C	17	46.0	15	40.5	4	10.8	1	2.7	37
D	34	80.9	6	14.3	1	2.4	1	2.4	42
Total	95	64.2	34	23.0	8	5.4	11	7.4	148

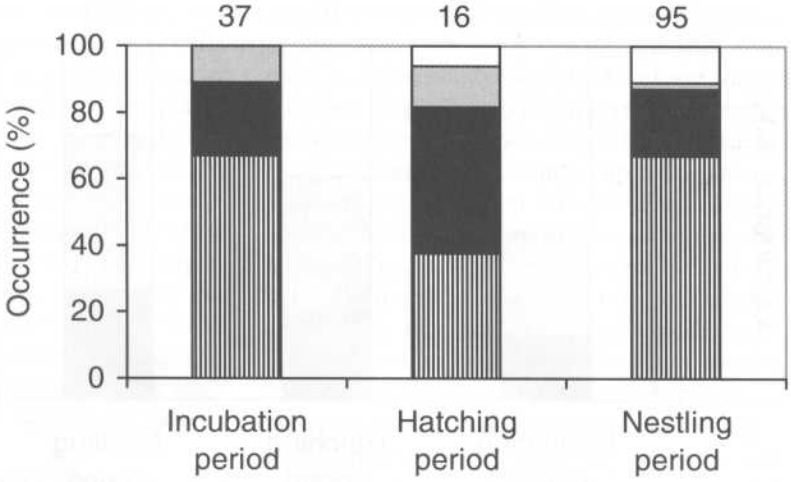

Fig. 1. Presence of adult Red-footed Falcons in the periods of incubation, hatching and nestling (white bars - without birds, grey bars - only male, black bars - only female, vertically striped bars - female and male). The figures above the bars denote the number of observations.

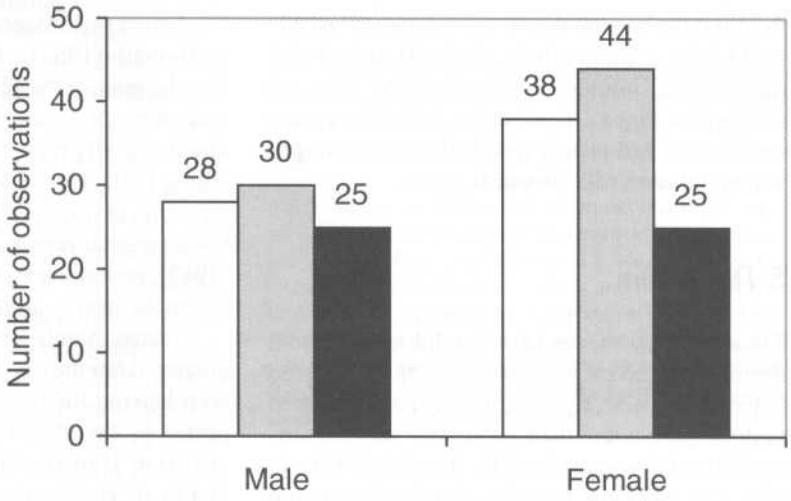

Fig. 2. Nest defence behaviour of adult male and female Red-footed Falcons (white bars - alarm, grey bars - repellence, black bars - attack). The figures above the bars denote the number of observations.

periods of incubation, hatching and nestling ($\chi^2 = 11.89$, df = 4, $P < 0.05$). It occurred five times that males, in an attacking glide, physically touched the man climbing the tree when he was only 1–0.5 m from the nest: (1) nest A on 24 June - in a quiet flight, the bird touched with the wing the head of the climbing man; (2) nest C on 22 June - in a calling flight, the bird touched with the wing the head of the climbing man; (3) nest C on 15 July - in a quiet flight, the bird touched with the wing the arm of the climbing man; (4) nest D on 16 July - in a quiet flight, the bird touched with

Table 2. Occurrences of nest defence behaviour of the parent birds during the inspections of the four nests (A, B, C, D).

Nest	Alarm		Repellence		Attack		Total
	n	%	n	%	n	%	n
A	21	43.7	16	33.3	11	23.0	48
B	11	39.3	17	60.7	0	0	28
C	18	40.0	11	24.4	16	35.6	45
D	16	23.2	30	43.5	23	33.3	69
Total	66	34.7	74	39.0	50	26.3	190

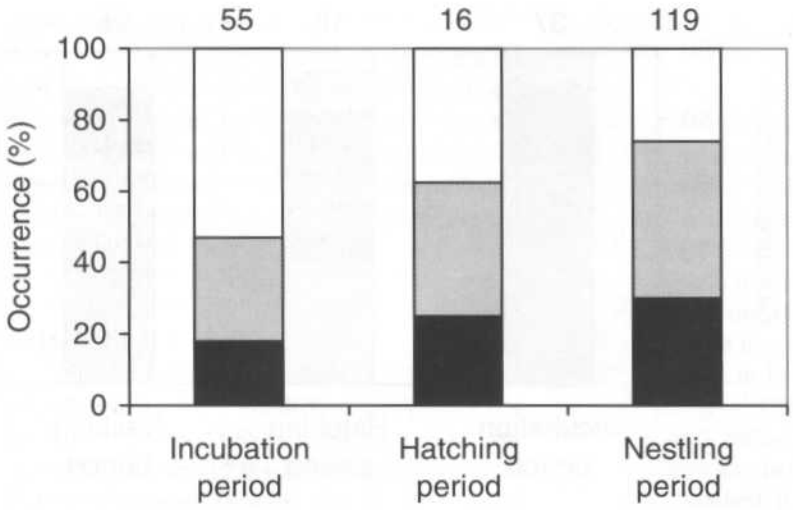

Fig. 3. Nest defence behaviour of adult Red-footed Falcons in the periods of incubation, hatching and nestling (white bars - alarm, grey bars - repellence, black bars - attack). The figures above the bars denote the number of observations.

the chest the head of the climbing man; (5) nest D on 24 July - in a quiet flight, the bird touched with the feet the shoulder of the climbing man and dropped on him a Green Bush-cricket *Tettigonia viridissima*. It was only nest B the inspections of which did not evoke physical attack.

5. Discussion

The daily disturbance of nests did not lead to a decrease in the breeding success of Red-footed Falcons. The nestlings rapidly became habituated to disturbance, and their behaviour was consistent with what was reported by Horváth (1964). In each nest only the underfed, slowly developing nestlings died that had hatched as third or fourth, similarly to the findings of Osmolovskaya (1939).

Despite the fact that the ratio of parent bird presence differed among the four nests, Red-footed Falcon parents stayed near the nest almost all the time, that is they attended the nests (Rowe 1947, Rettig 1978, Stinson et al. 1988). The attendance of parent birds to the nest differed between the periods of incubation, hatching and nestling, which can be attributed to the difference in the roles of the female and the male in nesting. For example, Newton (1979) remarked that the females of certain species are reluctant to leave the nest even when the male approaches with food.

Our findings from recording the sex of the bird that was leaving the nest upon disturbance in the incubation period were almost identical with those of Horváth (1963) who found inconsistently either the male or the female in the nest in the same hour of many successive days. The two sexes were almost equally represented in the sample of incubating birds. He visited the nests at dawn, in the morning, at noon, in the afternoon and at sunset, but no regular repetition could he discover. Cade (1982), nevertheless, noted that only the females sat on the nest at night.

During hatching the role of females was greater. After the eggs hatched, only females were seen leaving the nests. This finding can be supported by the observations of Carlier and Gallo (1989) or Hubert and Carlier (1992), who claim that in species in which both the female and the male take part in incubation, females are dominant. Females of such species do not allow the male near the nest during the days preceding and following hatching (Liversidge 1962, Wiley & Wiley 1981, Dewhurst et al. 1988, Village 1990).

Later on, parent birds did not fly off from the nest, instead they departed from the branch supporting the nest, from a neighbouring tree or abandoned Rook nest, as had been observed earlier by Horváth (1963) in Red-footed Falcons. Most probably the birds used the empty Rook nests not only for nesting, since Spaede-foot Toads were discovered in these nests, which are the main elements of the diet of Red-footed Falcons in the nesting season (Horváth 1955, 1956, 1964, Fülöp & Szlivka 1988, Haraszthy et al. 1994, Purger 1998).

We noticed that when the male handed over food, the female did not fly straight to the nest after receiving the prey, instead she landed on a nearby branch or an empty nest. Horváth (1964) reported that the adult birds always kill the prey before taking it to the nest, moreover, they tear off the wings and jumping legs of locusts and grasshoppers before offering them to the nestlings. It may be that the birds use the empty nest for "preparing" the food for the nestlings, and neither can the possibility be rejected that Spade-foot Toads were accidentally dropped in the nests by the adult birds, as a response to disturbance. Further studies are needed to clarify if Red-footed Falcons store or "prepare" food.

It is known that the defence of the nest from potential predators assumes the increase in the survival chances of the nestlings (Andersson et al. 1980, Greig-Smith 1980, Blandcher & Robertson 1982, Curio et al. 1984, Wallin 1987, Montgomerie & Weatherhead 1988, Redondo 1989). Our results showed that females, probably as a result of their more frequent presence at the nest, participated in the defence of the nest more times, but the ratios of the observed behaviour types did not differ between the sexes. Since both parents take part in incubation (i.e. the investments of males and females are similar), the chances of a successful renesting keep decreasing after hatching. According to Barash (1975) and Weatherhead (1979), the fact that potentially there is possibility for renesting, has an effect on the defence strategy of the parent birds, which implies that only the nest defence strategies are left for Red-footed Falcons after the young have hatched.

The nest defence behaviour of the adult birds showed significant difference among the four nests. This can be regarded as a result of differences in individual behaviour of various pairs, since successful pairs must defend their nest more intensively than those that even allow predation (Greig-Smith 1980, Blancher & Robertson 1982, Knight & Temple 1986, Breitwisch 1988, Wiklund 1990b). However, differences between various nest defence strategies can be explained also with the fact that clutch sizes were different, for Wiklund (1990a) claimed that the frequency of attacks by the female increased proportionately with clutch size.

The intensity of nest defence strategies was different in the incubation, hatching and nestling periods. As nesting proceeded and parental investment grew, the number of repellences and attacks increased proportionately. Kovács (1993) reported on aggressive Red-footed Falcon females that attacked humans. Our findings support what was assumed by Anderson and Wiklund (1987), namely that the more intensive nest defence behaviour of males in birds with reversed sexual size dimorphism can be explained with their greater agility. The fact that Red-footed Falcon males bring the nestlings much more food than females, moreover, they are able to raise the offspring alone (Horváth 1964), also support the statement that males are more agile. Since they fly to the nest more times, they are likely to notice potential intruders sooner.

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Selostus: **Punajalkahaukkojen pesän puolustuskäyttäytyminen ja häirinnän vaikutus lajin pesimämenestykseen**

Kirjoittaja selvitti vähän tutkitun lajin, punajalkahaukan, pesimäaikaista käyttäytymistä Serbian pohjoisosissa. Tutkimuksen tarkoituksena oli selvittää: 1) vaikuttaako päivittäin tapahtuva häirintä punajalkahaukkojen pesimämenestykseen, 2) onko naaras- ja koirasemojen pesäpaikalla läsnäolossa eroja eri pesien välillä ja pesinnän eri vaiheiden aikana sekä 3) kuinka emot reagoivat pesälle tunkeutujaan pesinnän eri vaiheissa. Päivittäinen pesillä vierailu ei vaikuttanut punajalkahaukkojen pesimämenestykseen. Sekä naaras- että koiraslinnut osallistuivat hautomiseen. Naaras- ja

koiraslintujen roolit olivat erilaisia pesinnän eri vaiheissa. Pesinnän edistyessä naaraan rooli kasvoi. Haudonta- ja pesäpoikasaikana olivat sekä koiras että naaras yleensä pesäpaikalla. Sen sijaan kuoriutumisaikana naaras oli läsnä pesällä useammin kuin koiras (86% vs. 14%). Poikasten kuoriuduttua, ainoastaan naaraslinnun havaittiin lähtevän pesästä. Myöhemmin emojen ei nähty lähtevän pesästä, vaan ne oleskelivat pesän läheisyydessä. Naaras puolusti pesää enemmän kuin koiraslintu, tosin ainoastaan koiraslinnun havaittiin koskettavan fyysisesti pesälle kiipeävää tutkijaa. Muuten punajalkahaukan pesän puolustuskäyttäytymisessä ei ollut eroja sukupuolten välillä. Sen sijaan puolustuskäyttäytymissä oli eroja pesinnän eri vaiheiden välillä. Pesinnän edistyessä emot muuttuivat agressiivisemmiksi.

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