Butll. GCA 11: 75-82, 1994

Influence of male-female relationships on parental behaviour in two pairs of Peregrine Falcons *Falco peregrinus*

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Two pairs of Peregrine Falcons Falco peregrinus brookei breeding in Quercy (South-west Massif Central, France) were observed from the period of courtship until the fledging of the young. The purpose was to test the following hypotheses: (i) the female has a stronger parental motivation than the male leading to differences in site and eyrie attendance and duties; (ii) the female and the male may have a similar parental motivation, but differences in site and eyrie attendance and duties arise from the relationship between the mates. The data tend rather to support the second hypothesis: the female's attendance at the whole site or at the eyrie is greater than that of the male; interactions between mates suggest that the female's domination over the male prevents him from performing parental duties; the female actually controls the site attendance schedule of her mate.

Key words: Peregrine Falcon, *Falco peregrinus brookei*, parental behaviour, male-female relationships, reversed sexual size dimorphism.

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Rebut: 14.07.94; Acceptat: 17.10.94

INTRODUCTION

Peregrine Falcons *Falco peregrinus* show important sex differences in parental investment (e.g. Hagen 1942, Cade 1960, Herbert & Herbert 1965, Nelson 1970, Glutz et al. 1971, Treleaven 1977, Cramp & Simmons 1980, Ratcliffe 1980, Monneret 1987). The male is the main food provider and also performs part of the incubation, while the female, larger and stronger than her mate, defends the territory, incubates the eggs, and then broods and feeds the young.

The interpretation of this sex difference is controversial. Hagen (1942), Ratcliffe (1980) and Monneret (1987) suggested that the parental instinct is weaker in the male than in the female. According to Monneret (1974), the male prevents the

female's aggressiveness by food transfers. Therefore, the male is thought not to hunt for the young but for the female. However, other authors (Herbert & Herbert 1965, Treleaven 1977, Cramp & Simmons 1980) suggested that the tendency to incubate and also the interest in the young are as strong in the male as in the female. Nelson (1970) found that the male Peregrine was immediately motivated to start bringing food for the young by the sight of newly hatched chicks or signals from the brooding female that hatching has occurred. Several authors (Herbert & Herbert 1965, Nelson 1970, Treleaven 1977, Cramp & Simmons 1980, Hustler 1983, Carlier 1992, Hubert & Carlier 1992) noted that the female controls the schedule of brooding shifts in the wild, the male often having to "beg" lengthily for his turn at brooding. Wrege & Cade (1977) stressed that the female's dominance as a characteristic of the pair relationship in large falcons was possibly necessary for successful reproduction. This dominance is conspicuous during mating (Gallo et al. 1991). Carlier & Gallo (1989) and Hubert & Carlier (1992) have investigated changes occurring in the behaviour of Peregrine mates during the hatching period, and noticed the importance of male-female relationships, particularly the female dominance at the eyrie. She "tolerated" or "did not tolerate" the male at the eyrie.

Therefore, two views or hypotheses about the determinism of parental behaviour can be put forward: 1) the female has a stronger parental motivation than the male leading to differences in attendance and duties at the eyrie; 2) the female and the male may have a similar parental motivation, but differences in site and eyrie attendance and duties arise from the relationship between the mates.

If the hypothesis of similar parental motivation in male and female combined with the female's domination is supported, a greater attendance of the female at the site and at the eyrie should be observed. Moreover, if the female's domination over the male has an influence on the performance of the male's parental behaviour, it should be expressed in the observed interactions.

STUDY AREA AND METHODS

Two mature adult pairs were studied during spring 1988. Both were breeding within river valleys in Quercy (south-west Massif Central, France).

Pair A performed most of its courtship around the nesting cliff of the previous breeding year. Then the female laid in a cavity of another cliff, above a village. Pair B bred on a cliff-face above a forest, perpendicular to the course of the river. The eyrie was a hollow ledge on the cliffside. In this paper the 'site' refers to the nest and the area around it that the pair actually occupied.

Observations were carried out from spots located at least 100 metres from the eyrie, where it was possible to watch the whole site and the inside of the eyrie without disturbing the falcons. A telescope with a 20-60 x zoom and 8x binoculars were used. A cassette recorder was used to record the behavioural descriptions and the time. The observer focused first on the eyrie, while frequently scanning the whole site to spot the birds that were likely to be there.

For site A, where courtship was observed, the observations extended from 16 February to 14 June and for site B from 6 March to 14 June. Site B replaced another site at which, after courtship observation, the choice of the eyrie prevented subsequent observation. The total observation time was 84 hrs 55 min for site A, spread over 11 observation periods, and 78 hrs 32 min, spread over 9 observation

periods, for site B. For each site, the observation usually extended over a whole day from dawn to dusk.

Data were grouped together in observation periods for each site. The periods never exceeded three days and were separated by at least five days. All the behavioural patterns were transcribed from the cassette recorder as successions of behavioural units, preserving the time and the location. According to the hypotheses set out, a location criterion is combined with an interaction / non-interaction criterion. Three main location units were taken into account : (i) the eyrie and its edge; (ii) the whole site (including the eyrie and all the places actually occupied by the falcons); and (iii) the site with the exception of the eyrie {i.e. (ii) - (i)}.

The Mann-Whitney U-test was used to compare attendances; the X^2 test and Fisher test were used to compare occurrence frequencies in categories; Kendall's test was used for correlations.

RESULTS

Comparison of the respective attendances of females at the sites, at the eyries only, and at the sites with the exception of the eyries

Overall attendance at the site did not differ significantly between females (U = 25.5; df = 9,9; P = 0.184) (Table 1), but there was no significant correlation (Tau = 0.4; df = 9; P = 0.133). The proportions of attendance were highest during incubation, but dropped with the hatching of the young. A high value was noted for site B when the young were on the wing. It corresponded to long roosting of the female on a tree on the cliff top of the crest at the boundary of the site.

Overall attendance at the eyrie did not differ significantly between females (U = 28.5; df = 9,9; P = 0.280) (Table 1), but there was no significant correlation between them (Tau = 0.432; df = 9; P = 0.105). Eyrie attendance of female A was lower than that of female B at least until the young were five days old. A considerable increase was noted for female A between incubation and hatching.

Overall attendance at the site with the exception of the eyrie did not differ significantly between females (U = 38; df = 9,9; P = 0.824) (Table 1); there was no significant correlation either (Tau = 0.235; df = 9; P = 0.377). It was clear that female A occupied the site intensively until the hatching of the young. This happened at the expense of attendance at the eyrie. Conversely, female B occupied the eyrie intensively right up till hatching. This happened at the expense of the rest of the site. Both females showed about the same site attendance afterwards.

Comparison of the respective attendances of males at the sites, at the eyries only, and at the sites with the exception of the eyries

Overall attendance at the site did not differ significantly between males (U = 37.5; df = 9,9; P = 0.790) (Table 1); there was no significant correlation either (Tau = 0.343; df = 9; P = 0.198). Male A tended to occupy the site longer than male B from incubation until the hatching of the young. When the young were over ten days old, male B tended to be more regular at the site than male A.

Overall attendance at the eyrie did not differ significantly between males (U = 24; df = 9,9; P = 0.136) (Table 1). Moreover, there was no significant correlation between them (Tau = 0.446; df = 9; P = 0.094). Male A was more regular at the eyrie until the young were over ten days old. Afterwards the proportions were close (slightly higher for A). It should be pointed

Dates	Attendance at the site				Attendance at the eyrie				At least 1 falcon at the eyrie	
	Pair A		Pair B		Pair A		Pair B		Pair A	Pair B
	M	F	M	F	M	F	M	F		
16–17.02	24 (c)	41 (c)	(no)	(no)	15 (c)	22 (c)	(no)	(no)	32 (c)	(no)
23–25.02	16	46	(no)	(no)	8	16	(no)	(no)	22	(no)
06–08.03	0	8	2 (i)	1000 (i)	0	0	0 (i)	100 (i)	0	100 (n)
02–04.04	73 (i)	83 (i)	11 (n)	100 (n)	73 (i)	28 (i)	1 (n)	99 (n)	100 (i)	100 (n)
09–11.04	26 (n)	79 (n)	5	96	25 (n)	74 (n)	2	95	99 (n)	97
17–18.04	19	60	18	48	18	17	3	12	34	15
25–26.04	9	41	12	44	9	10	12	15	20	26
01–02.05	7	21	26	28	4	0	0	3	4	3
12–13.05	2	28	13	27	1	2	0	2	4	2
22–23.05	2 (f)	0 (f)	3 (f)	62 (f)	1 (f)	0 (f)	1 (f)	0 (f)	1 (f)	1 (f)
13–14.06	0	0	0	0	0	0	0	0	0	0

Table 1. Percentage of male and female attendances out of the total observation time according to the pair and to the period.
(no): no observation. Phases = (c): courtship, (i): incubation, (n): nestling, (f): fledgling.

Taula 1. Percentatge de les atencions de mascles i femelles sobre el temps total d'observació per parella i període.
(no): sense observacions. Fases = (c): festeig, (i): incubació, (n): polls, (f): envol.

out that the maximum occurred during incubation for male A, whereas the maximum of male B occurred when the young were three weeks old (observation period 7).

Male B's overall attendance at his site with the exception of the eyrie was significantly higher than that of male A (Table 1), (U = 16.5; df = 9,9; P = 0.029). However, there was a significant correlation (Tau = 0.528; df = 9; P = 0.012). Apart from during courtship, male A stayed little at the site outside the eyrie.

Comparisons male/female

In terms of the proportion of observation time during which the female, on the one hand, and the male, on the other, were visible at the sites (Table 1), a positive correlation was obtained for pair A (Tau = 0.811; df = 11; P = 0.0005). Moreover, overall attendance was not significantly different for male and female A (U = 34; df = 11,11; P = 0.081). On the other hand, the correlation was not significant for pair B (Tau = - 0.197; df = 9; P = 0.459), in which the overall attendance was significantly higher for the female (U = 8.5; df = 9,9; P = 0.005).

Female A's overall attendance at the eyrie did not differ significantly from that of her mate (U = 60; df = 11,11; P = 0.973) (Table 1). Furthermore, there was a significant correlation between mates (Tau = 0.785; df = 11; P = 0.0008). On the contrary, there was no significant correlation between female B and male B (Tau = 0.126; df = 9; P = 0.637), and female B's attendance at the eyrie was significantly higher than that of her mate (U= 18.5; df = 9,9; P = 0.047). This

difference was nearly 1 to 100 until the young were over ten days old.

The comparisons of the time spent at the sites with the exception of the eyrie for the males and females did not yield any significant correlations (Pair A: Tau = -0.036; df = 11; P = 0.859; Pair B: Tau = 0.25; df = 9; P = 0.313) (Table 1). Female A's attendance was significantly higher than that of male A (U = 21.5; df = 11,11; P = 0.009). Considering that the male spent a great deal of time at the eyrie, it is assumed that his attendance at the whole site actually amounted to the attendance at the eyrie. For pair B, attendance was not significantly different between mates (U = 32; df = 9,9; P = 0.449). Before the young were ten days old, the female was scarcely seen at the site excluding the eyrie. Therefore, her attendance at the site amounted to her attendance at the eyrie.

Overall attendance at the eyries

Despite differences between pairs it is worth noting that there was a significant correlation between the two pairs for the proportion of observation time during which at least one adult was visible at the eyrie (Tau = 0.551; df = 9; P = 0.039).

Interactions male–female during the brooding shift

Pair A. Two incubation shifts and two brooding shifts with young of less than ten days of age were initiated by the male. Both incubation shifts were readily performed, one being associated with a food transfer; two others (brooded young a few days old) resulted in "reluctance" from the female, as she left after about 20 seconds, screaming the wailing call while the male adopted the horizontal Head-low bow). On the other hand, four reliefs were initiated and carried out immediately by the female (the male being present).

Pair B. Four shifts were initiated by the male but only two were carried out successfully. The first failure happened during the hatching period: when the male arrived, the female stretched out on the eyrie, uttering the wailing call for three minutes, this led to the male's departure. The second failure occurred on the occasion of food provision by the male when the young had hatched. The male rested on the eyrie edge with prey in his beak; the female displayed the same behaviour as above, leading to the departure of her mate after about four minutes. However, brooding relief was "accepted" twice when the eggs were pipped (but before the first "refusal"). Two reliefs were initiated and carried out immediately by the female.

The Fisher test was used to test the differences between males and females. Two patterns were taken into account : (i) fast relief; (ii) slow and refused relief. Females performed fast relief significantly more than males; conversely, males performed slow or refused relief more than females (Fisher test; B = 4, A + B = 7, C + D = 6, D = 0, P < 0.05).

Interactions male–female during prey bringing (Table 2)

The three feedings by males seen before the young were two weeks old occurred when the females were not at the eyries. They resulted twice in the quick arrival of the female and in the departure of the male. When the young were three weeks old, they were fed by males without any interference from the females. When the young were five weeks old, they were no longer fed beak-to-beak by the adults.

The X^2 test was used to test the differences between male and female in the patterns of supplying prey from the time of hatching until the adults first delivered

Pair	Sex	Periods and ages of young (days)					
		09–11.04	17–18.04	25–26.04	01–02.05	12–13.05	22–23.05
		A: 2d	A: 9d	A: 17d	A: 23d	A: 34d	A: 44d
		B: 7d	B: 14d	B: 22d	B: 28d	B: 39d	B: 49d
A	M	0	4 (1*)	1	3 (2*, 1)	2 (2)	4 (4)
	F	1	1	2	0	1 (1)	2 (2)
B	M	5 (1*)	1 (1*)	3 (1*, 2)	1 (1)	2 (2)	3 (3)
	F	1	3	4	2 (1)	1 (1)	0

Table 2. Distribution and pattern of prey delivery according to the period.
- For the females, the numbers without brackets refer to food bringing followed by feeding of the young. For the males, they refer to food bringing with transfer to the female which carries out feeding.
- The numbers in brackets with asterisks (males only) refer to the male feeding the young without preliminary transfer to the female.
- The numbers in brackets (without asterisks) indicate the number of times food bringing was not followed by parental feeding.

For male A at period 17-18 April and male B at period 9-11 April, the females interrupted the feeding by the males.

Taula 2. Distribució i tipus d'entrega de les preses aportades al niu segons el període.
- *Per a les femelles, els números sense parèntesi es refereixen al menjar aportat seguit del peixament dels joves. Pels mascles, es refereix al menjar aportat lliurat a la femella la qual s'ocupa de l'alimentació.*
- *Els números en parèntesi amb asterics (només mascles) es refereixen al mascle peixant els joves sense haver passat el menjar abans a la femella.*
- *Els números entre parèntesi (sense asteriscs) indíquen el nombre de vegades en què el menjar aportat no va ser donat pels pares.*

Pel mascle A en el període 17-18 d'abril i el mascle B en el període 9-11 d'abril, les femelles van deturar l'alimentació dels joves pels mascles.

food to the nestlings and left it for the nestlings to tear up for themselves (observation periods: site A 5-8; site B 5-7). Two patterns are considered: (i) food provisioning followed by appropriation of the food by the mate, which then performs the complete feeding, and likewise food provisioning to the nest with initiation of feeding, followed by an interruption by the mate which then resumes feeding; and (ii) food provisioning followed by complete feeding. Females performed significantly more of sequence (ii) than males; the opposite was true for males ($X^2 = 13.7$, df = 1, $P < 0.001$).

DISCUSSION

Results, although based on a small sample size, suggest that both sexes were attracted by the site, and especially by the eyrie, from the period of incubation until the young were ten days old. In pair B, as this resulted in competition for presence at the eyrie, the female (larger and stronger) was usually likely to monopolize it, the male remaining in another part of the site. Male A was able to attend the eyrie longer than male B, so the female attended the remainder of the site correspondingly more. When the young were

over ten days old a high attendance was noted at the site with the exception of the eyrie in both females; this was also the period of maximum eyrie attendance for male B, as if he was taking advantage of the distancing of the female. When the young were over four weeks old, their frequent "begging" behaviour did not allow the adults to stay at the eyrie. The females' domination over their mates was conspicuous during brooding shifts and prey provisioning by the males, which were able to reach the eyrie only if their mates allowed it (Carlier & Gallo, in press). This female domination in landed interactions was more pronounced for pair B than for pair A and this was reflected in the male's attendance: male B did not stay at the eyrie for a long time. These results, concerning pair B, support those of Carlier (1993) collected for five Peregrine pairs. Pair A reveals a more 'equal' distribution of the duties.

Hubert (1990) concluded from a study of the Buzzard *Buteo buteo*: "the male seems to have the same submissive behaviour toward the female and the same motivation as his mate to brood throughout the brooding period : the result is that it is the female behaviour which determines the time spent at the eyrie by the male." Hubert & Carlier (1992) confirmed this assumption by comparing the Peregrine and the Buzzard.

Therefore, it seems that there is a strong influence of male-female relationships on the performance of the male's parental behaviour: the differences in parental roles do not simply result from the reduced parental motivation in the male. We should conclude therefore that the second hypothesis applies, i.e. the male and the female may have similar parental motivation, but differences in site and eyrie attendance and duties arise from the relationship between the mates.•

ACKNOWLEDGEMENTS

I am grateful to Vincent Héaulmé for his help in the field and to Peter Winterton for his valuable assistance in writing.

RESUM

Influència de les relacions mascle-femella en el comportament paternal de dues parelles de Falcó Pelegrí *Falco peregrinus*

Es van estudiar dues parelles de Falcó Pelegrí Falco peregrinus brookei que nidificaven a Quercy (sud-oest del Massís Central francès) i es van prendre dades des del festeig fins a l'envol dels joves, amb l'objectiu de comprovar aquestes dues hipòtesis: (i) la femella té una motivació maternal més forta que el mascle, la qual cosa comporta diferències en l'atenció que dedica al niu i tasques relacionades; (ii) la femella i el mascle tenen una motivació paternal similar i les diferències d'atenció al niu sorgeixen de les relacions entre la parella. Les dades obtingudes donen suport a la segona hipòtesi: l'atenció al niu de la femella és superior a la del mascle i les interaccions entre la parella suggereixen que la dominació de la femella sobre el mascle impedeix a aquest últim dur a terme les seves tasques paternals. Les femelles arriben a controlar l'horari d'atenció al niu per part del mascle.

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