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AERIAL FOOD TRANSFER AS A DEMAND BEHAVIOR IN THE MARSH HARRIER

CARMELO FERNÁNDEZ[1]
Estación Biológica de Doñana
CSIC
Avda, Mª Luisa s/n
Pabellón del Perú, 41013 Sevilla, Spain

PAZ AZKONA
Soc. Ugarra
Tafalla 34-4ª
31003 Pamplona, Spain

Abstract.—Sixty percent of the food supplied by male Marsh Harriers (*Circus aeruginosus*) was transferred to the female in the air when she was present in the territory. The frequency of aerial food passing increased as the breeding cycle advanced, from 26% during incubation to 77% in the late nestling stages, and also increased with increasing brood size. This may be explained by a greater female demand behavior as the food requirements of the brood grow. Thus aerial food transfer may be interpreted as a female demand behavior, which forces the male to increase hunting effort. The use of the aerial food transfer as a demand behavior among raptors should be limited to maneuverable species with reversed sexual dimorphism and female dominance.

EL TRASPASO DE CEBAS EN VUELO COMO CONDUCTA DE DEMANDA DE ALIMENTO EN *CIRCUS AERUGINOSUS*

Sinopsis.—El 60% de las cebas aportadas por los machos del Aguilucho lagunero (*Circus aeruginosus*), cuando las hembras estaban presentes en el área de nidificación, fueron transferidas en vuelo (n = 283). La proporción de cebas en vuelo aumentó conforme avanzaba el ciclo reproductivo, de 26% durante la incubación a 77% en la última fase de estancia de los polluelos en el nido, y con el tamaño de las polladas. Esto puede ser explicado por una intensificación en la conducta de demanda de alimento asociada a un incremento en las necesidades alimenticias de los polluelos. Así, el traspaso de cebas en vuelo puede ser interpretado como un comportamiento de demanda de alimento por parte de las hembras, que obliga a los machos a incrementar el esfuerzo de caza. En las rapaces, el traspaso de cebas en vuelo debe estar restringido a las especies más ágiles, con dimorfismo sexual inverso y dominancia por parte de las hembras.

Male Marsh Harriers *Circus aeruginosus* transfer food items to females in flight during the incubation and nestling phases (Cramp and Simmons 1980, Johannesson 1975). Hypotheses regarding the significance of aerial food passing during the breeding period include: (1) maintenance of pair bonds (Lack 1940, Watson 1977), (2) avoidance of food loss by missing small nests (Newton 1986), (3) prevention of chick aggression towards small adult males (Newton 1978, 1986), and (4) reduction of predation on nests (Watson 1977) or at terrestrial transfer sites (Simmons 1991).

In this study we evaluate the relative importance of three food transfer methods (to the nest, on the ground and aerial) used by Marsh Harriers during the breeding season. We analyze variations in the use of these

[1] *Current address: Soc. Ugarra, Tafalla 34-4ª, 31003 Pamplona, Spain.*

transfer methods during the breeding season and in relation to brood size. We suggest that aerial food transfer during breeding may be a function of female demand behavior, which informs the male of the hunger state of the young and stimulates male hunting effort.

STUDY AREA AND METHODS

The study was conducted in spring 1990 on two nature reserve wetland areas (El Juncal and Dos Reinos) in the Upper Ebro Valley (Navarra, Northern Spain). Ten monogamously breeding pairs were observed, two in El Juncal and eight in Dos Reinos (Fernández 1991). Observations were made by two observers equipped with binoculars (8 × 35) and telescopes (20–45 × 60) from fixed positions about 500 m from the nests. The breeding period was divided into five stages: incubation and four periods of 11 d each during the nestling stage. A total of 631 h of observations was made: 128 h during incubation, and 131, 124, 140 and 108 h, respectively, in each four nestling stage. Aging of broods was achieved by measuring body development of the chicks in the nest (Altenburg et al. 1987).

Time spent by either the male or the female on the nest and in the nesting area (on the wetlands) was recorded. Time spent out of the nesting area was considered as a measure of hunting time (Altenburg et al. 1982). For each food item delivered, a record was kept of: (1) sex of the adult supplying prey; (2) presence of female in the nesting area; (3) type of delivery: to the nest (directly to the chicks on the nest), on the ground (to the female out of the nest) or aerial transfer (to the female in flight); and (4) success of aerial passes, noting the dropping and loss of food items.

For statistical estimates only prey items supplied by the male when the female was present were considered. Statistical differences in the proportion of three types of food transfer during the five breeding stages were tested by means of chi-squared test in 3 × 4 contingency tables (Sokal and Rohlf 1969). Similarly, we compared the frequencies of three methods of food transfer in relation with the size broods (comparing pairs with 1, 2, 3 or 4 chicks) using chi-squared test. Also, we calculated Pearson's correlation coefficients (r) between the proportion of food transfers by males in flight, on the ground or in the nest and the five age intervals of the chicks (Sokal and Rohlf 1969).

RESULTS

A total of 467 prey deliveries was observed (0.74 food item/h) of which 372 (79.7%) were supplied by the male. In 283 (76.1%) of these 372 cases the female was present in the nesting area. The females supplied directly to the nest 85 (18.2%) food items, probably hunted by themselves.

The females almost never left the nest during incubation or the first stage after hatching (1–11 d), whereas at the end of nestling rearing (34–44 d) females only spent 30.1% of their time in the nesting area (Table 1). Males spent 43.8% of their time around the nest during incubation but only 25.5% at the beginning (1–11 d) and 12.6% at the end (34–44 d)

TABLE 1. Time spent in nesting area and number of prey items supplied by male and female Marsh Harriers during breeding period.

	Incubation	Nestling phase			
		1–11 d	12–22 d	23–33 d	34–44 d
% time spent by females in nesting area	100	100	93.5	57.2	30.1
% time spent by males in nesting area	43.8	25.5	21.7	12.8	12.6
Total food items supplied by hour	0.43	0.53	0.81	0.97	0.88
% supplied by females	—	—	8.0	29.1	41.6
% supplied by males	100	100	92.0	70.9	58.4

of the nestling stage. As a result, the number of food items brought directly to the nest by the male when the female was absent was higher in the latter stages of breeding.

The proportion of food transfers by males in flight, on the ground, and in the nest when females were present (Table 2) varied over the breeding period ($\chi^2 = 81.53$, df = 8, $P < 0.001$). Aerial transfers increased as the breeding cycle advanced ($r = 0.892$, df = 4, $P < 0.05$). Conversely, ground transfers, very frequent during incubation, decreased notably over the nestling period ($r = -0.980$, df = 4, $P < 0.001$). Numbers of food items brought directly by males to the nest when females were present in the territory were always very low (≤23%), increasing slightly as the chicks developed ($r = 0.977$, df = 4, $P < 0.001$) (Fig. 1). On 12 occasions females flew to receive food but were refused by the male (6.6%, $n = 181$), who delivered food on the ground (5.5%) or to the nest (1.1%).

We noted a relationship between brood size and type of food pass (Table 3). Aerial transfers were more frequent in pairs with larger broods ($\chi^2 = 17.95$, df = 6, $P < 0.01$), though also this could be due to the greater skills or experience of the most successful breeding pairs.

TABLE 2. Frequency and variation in the modes of food pass from male to female Marsh Harriers during breeding period.

	Incubation	Nestling phase				Total
		1–11 d	12–22 d	23–33 d	34–44 d	
Total food items supplied by males	55	70	94	97	56	372
Food supplied by males when females present	55	70	79	53	26	283
Transfers in nest	0	6	9	8	6	29
Transfers on ground	41	24	14	6	0	85
Aerial transfers	14	40	56	39	20	169
Food items dropped (lost)	0	2 (1)	3 (0)	1 (1)	0	6 (2)

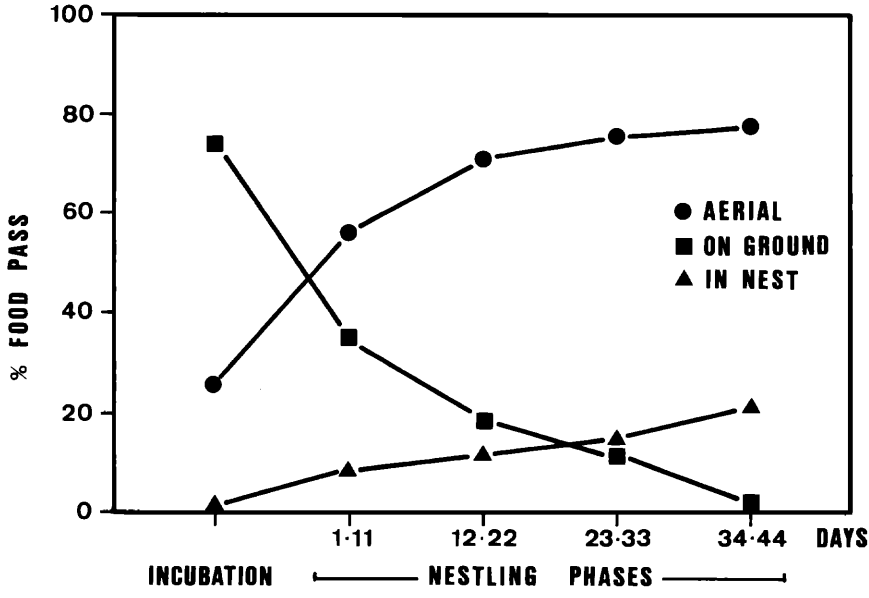

FIGURE 1. Variation in the proportion of three types of food pass (in the nest, on the ground and aerial) from male Marsh Harriers during breeding period when females were present in the nesting area.

Food items were dropped in six (3.6%) of the 169 aerial transfers attempted. Two of these items were lost, with adults unable to find them either in the water or among cattails (*Typha* spp.). This represents a loss of 1.2% of aerial delivered food items.

DISCUSSION

Various authors have suggested that aerial food passing in raptors is a means of pair bonding (Lack 1940), or a system to avoid food loss by missing small nests (Newton 1986) or nests situated in areas of dense vegetation (Watson 1977). Another hypothesis is that, by transferring food away from the nest, the small adult male avoids aggression from his large (particularly females) offspring (Newton 1978, 1986). Finally, in the case of harriers, there are two additional hypotheses that may explain aerial transfers: (1) aerial food passing is a method to avoid nest detection and nest predation in a genus with particularly conspicuous males and nests on the ground (Watson 1977), and (2) the safe substrates (such as trees or cliffs) used by other raptors to transfer food are not available to harriers (Simmons 1991). These hypotheses, however, hardly explain the changes in frequency of food passing that take place in Marsh Harriers during breeding and with brood size.

During our research we observed that there were females who controlled the mode of food passing, because the females were rarely refused

TABLE 3. Food passing patterns from male to female Marsh Harriers depending on brood size.

Brood size	*n*	Type of food pass			Total
		In nest	On ground	Aerial	
1 chick	2	5 (17.9%)	6 (21.4%)	17 (60.7%)	28
2 chicks	3	14 (17.1%)	24 (29.3%)	44 (53.7%)	82
3 chicks	1	1 (5.9%)	4 (23.5%)	12 (70.6%)	17
4 chicks	4	9 (8.9%)	10 (9.9%)	82 (81.2%)	101
Total	10	29	44	155	228

by males when they flew to receive food (cf. Simmons et al. 1987). We suggest that, besides other functions, aerial food transfer during breeding has a component of demand behavior that serves to inform the male of the hunger state of the female and the young. Thus, the progressive increase in aerial transfers would be due to an increase in the brood's food requirements, which stimulates the female to go out to collect food from the male before he has time to deliver it to the nest or leave it on the ground. The fact that aerial passes were more common in pairs with larger brood sizes and greater food requirements seems to support this view. As a demand behavior the aerial food transfer may be similar and complementary to dismissal screams and aggression described in other birds of prey (Balfour 1957; Haverschmidt 1953; Newton 1978, 1979, 1986; Schnell 1958; Sherrod 1983; Watson 1977) and could be related to reversed sexual dimorphism and female dominance (Smith 1980).

The main benefit of the female forcing the male into aerial food passes would be to increase male foraging rate (Cade 1960, Schnell 1958). The results of Altenburg et al. (1982) as well as those from this study suggest that monogamous male Marsh Harriers spend more time foraging as the breeding cycle advances. Increased male foraging time could result in two ways: (1) time saved in food transfer, as suggested by Simmons (1991), and (2) demand behavior of females stimulating the males when females come out to receive prey items.

Undoubtedly the advantages of aerial transfers are partially offset by the risk of food loss (Watson 1977), but as we have seen, losses in the Marsh Harrier, as well as in other harriers (Jiménez and Jaksic 1988, Simmons 1991), are insignificant. Losses are probably compensated by extra hunting time and the consequent increase in food items supplied by the male. In other raptors, which are not able to capture birds in flight, or whose staple prey is heavy (e.g., large mammals) the risk of food loss would be much greater and not compensated by increased food searching time. Then one would expect the use of aerial food passes as a demand behavior among birds of prey that are aerially maneuverable, that hunt handy prey and that have reversed sexual dimorphism, as occur in genera *Circus, Falco* and *Accipiter* (Cade 1960, Jiménez and Jaksic 1988, Newton 1986, Simmons 1991, Watson 1977).

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