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Analysis of the nestling feeding behaviour in the female common buzzard

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ABSTRACT. *Analysis of the nestling feeding behaviour in the female common buzzard.*- The nestling feeding behaviour of the female Common Buzzard *Buteo buteo* was recorded in nature by video cameras focused ontwo nests. 75 feeding sessions were analysed and the descriptive statistics used revealed modifications in both females feeding behaviour. From 0 to 7-8 days after hatching, feeding was characterised by consumption of food morsels by the female. From 7-8 to 30 days after hatching, the females fed the nestlings more intensively and in a more similar manner in both nests. The proximity of the male sometimes disturbed feeding activity. After 30 days, the females behaviour seemed inhibited by the appearance and the behaviour of their nestlings. An analysis of the female feeding behaviour is suggested here, in terms of change in the motivations of females who live conflictual situations.

KEY WORDS. *Buteo buteo*, Behaviour, Motivation, Feeding, Parental care, Nestling

Introduction

The feeding behaviour of young birds of prey has been described by several authors. Food is distributed to the nestlings by the female who holds the prey in her talons, tears off small morsels and presents them to the young while ingesting some morsels herself. This has been called active feeding behaviour (Jenkins, 1978) as opposed to the behaviour observed when the nestlings are able to feed themselves, where feeding becomes a simple prey delivery. This study concerns active feeding behaviour only.

Studies concerning feeding behaviour in raptors have delt with feeding occurrence (Palmer et al., 1958; Rettig, 1978; Gargett, 1990), length of feeding (Liversidge, 1961; Collopy, 1984), circadian rhythms of feeding (Wiley & Wiley, 1981; Jenkins, 1978; Newton, 1978), or number of morsels consumed per family (Poole, 1989).

The ultimate approach of the studies on feeding behaviour concerns the level of minimal parental care required to raise a clutch. The adult's fitness would decrease if its parental investment reduced its chances of survival and of reproducing during the following season (Trivers, 1972). Parental feeding effort would thus require a balance between food conditions (quality and quantity), the size of the clutch, and the adults' physical condition, maximising the number of viable nestlings (Bengtsson & Ryden, 1983).

The proximate causes affecting parental feeding (studied in passerine and marine birds) are the age of the clutch (Gibb, 1950; Kluyver, 1961; Van Balen, 1973), the size of the clutch (Royama, 1966), and the "hunger level" of the clutch (Perrins, 1965). Artificial reduction or increase in nest size are followed by adjustments in feeding effort (Von Haartman, 1954). The nestlings' hunger level is expressed by its begging behaviour, producing both visual and acoustic signals according to the age and the hunger level of the clutch (Henderson, 1975; Bengtsson & Ryden, 1983).

The proximate factors studied explain variations in parental feeding behaviour according to external factors (age, size, hunger level of the clutch) that stimulate parental behaviour; but the feeding behaviour may not be reducible to a simple stimulus-response system. Internal factors, such as motivation have also to be taken into account. Indeed, in a similar environment, a given stimulus can produce different kinds of behaviour, depending on the motivation of the bird (Mc Farland, 1990). Is a motivational mechanism able to describe the observed feeding behaviour?

The aim of this paper is then to describe the behaviour of the female Common Buzzard *Buteo buteo* when feeding her offspring and to analyse this behaviour in terms of motivation for the female: how does the female's feeding motivation fit to the age of the young? How describing the observed feeding behaviour in terms of motivations ?

Methods

Area and nest-sites

Nest-site characteristics have been previously described (Hubert, 1992; Hubert, 1993). We observed five pairs of buzzards nesting in the forest of Chizé (Deux-Sèvres, France), which is mainly composed of beech (*Fagus sylvatica*), oak (*Quercus pedonculata*) and pine (*Pinus sylvestris*). Nest trees were either in beech, oak or pine, and were located near pathways, to facilitate a quiet and rapid approach. Nests were at a height of 14-20 m. Two nests were monitored by video camera and three by direct observation. Observations were made from 2 May to 10 June 1991.

Direct observation

Three nests (nests C, D, and E) were monitored from ground level with telescope (20-60x) and binoculars (8x) from observation sites, 20-40 m from the nests for a total of 168 hr. The three nests were observed each successively in the morning for about 6 hr each per d. Nest C, containing one young, was observed directly from 4-24 d after hatching then by video from 28-45 d. Nest D, containing three young, was observed 5 d before to 10 d after hatching, thereafter the whole clutch has been predated. Nest E, containing 3 young at the beginning, was observed 11-34 d. after hatching, but two young were killed by sibling competition (respectively at age 14 and 32) and the last one was recovered died under the nest at age 37.

Video recorded nests

A video system, composed of a camera and a portable recorder powered by an automobile battery, was placed at two nests (A and B) containing each two eggs. The cameras (each protected by a plexiglas and wooden box, camouflaged by tree branches) were installed in trees 3-4 m above and 8 to 12 m from the nests. Each morning, at a fixed solar time, a new 4-hr tape was placed in the recorder, itself on the ground. This sampling regime was chosen because it appeared to be the time of maximum nesting activity in a preliminary study of full-day regime (Hubert, 1990). Recording was done from 5 d before hatching until 18 d after hatching for nest A. The second young of nest A was killed by a predator in its 18th day of life (the first one died by sibling competition at 4 d) thus the video system was moved to nest C. Nest B was recorded from 13 d before to 32 d after hatching, only one egg hatched, and this young has been monitored until observations came to end (10-06-91, at 32 d.). A total of 324 hr were filmed at the three nests (A, B, and C). Only the young of nest C was observed until flight, 43 days after hatching.

Data

Videos were examined with a detailed ethogram, describing movements, postures performed and the location of the behaviour in the nest. The ethogram includes 127 acts, but only the 28 acts occurring in feeding sequences and appearing in correspondence analyses are described (table 1). Videos were analysed once, by the same worker (C.H.), usually at the normal speed, but feeding bouts were watched with the slow motion. Feeding activities are coded by the letter F (ex. F1 = put down the prey, F2 = tear off a morsel, F3 = present a food morsel to the young, etc.). The stereotyped feeding session comprises a repetition of F2-F3 acts (tearing off a morsel and presenting it to the young). A feeding session as described here is defined by a series of F(n) acts, limited in its context to the 4 acts preceding the first F(n) act up to the 3 acts after the next non F(n) act. Only F(n) acts and their defined context are analysed here. Data from direct observation nests were mainly used to insure that recorded nests were consistent with other nests, but could not be as detailed as data from recorded nests.

TABLE 1. List of behavioural acts of the female buzzard at the nest during feeding sessions.
[Lista de los actos de comportamiento de la hembra de Ratonero común durante las sesiones de alimentación.]

BRAN: moving nesting material (branches)
CALC: calling from the nest cup
CALR: calling from the nest rim
F1 : laying down the prey
F2 : tearing the prey into morsels
F3 : giving a food morsel to the young
F4 : bringing the prey back to herself
F5 : morsel refused by the young
F6 : ingesting morsels
F7 : picking up fallen morsels
F8 : pecking at morsels
F? : non-identified feeding behaviour
FLY: flying away
GAC : glances around from the nest cup
GAR : glances around from the nest rim
GUC : getting up
GYR : glances on the rim toward the young
GYC : glances in the nest cup toward the young
INC : brooding
LPR: landing on the rim with prey in talons or beak
LZR: landing on the rim without prey or branches
PBER: begging posture
PDOR: dominance posture
PRC: preening in the nest cup
PRR: preening on the nest rim
SDC : stepping down into the nest cup
SUR : stepping up to the rim
TUC : turning in the nest cup
TUR : turning on the nest rim
WALR: walking on the rim
WPR : walking on the rim with prey in talons or beak

Statistical analysis

Statistical analysis of behavioural sequences used SPAD.T software which can process a large number of diversified lexical data (Lebart & al., 1984; Morineau, 1984; Lebart & Salem, 1988). Correspondence analysis were applied to the feeding sessions recorded in nest A and in nest B. Correspondence analysis (CA) describes charts with feeding sessions in lines and behavioural items in columns and gives graphic representations of associations between lines and columns. Days with similar behavioural profiles are represented closer. Contrast between periods as well as modification of feeding behaviour along the study are fully described and characterised by specific activities. Feeding sessions were grouped together day by day. Each group of sessions was labelled with the letter of the nest (A or B) followed by a number indicating the age of the young (e.g. B23: sum of feeding sessions observed in nest B when the young was 23 days old). Days without monitored feeding sessions do not appear on figures (A1, B2, B11, B24, B29, B32).

Results

Length of feeding sessions and delay between two sessions.

111 feedings in all were observed (75 filmed on

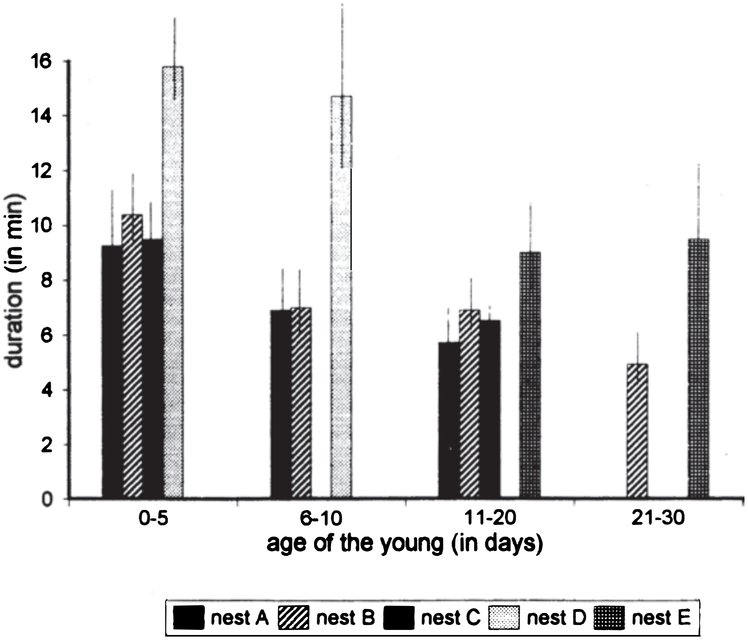

FIGURE 1. Mean feeding duration (in min) versus age of the young. Bars indicated ± SE.
[Duraciones medias de alimentación (en minutos) con respecto a la edad del jóven.]

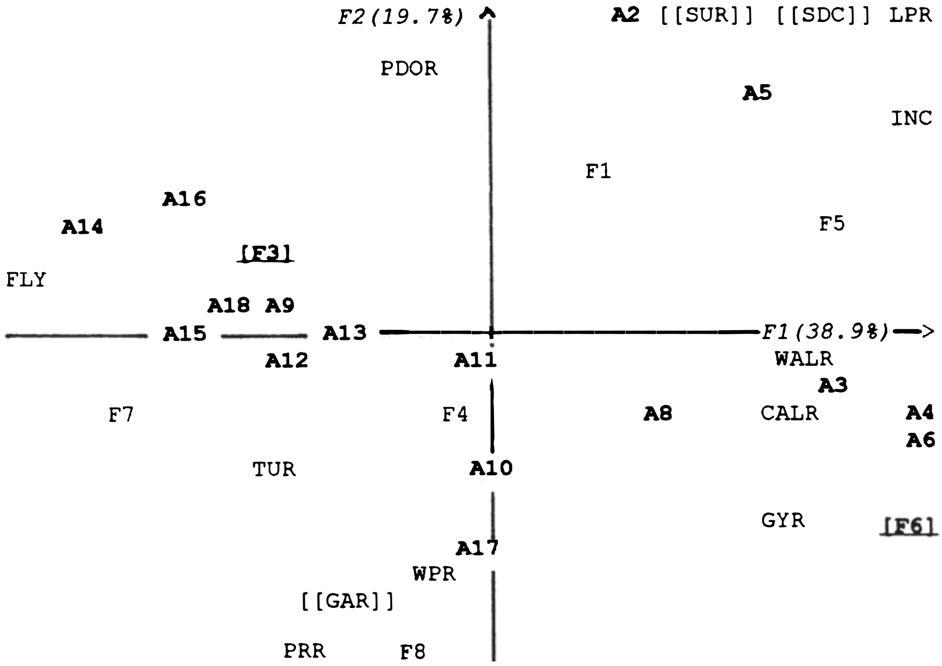

FIGURE 2. Correspondence analysis (F1 x F2) of feeding sessions at nest A. Feeding sessions are indicated in bold characters. Acts intervening more in the formation of axis 1 are indicated by a bold-underlining, e.g. **F6**. Acts intervening more in the formation of axis 2 are indicated in double square brackets, e.g. [[GAR]]; acts having some importance in the formation of axis 2 are indicated in single brackets, e.g. [F3].

[Analisis de correspondencia (F1 x F2) de las sesiones de alimentación del nido A.]

video in nests A and B and 36 by direct observation in C, D and E). Feeding occurred at an average of every 90±5.5 min., was performed only by the female (except for two attempts by the male in nest B). The average feeding time was 8.6±0.52 min. There was a slight decrease in feeding time as the nestlings matured (fig. 1). In addition, feeding time was proportional to the number of young : in nests D and E (with 3 young each), feeding time was definitely longer than in the other nests. On the other hand, feeding sessions were not much more frequent in nests with 3 nestlings (75±9.7 min) than in nests with only one (94±10.57 min.). Young were fed by the female until 25-27 days of age except in nest B where the nestling seemed slightly retarded compared to the average (at 31 days, it was still incapable of eating alone and its feathers were less developed than in other young of the same age).

Comparative analysis of food sessions in nests A and B (video recorded)

Nest A (fig. 2)

The points representing feeding days go from A4-A6 to A14-A16, with, however, intermediate days (A10, A17), thus showing 2 main feeding styles:

- style 1 (A2, A3, A4, A5, A6, A8) characterised by the ingestion of food morsels by the female (F6

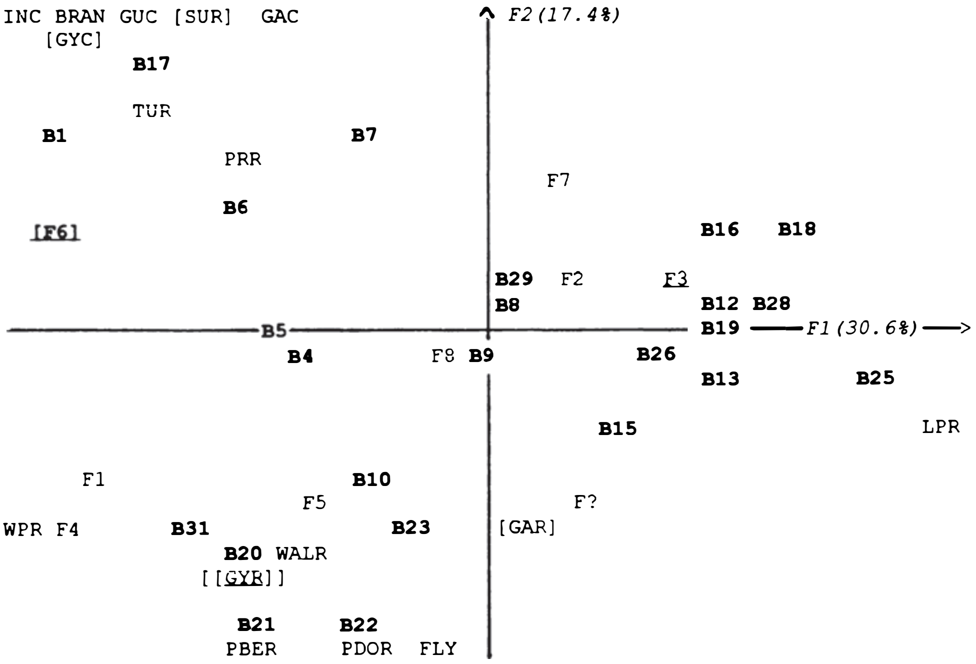

FIGURE 3. Correspondence analysis (F1 x F2) of feeding sessions at nest B. Feeding sessions are indicated in bold characters. Acts intervening more in the formation of axis 1 are indicated by a bold-underlining, e.g. **F 6**. Acts having some importance in the formation of axis 1 are indicated by single underlining, e.g. F3. Acts intervening more in the formation of axis 2 are indicated in double square brackets, e.g. [[GYR]]; acts having some importance in the formation of axis 2 are indicated in single brackets, e.g. [GAR].

[Analisis de correspondencia (F1 x F2) de las sesiones de alimentación del nido B.]

alone accounts for 50% of the variance of the first factor) and by a very low rate of F3 (presenting morsels to the young). These days are also similar because of the number of glances to the chick (GYR, GYC), by movements from nest rim to nest cup (SDC, SUR) and by brooding, preceding or following feeding sessions. However, days A2 and A5 are quite distinct from A3, A4, A6 and A8 along axis 2 because of the nearly total absence of scanning behaviour (ARS) during feeding sessions.

- style 2 (A9, A11, A12, A13, A14, A15, A16, A18) characterised by another feeding style with a high rate of F3 (presenting morsels to the nestling) and with a very low rate of F6 (female ingesting morsels) and GYR (glances to the young). Points are rather close each others, showing the homogeneity of this feeding style.

Between these two distinct styles, there is some regression to a style closer to A4-A6, that is characterised by high surveillance activity and slower rate of actual feeding (A10 and A17).

Nest B (fig. 3)

The correspondence analysis disclosed three groups of points, showing three feeding styles:

- Style 1 (B1, B4, B5, B6, B7) characterised by a high rate of F6, a low rate of F3 and by activities related to brooding (INC, GYC, SUR, GUP).

- Style 2 (B12, B13, B15, B16, B18, B19, B25, B26, B28) characterised by a highly intensive series of feeding sessions (very numerous F2-F3), and rare occurrences of F6. Points are rather close each others, showing the homogeneity of the feeding sequences.

- Style 3 (B20, B21, B22, B23) characterised by a high number of activities scanning the environment (GAR) and the young (GYR).

Feeding styles 1 and 3 demonstrate much less intensive feeding than style 2 (occurrence of F3) and are thus grouped together on axis 1. The female was agitated and showed ambivalent behaviour. In Style 1, she gave little food to the chick and ingested most of the food while in Style 3, she did not feed the young much because she was too busy scanning the environment and watching the young. On B21-B22-B5, the male landed on the nest with prey during several food sessions. On B26, the male also landed on the nest during feeding, but without prey: B26 lies far from B20, B21, B22. It is thus the male WITH prey that produced the female's scanning during feeding. During feeding on B23, the male did not land on the nest although he remained in the proximity of the nest without landing, thus inducing increases in scanning behaviour by the female. The presence of the male during feeding induced either dominance posture (PDOR) or begging posture (PBER) by the female.

Discussion

Data from direct observation nests showed a feeding pattern in duration and frequency that was comparable to video recorded nests. The video recorded nests could be then considered as not atypical for the buzzard population studied.

Our results showed that (1) females' feeding behaviour can be characterised by three main styles, according to the age of the young or male's interactions, (2) the females' feeding behaviour was much more variable during the first days of life of the young than after. Feeding seemed stereotyped after the young was over 8-9 days, (3) the first feeding sequences were characterised by an ambivalent behaviour of the females ; even if the young was not always receptive to the morsel presented, some acts of the females can be only explained by their ambivalence, such as movements on the nest rim, ingestion of most torn morsels *a priori* aimed at the young (small pieces). Thus, the feeding behaviour cannot only be considered as dependent on external factors but also on internal factors. Results could be then analysed in terms of motivation:

During the first days of life of the young (from the first day to the seventh or eighth day), both females fed their chicks rather similarly : feeding sequences were characterised by a great number of food morsels ingested by the females. In this period, the female may be particularly hungry because she usually lose weight (Village, 1990) and could live off body fat reserves (Poole, 1989). She may stopped brooding because of the association of her hunger and the presence of prey in the nest. But the chick, no longer warm from brooding, began to call and moved about. Calls of young birds was shown to be a sign-stimulus, inducing parental care (Tinbergen, 1971). The feeding behaviour of the first days could be then considered as a conflict between the hunger motivation of the female and the motivation to feed the calling chick. This ambivalence could give rise to the numerous movements on the rim and to tearing the prey into small pieces. This situation completely absorbed the female's attention so that she did not always scan the environment during the first few days of feeding. This period corresponds to an obligate adjustment between the female and her offspring. It is worth noting that the female ate first and tore off small morsels as if she were to give them to the chick but ate them herself without offering most of them to the chick, whereas later (from 9 to 30 d after hatching), the female fed the young first, until it is satiated, and ate the rest of the prey if any.

During feeding sessions of style 2 (from 9 to 30 days after hatching), both females fed their young intensively (few behavioural acts other than F2-F3) and the feeding sequences during this period showed a great homogeneity. The motivation of the female to feed the young showed no ambivalence, the adjustment between the female and her offspring was achieved : the female landed on the nest (with or without prey) or took the prey in begging posture from the male who landed on the nest. The young called and moved about ; the female brought the prey back to herself, tore it to pieces that she gave to the young, feeding it until it was satiated. Then she quickly ate the rest of the prey, if any, without tearing it to pieces, or she picked at morsels remaining on branches of the nest.

Finally, in the feeding sessions of Style 3, the female's behaviour showed ambivalent motivation between feeding the young and scanning the environment or the young. In its beginning, the feeding sequence was identical to Style 2, but the male's proximity disturbed feeding behaviour. The female's behaviour could be thus considered as a balance between her motivation to feed her young and her motivation to get prey from the male.

Later, when the nestling fed itself alone (after around 30 days old, varying from nest to nest), the time adults spent in the nest was limited to bringing food (nest C, filmed) and the young threw itself at the adult, took the prey in begging posture, turned around and mantled the prey with its wings and tail spread, and immediately ate it (usually swallowing it whole). Then, if the adult was still present, the young turned back to the adult in begging posture, the adult then flew off. The behaviour of the female was altered by the behaviour (mantling, begging) and the appearance of the young (its back feathers have grown in, only its head and neck are still covered with down). The female was perhaps still motivated to feed it but the young's behaviour inhibited her. Moreover, the young resembled less and less a nestling, more and more an adult buzzard, which, for the female, induced an attitude of alert when she landed on the rim. She may have less tendency to leave the prey to her young if it did not adopt a begging posture. Her behaviour could be thus considered as a balance between her motivation to feed it and her motivation to avoid contact with her nestling.

In conclusion, the female's feeding behaviour is not only dependent on external stimuli (age of the young, behaviour and aspect of the young) but also on her motivational state: conflictual situations emerge from different kinds of motivation, such as her hunger motivation versus the feeding of the young, the feeding of the young versus getting prey from the male. Furthermore, it seems relevant to consider that even if the feeding behaviour is a "natural" drive of the bird, it is based on a conflictual situation and needs an adjustment between the female and the young.

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Resumen

Análisis del comportamiento de alimentación de los pollos por la hembra de ratonero común.

Se ha filmado, con equipo de video dispuestos sobre dos nidos, el comportamiento de alimentación de los polluelos de dos parejas de ratonero común (*Buteo buteo*) en situación natural. 75 secuencias de alimentación han sido analizadas y los estadísticos descriptivos utilizados ponen de manifesto una evolución de este comportamiento en las hembras. Desde 0 a 7-8 días después de la salida del huevo, la hembra consume la mayor parte de los trozos de carne destinados "a priori" al polluelo. Desde nueve hasta treinta días, las hembras alimentan a los polluelos de forma muy eficaz y muy similar entre los dos nidos. Solo la interacción con el macho perturba la actividad de alimentación del polluelo. Después de 30 días de vida del polluelo, las hembras parecen inhibidas por el aspecto y el comportamiento de los jóvenes. Se analiza el comportamiento de alimentación en términos de modificaciones en la motivación de la hembra.

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