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SHORT COMMUNICATION

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Feeding and reproductive behaviour in fallow bucks (*Dama dama*)

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Abstract Observations on individually marked fallow deer (*Dama dama*) in central Italy were performed over 2 years in order to analyse time budgets of four age and sex classes. The aim was to test whether feeding activity was influenced by mating activity, forage quality or physiological constraints during the rut. Only adult males (bucks) completely ceased feeding during the rutting season, well before the actual start of mating behaviour and concurrently with the phenomenon of scent-urination, and spending most of their daily time completely inactive. All other age and sex classes were unaffected in their feeding behaviour by the rutting season. Indeed, females and young males showed a marked increase in grazing in response to an improvement in forage quality from summer to autumn. These results seem to confirm the hypothesis that hypophagia, displayed only by bucks, may be of no adaptive value in itself. On the other hand, it may be a by-product of other physiological processes occurring during the rut, inducing scent-urination, which plays an important role in intraspecific recognition and sexual attraction.

Introduction

Temperate areas, exposed to cyclical environmental conditions, host animals which over time have adapted to the successful use of seasonally available resources. Seasonal reproduction and annual variations in metabolism, body weight and food intake represent two cyclic phenomena having a clear adaptive value. The first defines the time of year during which there will be the best survival conditions for the newborn, while the second keeps the budget between energetic losses and food resources positive (McMillin et al. 1980). Therefore, voluntary forage intake reduction is an important factor in promoting such processes (for ungulates see: red deer, *Cervus elaphus*, Brown et al. 1979; reindeer, *Rangifer tarandus*, McEwan 1968; roe deer, *Capreolus capreolus*, Drozdz and Osiecki 1973; moose, *Alces alces*, Miquelle 1990; bison, *Bison bison*, Maher and Byers 1987). This condition occurs twice a year; in winter, when there are few available resources (with an evident adaptive value) and, only in adult males, during the breeding season, when they should have a higher food intake to face energetic expenditure linked to reproductive activity. The mechanism governing this last phenomenon in mammals is not clear, and most data come mainly from captive animals (McMillin et al. 1980; Suttie and Simpson 1985) or from single individual cases (Kitchen 1974; Clutton-Brock et al. 1982). Studies on bison (Maher and Byers 1987) noted a close relationship between appetite suppression and male age: the oldest males, with the highest reproductive success, strongly reduced their forage intake during the breeding period. Two hypotheses were proposed to explain this voluntary hypophagia: (1) time normally allocated to feeding is supplanted by rutting activities (Geist 1982), because any behavioural activity restricts another one (Coblentz 1976; Lincoln and Short 1980), with an evident adaptive value; (2) feeding cessation is related to physiological processes occurring during the reproductive period as a result of changes in testosterone levels (Suttie and Simpson 1985) or in endogenous opiate antagonist (Plotka et al. 1985), with no direct adaptive value. Moreover, as Miquelle (1990) observed in moose, a strong time coincidence exists between hypophagia and "scent-urination", which is responsible for the pungent odour of adult males' urine during this period and related to high testosterone levels. Here we test whether, in fallow deer, (1) feeding reduction would give more opportunities to adult males to spend time in reproductive activities, or (2) hypophagia is the result of physiological processes coming from hormonal cycles during the rut, possibly associated with scent-urination.

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Materials and methods

The study area is a deer park of 42 ha within the Maremma Natural Park, Tuscany, Italy. The climate is Mediterranean with mean annual rainfall about 650 mm. Fallow deer population consisted of about 120 and 150 head in 1991 and 1992, respectively. Observations were conducted from June 1991 to April 1993 (1,350 h observations) and were almost evenly distributed during the day.

We classified fallow deer into four categories: adult females (>12 months), adult males (>48 months), yearlings males (12–24 months old), and subadult males (24–48 months old). All were identified with ear-marks and their time budget was recorded monthly by focal sampling with scan-sampling (scans of 2 min and sessions of 120 min). The following behaviours were sampled: lying, standing, feeding, ruminating, moving, self-grooming, other activities. From 10 to 30 September in 1991 (pre-reproductive period), a continuous sampling was also performed on males in order to record activities linked to reproduction such as scent-urination and roaring. The mating period was defined by the first and last copulation observed (1991 from 1 to 13 October; 1992 from 28 September to 10 October) and then a supplementary time budget was performed: all males were analysed every 2 days, for at least 60 min each. We kept a monthly record of food availability by sampling grass from ten evenly distributed plots: the grass was cut in squares of 30 cm. Green grass was separated from dry grass and (1) the total amount of grass and (2) the green part of the sample were weighed, assessing the total percentage of green and the amount of available forage.

For statistical analyses, non-parametric tests were used; significance was set at $\alpha<0.05$.

Results

In 1991 and 1992 there were, respectively, 20 and 21 bucks in the Park of which four and seven were observed mating. The first buck observed scent-urinating was recorded on 13 September in 1991 and on 12 September in 1992. This behaviour was observed in all bucks on 27 September 1991 and on 26 September 1992 (with one exception, see below). No subadult male was ever observed scent-urinating. Other reproductive behaviours started between 10 and 12 September, apart from roars, shown only by adult bucks, which were heard from the last 10 days of August. In 1992, one buck (Y/G) had a tumour of the preputial gland, preventing him from scent-urinating.

Data sets were obtained for one pre-reproductive period (10–30 September 1991), two reproductive periods (1–13 October 1991 and 28 September–10 October 1992), and one post-reproductive period (second half of October 1992). In addition, monthly time budgets were collected outside the rut for the purpose of comparison.

In the 1991 pre-reproductive period, we found differences among classes in feeding, lying and reproductive behaviours (K-W, ANOVA, df=3, respectively χ^2=13.55, P=0.004; χ^2=23.27, P<0.001; χ^2=11.84, P=0.008). From 10 September, forage intake by bucks decreased dramatically to 8.2% of time budget, whereas females, yearlings, and subadult males maintained higher feeding time rates (28%) (M-W, U-test, $n_{1,2}$=8, respectively U=8, P=0.012; U=4.5, P=0.004; U=8, P=0.012). Adult males spent more time lying (68%) than did females and young males (M-W, U-test, $n_{1,2}$=8, U=8, P=0.012 for both). They spent most time lying down idle, not guarding mates or defending harems.

In both reproductive periods sex and age classes showed markedly different activity budgets (Fig. 1) (KW, ANOVA, df=3, feeding: χ^2=31.76, P<0.001; ruminating: χ^2=8.78, P=0.03; lying: χ^2=9.38, P=0.024; reproductive behaviours: χ^2=9.77, P=0.02, in 1991; feeding: χ^2=27.72, P<0.001; ruminating: χ^2=10.19, P=0.02; lying: χ^2=9.73, P=0.02; reproductive behaviours: χ^2=14.71, P=0.002, in 1992). Unlike females, yearlings (M-W, U-test, $n_{1,2}$=8, U=0, P<0.001 for both years) and subadult males (M-W, U-test, $n_{1,2}$=8, U=0, P<0.001 in 1991, U=1, P=0.001 in 1992), the bucks showed an evident hypophagia: during the first rutting season they reduced feeding and ruminating up to 4.8% and 2.4% of their time budget and up to 5.7% and 0.9% during the second rutting season. Adult males spent most of their time budget lying down (55% in 1991, 60% in 1992); more than yearling males (M-W, U-test, $n_{1,2}$=8, U=4.5, P=0.004 in 1991, U=7, P=0.009 in 1992), than females in 1992 only (M-W, U-test, $n_{1,2}$=8, U=8, P=0.012), but not more than subadult males over the two years (M-W, U-test, $n_{1,2}$=8, U=18, U=15, P>0.05) (Fig. 2). During the rut, all males (the adults had the highest rate, i.e. 7.5%) were more engaged in reproductive activities than were females (which spent only 0.4%).

During the 1992 reproductive period, the Y/G male with the preputial gland tumour did not cease feeding, but actually increased this activity, with a range between that of female and that of yearling (Fig. 2); however, none of his approaches to females was successful.

In the 1992 post-reproductive period, very high food intake was noted in all the classes, comparable with the spring intake; statistical analysis did not record any significant difference among classes in the activities of feeding, ruminating and lying (K-W, ANOVA, df=3, χ^2=3.06, P>0.05).

Statistical tests showed a high between-months variability in feeding behaviour for adult males during the 1991–1992 (K-W, ANOVA, df=6, χ^2=30.74, P<0.001) and 1992–1993 sampling periods (K-W, ANOVA, df=6, χ^2=35.07, P<0.001), with the highest values in April and the lowest in October (M-W, U-test, $n_{1,2}$=8, U=0, P<0.001), in spite of the highest availability of forage (Fig. 3a, b). Females clearly spent more time feeding in September and October (47% and 70%) than did bucks (Fig. 3a, b).

Although autumn rains improved the quality and amount of forage, adult male feeding activity during the two rutting seasons was not correlated with quality and availability of food (Spearman's test, n=7, rs=0.32 and rs=–.25, P>0.05). Conversely, female and yearling male food intake was positively correlated with forage quality over the two years (n=7, rs=0.99, P<0.001 for both) (Fig. 3a, b).

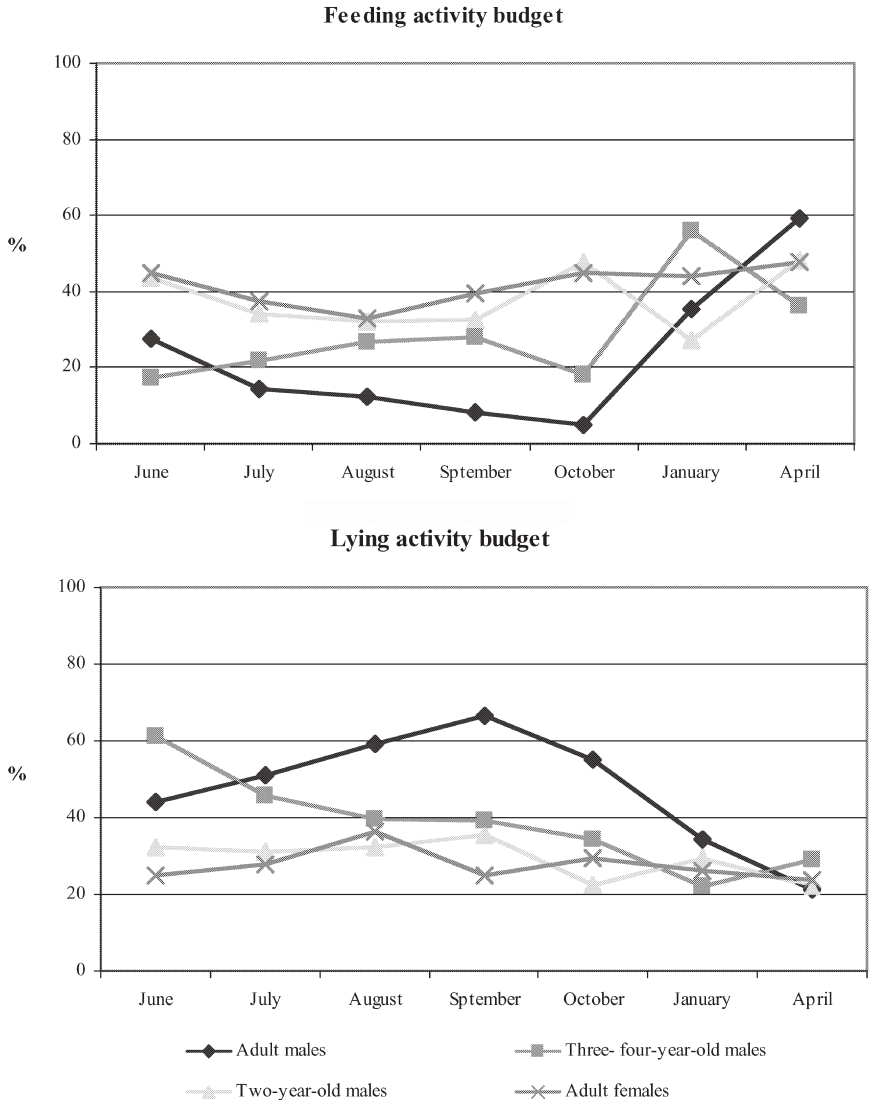


Fig. 1 Percentage of monthly feeding and lying activity budget in fallow deer (*Dama dama*) by sex and age class from June 1991 to April 1992

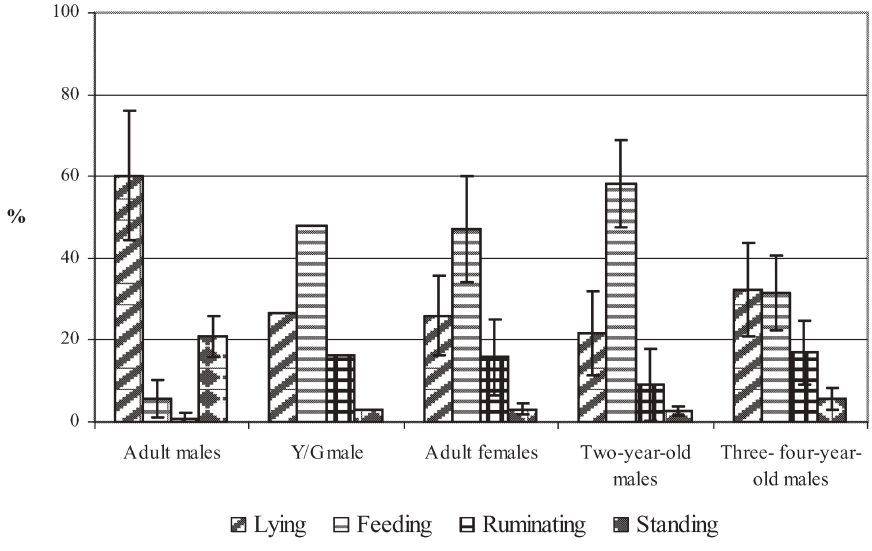


Fig. 2 Sex and age class (and Y/G male) time budget for the activities of lying, feeding, ruminating and standing in fallow deer (*Dama dama*) during the 1992 rutting season expressed as mean percentage and SE

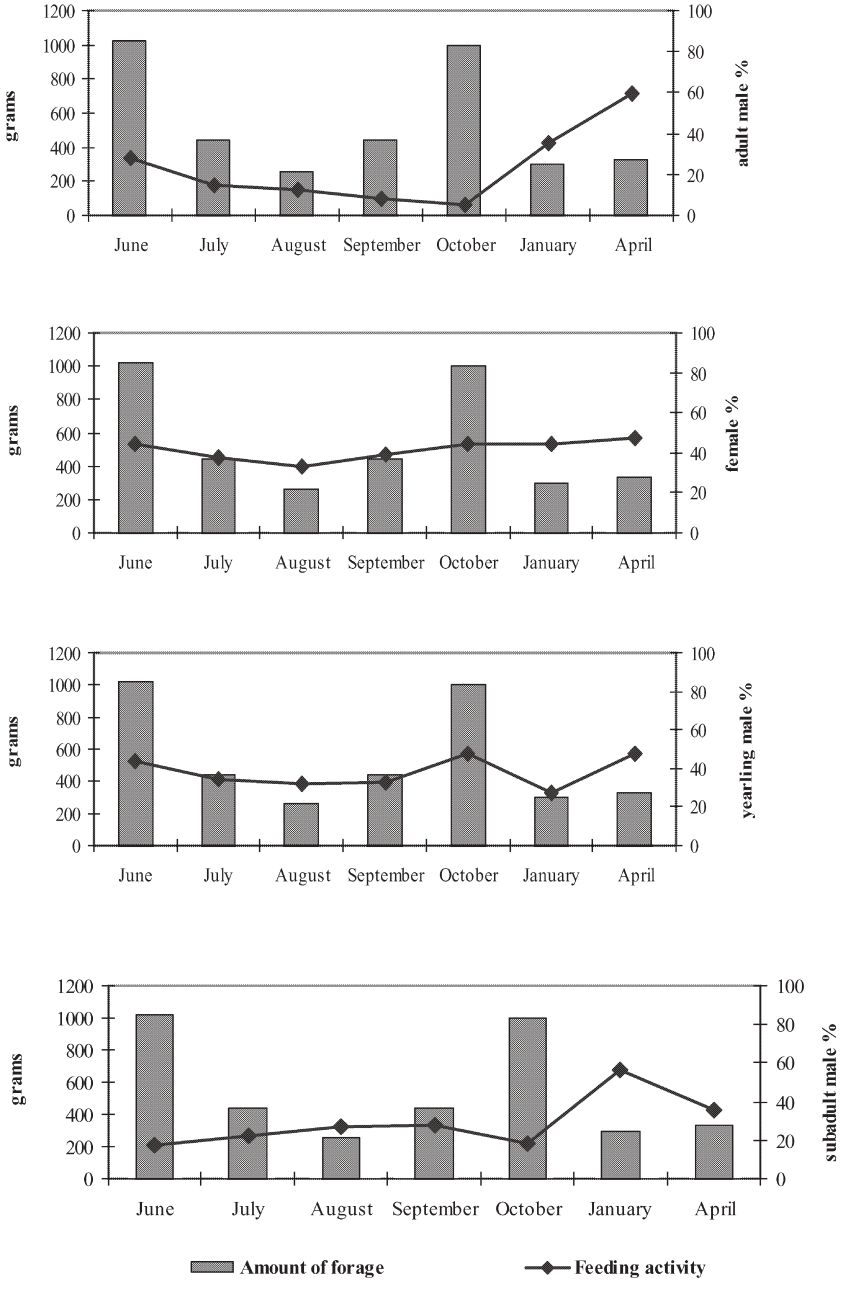
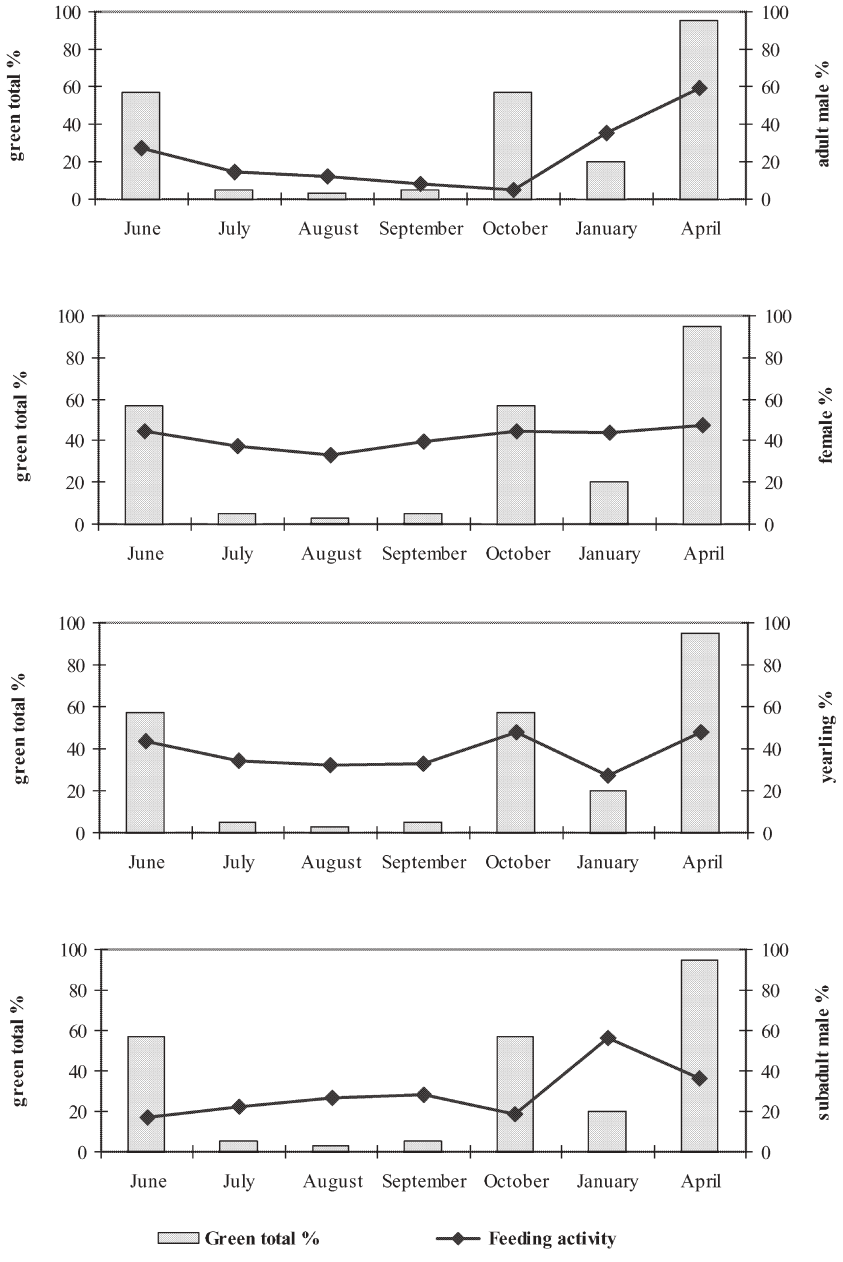


Fig. 3 a Relationship between the amount of available forage and feeding activity, by sex and age class of fallow deer (*Dama dama*) in the 1991–1992 period. **b** Relationship between total percentage of available green forage and sex- and age-class feeding activity in the 1991–1992 period

Discussion

Fallow deer, like other ungulates (Illius and Gordon 1987; Mysterud 1998), have seasonal variations in diet. In particular during the breeding season, feeding activity in fallow deer was age- and sex-dependent: subadult males slightly reduced this activity; yearling males never ceased feeding and actually increased food intake as much as females in response to better forage quality and higher availability. Only bucks dramatically reduced their forage intake simultaneously with reproductive behaviours exclusive to this age class, but well before the first copulation. Reproductive success in ungulates is strictly linked to weight and social maturity (Clutton-Brock et al. 1982; Apollonio et al. 1989); so subadult males and yearlings, not successful in approaching females, seem to have more time to spend in feeding than do adults. However, the explanation of this phenomenon is more complex because the reduction in food intake occurred in adult males well before the first copulation was observed and had a marked time coincidence with scent-urination. The results obtained do not seem to confirm the hypothesis that bucks have no time for feeding because of reproduction (Geist 1982), because those in our study spent only 7.5% of their time budget in reproductive activities. Moreover, only a few males of a population were able to mate, while all adult males, in normal body-condition, exhibited this hypophagia. In fact bucks, unlike the other classes, spent more than 60% of their activity budget lying idle on the ground, not guarding individual females or defending

Fig. 3 (continued)



harems, and more than 14% of their time standing inactive, not looking for forage, which during the rutting period, at the beginning of autumn, was abundant and of high quality. Therefore it seems more likely that the phenomenon could be related to physiological processes possibly linked to hormonal changes recorded during the breeding season. Exclusive adult fallow deer male behaviours are olfactory communication, especially scent-urination (Kennaugh et al. 1977), and acoustic communication, i.e. groaning (McElligott and Hayden 2000). The latter activity occurred earlier than hypophagia, while a strong time relation emerged between food suppression and scent-urination due to development of the preputial gland, accountable for the pungent odour resulting only from adult male urine. As for other ungulates, scent-urination is associated with a strong odour of urine, which is closely age- and weight-dependent, occurring in species reducing food intake (Coblentz 1976; Espmark 1964; Bowyer 1981; Miquelle 1990). Considering that in all macrosmatic animals (i.e. having a well-developed olfactory mechanism), pheromones play a leading role in intraspecific recognition and in sexual attraction, permitting the identification of each member of a particular social group and signalling his social status (Tang-Martinez et al. 1993), we noticed that hypophagia and scent-urination occur at the same time, suggesting that the physiological processes inducing scent-urination and preputial gland activity may be the same as for appetite suppression in adult males. In fact, the unmodified food intake of the adult male that had a preputial gland tumour (causing necrosis of the tissue and the attached glands) may give more support to our hypothesis. During the rut,

this buck did not reduce forage intake but even increased the time spent feeding as much as females did. Therefore, it seems probable that the advantages deriving from scent-urination, which could be important for increasing reproductive success, are high enough to balance the cost of hypophagia. Urine odour could provide specific information about reproductive state, physical condition and energy level (Doty 1986). This is important for both sexes because, on the one hand, females interact with many males before copulating, and individual odours may be a key factor in the cues used to assess the social and physical status of bucks. A scent-matching mechanism (Gosling 1982) could be invoked to explain such a process.

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