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ARTICLE

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Feeding competition within a feral goat population on the Isle of Rum, NW Scotland

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Abstract This study investigated feeding competition within and between different age–sex classes of feral goats (*Capra hircus*) on the Isle of Rum (northwest Scotland) from August to November 2000 (inclusive). Although contests in a feeding context were common, most were relatively passive: little overt agonistic behaviour was observed between opponents and the distance between feeding animals involved did not change significantly after an interaction. Month (but not sex or habitat type) had a significant effect on feeding interaction rates, and the proportion of interactions involving more intense forms of conflict was highest in November when forage availability was beginning to decline. The results show that the initiator won most feeding encounters, with adult males being dominant over females. The ability to win conflicts increased with age for both males and females. However, it decreased sharply for adult males older than 5 years, which may, in part, explain the reduced overwinter survival of these individuals.

Key words Feeding competition · Agonistic behaviour · Sex differences · Feral goats

Introduction

Large herbivores generally feed on widely dispersed resources, and it has therefore been suggested that the aggression between members within groups is relatively unimportant for these species (Geist 1974; Wittenberger 1981). Rather, most competition between ungulates is likely to be indirect, resulting from depletion of food by animals that have already passed through an area (Jarman 1974; Illius and Gordon 1987). However, several studies have reported apparent (or even high) levels of feeding competition for northern ungulate populations, particularly in winter (red deer *Cervus elaphus*: Appleby 1980; Thouless 1990; Roosevelt elk *Cervus elaphus roosevelti*: Weckerly 1999; caribou *Rangifer tarandus*: Barrette and Vandal 1986).

Contests between animals competing for resources are potentially mediated by two main behavioural mechanisms. First, individuals may attempt to displace one another actively from the resource in question, the outcome being determined by overtly aggressive behaviour. Second, subordinate individuals may avoid costly conflicts by moving to locations away from dominant animals (Barton 1993). Several studies of ungulates under natural conditions have shown that there are aggressive interactions involving displacement at feeding sites. Appleby (1980) used an indirect approach (by comparing the proportion and total frequency of interactions that involved feeding replacement) to study red deer stags and showed that both the frequency of feeding replacements and the proportion of total interactions between stags were highest in winter when food availability was lowest. However, Thouless (1990) later demonstrated that aggressive interactions have little direct effect on access to food, and that feeding competition between red deer hinds is largely a passive process. Thouless (1990) therefore suggested that feeding interactions are typically limited to subtle displacements, most of which do not involve open aggression and incur only minimal costs for the aggressor.

Most of the studies on feeding competition in ungulates have been restricted to within-sex interactions, in most cases with a focus on females (e.g., Lovari and Rosto 1985; Hirotani 1990; Thouless 1990; Hass 1991; Thompson 1993; Fairbanks 1994; Greenberg-Cohen et al. 1994; Côté 2000a, 2000b) and rather few studies of males (e.g., Appleby 1980). Although there have been many other studies of agonistic behaviour in ungulates, these have typically not been limited to feeding contexts, and may thus have confounded competition for food with competition for other resources (e.g., mountain goat *Oreamnos americanus*: Risenhoover and Bailey 1985; Masteller and Bailey 1988; feral horse *Equus caballus*: Lenarz 1985; Rutberg and Greenberg 1990). By comparison, there have been few studies that have investigated feeding competition both between and

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within the two sexes in ungulates: one of the few exceptions is Barrette and Vandal (1986), who studied competition between the two sexes in a small sample of caribou at winter snow holes.

In many dimorphic ungulates (e.g., red deer: Clutton-Brock et al. 1987; Conradt 1999; Alpine ibex *Capra ibex ibex*: Bon et al. 2001; Rocky Mountain mule deer *Odocoileus hemionus hemionus*: Main and Coblentz 1996; white-tailed deer *Odocoileus virginianus*: Kie and Bowyer 1999), sexual segregation is common outside the breeding season. While feral goats (*Capra hircus*) are no exception, the level of segregation in the population inhabiting the Isle of Rum is modest and rather unstable (Shi et al. 2005), with adult males and females forming mixed groups even outside of breeding season. However, mixed-sex foraging groups are especially common during and after the rut (August through the autumn months) when individual males may spend days at a time with a group of females. Hence, goats offer a rare opportunity to investigate feeding competition between as well as within age–sex classes of feeding animals.

In this study, we examine feeding contests and their consequences between and within the two sexes of goats. We focus on the period August to November since foraging in mixed-sex groups is particularly common at this time (see Shi et al. 2005). We only consider contests that occurred when the recipient was feeding. While we excluded from consideration between-sex contests that appeared to be motivated by male sexual interests, we do not necessarily assume that all other interactions are concerned explicitly with competition for food. Our concern is not with the motivation for contests as such, but with their consequences for the recipient: our interest thus lies in whether such interactions disrupt the recipient's feeding activity, thereby imposing a foraging cost on it. The most explicit form that such disturbance can take is when the recipient abandons a feeding site to the initiator of the attack.

Materials and methods

Study area and population

This study was conducted from August to November 2000 (inclusive) on the Isle of Rum (57°0′N, 6°20′W) off the northwest coast of Scotland. The Isle of Rum has been described in detail by Eggeling (1964), Clutton-Brock et al. (1982), Clutton-Brock and Ball (1987) and Gordon (1989a).

The main study area was located on the west coast of the Isle of Rum between Harris Bay and Glen Guirdil. The main area comprised a 10-km section of cliff-line rising precipitously from sea level to between 150 and 450 m above sea level. There were about 190 feral goats (sex ratio approximately 1:1) living in the main study area. Coat colour and horn shape of adult goats are highly variable in the Rum population, so that each adult individual can be easily identified (Dunbar et al. 1990). Goats can be aged in the field by counting the number of distinctive growth "rings" on the horns (normally one per year in Rum population) (Bullock and Pickering 1984; Dunbar et al. 1990), although some caution needs to be exercised in aging females above 2 years of age. Goats less than 12 months old (lacking a full first horn ring) were classed as kids; those aged 12–24 months (i.e., with a single growth ring) as yearlings. Adults were more than 2 years old.

In 2000, the rut was unusually late, and occurred in September and October. The females give birth mainly in February and kids begin to feed themselves after their first 2–3 weeks (Pickering 1983; Gordon et al. 1987).

The feral goats sometimes feed alone but more usually do so in loosely associated groups whose sizes range from 2–51 (with two to three being the modal group size) (Shi et al. 2005). The composition and membership of the groups are very changeable, with individuals joining or leaving frequently as the animals forage across the landscape. Although there are about nine main categories of vegetation communities in the study area (see Clutton-Brock et al. 1982; Gordon 1989b for details), the goats mainly used just four of them (i.e., *Agrostis*/*Festuca* grassland, wet heath, *Calluna* heath and herb-rich heath) (Shi 2002). The beach was also heavily used by goats (both for access to seaweed as a food source and for shelter at night or on stormy days), especially during autumn and winter. However, we excluded the data collected on the beach from the present analyses because seaweed acts like an artificial food source, forcing animals close together and thus leading to increased levels of feeding interactions (Thouless 1990; Veiberg et al. 2004).

Data collection and analysis

The data on feeding competition were collected from August to November 2000 using focal animal sampling and ad libitum sampling (Altmann 1974). The animals quickly habituated to the presence of the observer and could be watched at a distance of 10–15 m.

The focal animal (adult or yearling, but not kid) was chosen randomly from among the animals that were feeding in a group, providing at least half the members of the group were active. The focal animal was watched for 30 min. During the sampling period, the focal animal often stopped feeding or moved out of sight due to the topography. On such occasions, sampling was suspended; if the focal animal did not start feeding again within 5 min, the sample was terminated. Only those samples that lasted for a minimum of 20 min were included in the analyses reported here. Focal-animal observations were terminated if the focal animal bedded down, walked out of sight or moved > 30 m from the group (Fairbanks 1994).

During observations, all agonistic interactions between the focal animal and any other individual were recorded, including sex and age of the winner and loser and the specific behaviour exhibited. For each sample, the following were recorded:

1. The sex and age of the focal animal.
2. The habitat type in which the focal animal was feeding.

3. Size and composition of the group.
4. Proximity of other individuals: distance to the nearest neighbour of the focal animal at the end of each 5-min interval.
5. All interactions when the focal animal approached or was approached by another individual (sex and age recorded). Approach was defined as any occasion when an animal moved to within two-body lengths (about 2–2.5 m) of another individual (see also Côté 2000b).
6. All interactions when the focal animal displaced or was displaced by another individual (sex and age recorded). Displacement was defined as any movement greater than one-body length that followed an approach. The activities of the focal animal and the opponent immediately prior to and after the agonistic interaction were also noted.

Agonistic behaviours were categorised according to the occurrence and form of threats used, following Shank (1972), Appleby (1983) and Côté (2000b):

1. Submission: orientation avoidance (slowly avoiding the opponent by walking or feeding) and rush avoidance (quickly moving away from the opponent).
2. Light threats: displacement or prevention of approach by lifting head.
3. Heavy threats: sudden movement towards conspecifics, horn threats (nodding or head-tossing).
4. Physical attacks (i.e. fighting): rearing up and slapping with the forefeet (boxing); using the horn in physical contact.

Following Hand (1986), the initiator, recipient, winner and loser were noted for each interaction. The outcome of agonistic encounters was defined as resolved when one of the opponents withdrew (i.e., moved more than one goat body length while showing submissive behaviour). The analyses include only those interactions where the recipients were feeding. Sexually motivated interactions can usually be distinguished from other types of interaction because the male persistently harasses the female, and follows her when she moves rather than simply occupying her feeding site. The rates at which the focal animals were involved in interactions, either as aggressor or victim, were calculated as the number of interactions per minute within each focal sample (Thouless 1990; Barton and Whiten 1993).

In order to minimise the risk of pseudoreplication, we never recorded feeding competition data on more than two focal animals in the same group on any given day. Although individual animals were likely to be observed more than once during the whole study period, observations of the same animal on different days under different environmental and social contexts are not likely to be strongly autocorrelated or to result in pseudoreplication (Molvar and Bowyer 1994).

When continuous variables were used with parametric statistical tests, data were first checked for normality (Kolmogorov-Smirnov, with $P = 0.05$). Only mean nearest-neighbour distance was not normally distributed, but ln-transformation was sufficient to achieve normality. When data are in the form of percentages, nonparametric tests are more appropriate; in these cases, we used the marginally less powerful Kruskal-Wallis test as an alternative to conventional ANOVA.

It should be noted that, in this paper, "dominant" and "subordinate" refer only to dyadic relations, and they only come from interactions in a feeding context. They are not related to rank within the population (Thouless 1990). The term "interaction" refers only to interactions over forage (feeding), not competition for other resources or interactions initiated by males as part of courtship behaviour.

During the whole study period, a total of 154 focal watches were conducted (88 for adult females, 56 for adult males and 10 for yearling females; yearling males were too rarely seen to be included). The total sample time was 4,341 min.

Results

Types of feeding interactions

During the 154 watches, 1,050 agonistic feeding interactions were recorded involving the focal animal as either initiator or recipient of the aggression. In 635 of these, the contest was won by the initiator (i.e., the initiator displaced the opponent and occupied its feeding site). On a further 164 occasions, the initiator lost the interaction because the recipient ended up taking over the initiator's feeding site (e.g., the initiator approached the recipient to some distance, but then turned around or just ran away, and the recipient then occupied the initiator's feeding site). The remaining 251 feeding interactions resulted in no obvious winner. Feeding interactions in which one individual displaced the other were thus three times more common than undecided interactions (76 vs 24%, respectively), suggesting that the disruption of feeding by other goats is relatively common among the goats on Rum.

Rates of interaction

Rates of interaction between feeding goats (interactions/min) were analysed by a three-way ANOVA with sex, habitat (four main types: see "Materials and Methods" section), month (August to November inclusive) and the interaction between habitat and month as independent variables, and interaction rate as the dependent variable. The results show that month significantly affected interaction rate ($F_{3,138} = 5.29$, $P = 0.002$), with interaction rates being highest in November. In contrast, neither sex ($F_{1,138} = 0.76$, $P = 0.386$) nor habitat type ($F_{3,138} = 0.46$, $P = 0.711$) affected interaction rates independently of month, although the interaction rates were lower on the *Agrostis*/*Festuca* grasslands (the habitat with the least patchy vegetation) than on other types of habitat. There was no significant interaction effect between month and habitat type ($F_{8,139} = 1.30$,

$P = 0.248$). Post hoc (least squares difference, LSD) analyses revealed that there were significant differences in the interaction rates between August and October ($P < 0.001$), August and November ($P < 0.001$), September and October ($P < 0.001$), and September and November ($P < 0.001$) (Fig. 1).

In addition to the variation in interaction rates with month, the percentage of all interactions which resulted in feeding displacement (i.e. those in which one individual displaced and fed in the place occupied by its opponent) differed significantly between months (Fig. 2: Kruskal-Wallis $\chi^2 = 83.25$, d.f. = 3, $P < 0.001$). The percentage of displacements exceeded 80% in October and November (when forage productivity was declining rapidly), but was considerably lower in August (when plants were still growing). Although some of this difference might be attributed to the disruptive effects of the rut (males harassing females in order to initiate sexual interactions), the fact that the rate of displacements continued to rise through November after the rut had ended suggests that forage quality is likely to have been an important factor.

Outcomes of feeding contests

Males won most of the interactions with adult females (2 × 2 χ^2 test: $\chi_1^2 = 84.12$, $P < 0.001$), yearling females ($\chi_1^2 = 22.64$, $P < 0.001$) and kids ($\chi_1^2 = 35.00$, $P = 0.004$) (Fig. 3). Similarly, Fig. 4 shows that adult females won most of their feeding interactions with yearling females ($\chi_1^2 = 51.00$, $P < 0.001$) and other females' kids ($\chi_1^2 = 52.56$, $P = 0.007$). However, adult females were more tolerant of their own kids than they were of other individuals' kids ($\chi_1^2 = 113.81$, $P < 0.001$). With their own kids, adult females did not win more often than might be expected by chance ($\chi_1^2 = 4.18$, $P = 0.428$) (Fig. 4).

Of the 1,050 feeding interactions, 112 involved yearling females as either initiators (34.8%) or recipients (65.2%). Of these, yearling females won only 23.2%, and were dis-

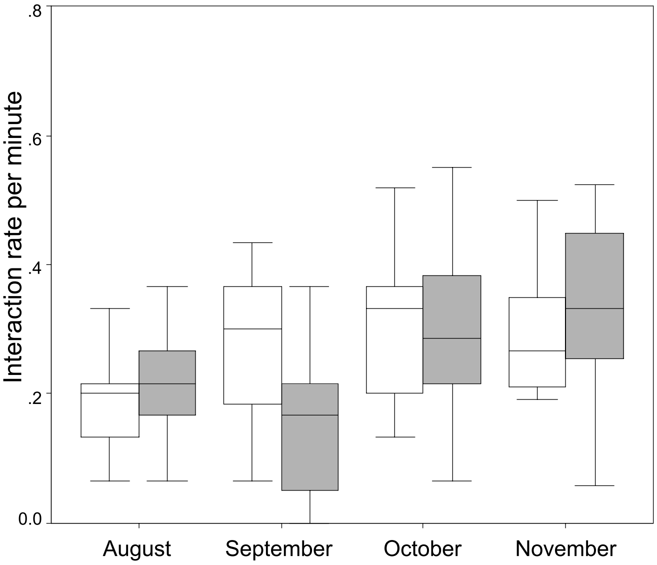

Fig. 1. The rate of feeding interactions (median number of interactions per minute, ±50 and 95% ranges) between goats from August to November. *Open bars* Male subjects, *hatched bars* female subjects

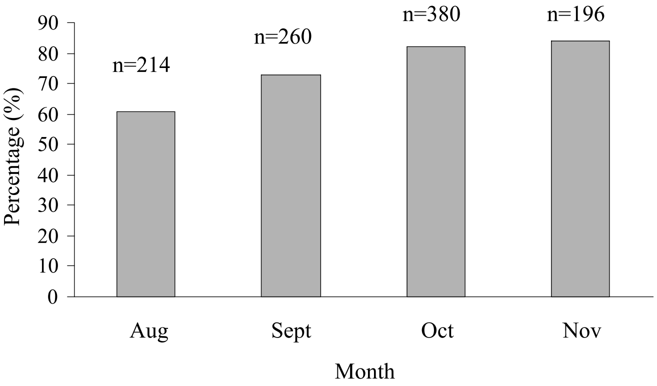

Fig. 2. Occurrence of feeding competition as a percentage of all feeding interactions in different months. Sample sizes (the number of all feeding interactions recorded in each month) are given *above each bar*

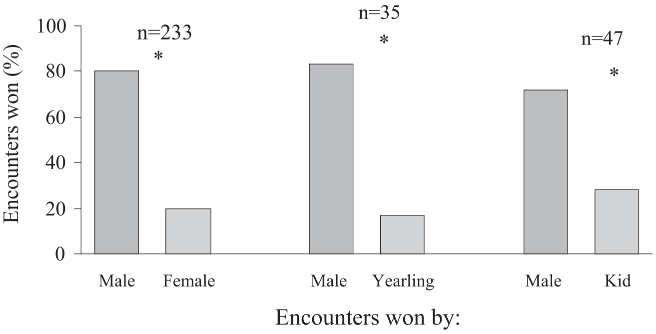

Fig. 3. The outcome of feeding interactions between adult males and other age–sex classes (adult females, yearling females and kids). The number of feeding encounters (n) is shown for each type of comparison. *Asterisks* indicate that the difference between the two categories being compared is significant ($P < 0.05$)

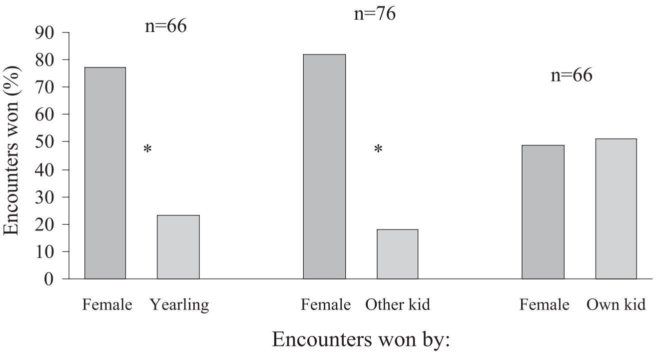

Fig. 4. The outcome of feeding interactions between adult females and other age–sex classes (yearling females, other females' kids and female's own kid). The number of feeding encounters (n) is shown for each type of comparison. *Asterisks* indicate that the difference between the two categories being compared is significant ($P < 0.05$)

placed by the opponent in the remaining cases (76.8%). Yearling females were thus significantly more likely to be displaced from their feeding sites by the opponent (either adult males or females) than to displace the opponent ($\chi_1^2 = 31.08$, $P < 0.001$).

A total of 312 feeding encounters were recorded between adult individuals of the same sex but of different ages. Of these, 16.9% were between adult males and 83.1% between adult females. The outcome of these contests is shown in Fig. 5. Most such encounters were won by the older animal. [Goats continue to grow with age (at least up to the age of 84 months: Saunders 2000), and more importantly, their horns grow throughout life; we therefore use age here as a proxy for body and/or horn size: the latter is probably particularly important in determining the outcome of fights.] The role of age (or body size) in determining the outcome of such encounters differed between males and females. For males, the percentage of encounters won by the older individual did not differ significantly from chance ($\chi_1^2 = 1.21$, $P = 0.784$), but older females won a significantly higher proportion of all-female encounters than younger females did ($\chi_1^2 = 73.52$, $P = 0.005$).

Only 31 of the feeding encounters occurred between adult individuals of the same age but different sexes. Since males are absolutely larger than females once they are adult (> 2 years old), it is not surprising to find that males won all of these encounters and were absolutely dominant over females of the same age in feeding competition ($\chi_1^2 = 13.56$, $P = 0.005$).

The percentage of feeding encounters won by individuals of a specific age group (as either initiator or recipient) was used as an index of their relative ability to win encounters against individuals of the same sex. For both males and females, the probability of winning feeding encounters increased with age, with 5-year-old males and 6-year-old females having the highest probabilities of winning (Fig. 6). However, males' ability to win feeding contests decreased sharply after 5 years of age, whereas females showed only a very slight decrease in the frequency of wins after age 6 years.

Agonistic behaviour during interactions

Not many feeding encounters involved overtly agonistic behaviour, and most of the encounters were resolved by active submissive behaviour (i.e., either initiator or recipient moving away or rapidly retreating) in response to the initiator's approach. Of the 799 feeding contests in which there was an obvious winner, 652 (81.6%) were resolved by submissive behaviour in response to the initiator's approach without need of overt threat ($\chi_1^2 = 404.10$, $P < 0.001$), and the recipients were most often responsible for this. Only 2.4% of the contests were resolved by overt fighting between the two opponents, and the remaining contests were resolved either by light threat (11%) or by heavy threat (5%).

Possibly because feeding contests rarely involved heavy threats or physical fights, the distance between the two opponents did not change greatly after an interaction even though interactions often resulted in the displacement of the recipient of a challenge (mean ± SE distance: 3.4 ± 1.5 m before vs 3.3 ± 1.6 m after the interaction: $F = 0.247$, $n = 143$, $P = 0.763$). Since the majority of challenges resulted in the displacement of the recipient of the challenge (see above), this suggests that, on average, the recipient moved about 3 m as a result of the challenge. In effect, it maintained about the same distance between itself and the initiator at all times.

Discussion

Studies of feeding interference in ungulates have suggested that a passive form of interference might be more important and widespread among grazing ungulates feeding on relatively uniform herbage than has been supposed (Appleby 1983; Thouless 1990). The present study showed that although many of the feeding interactions between feral goats resulted in displacement, most of them were resolved by submissive behaviours by either the initiator or the

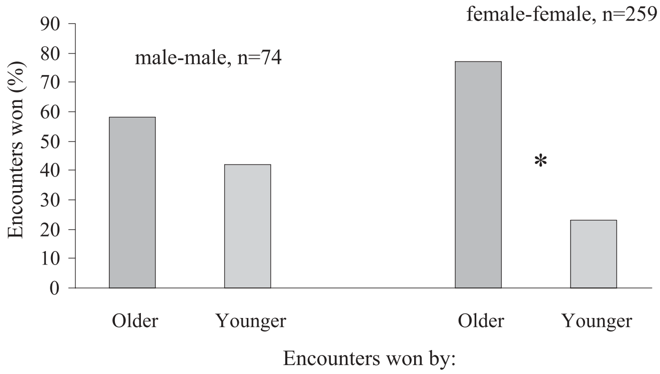

Fig. 5. Outcome of feeding encounters between adult individuals of the same sex. The number of feeding encounters (n) is shown for each type of comparison. *Asterisks* indicate that the difference between the two categories being compared is significant ($P < 0.05$)

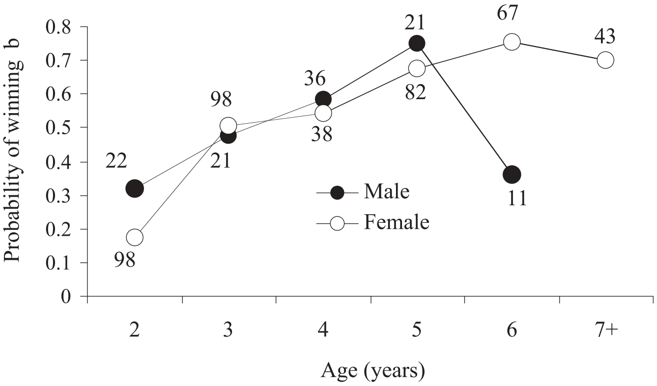

Fig. 6. The relationship between age and the probability of winning feeding encounters between individuals of the same sex, either as initiator or recipient (see text for details). Sample size (number of feeding encounters) is shown *beside each point* on the graph

recipient without the use of overtly agonistic behaviour. Furthermore, the distance between the two opponents did not change greatly after the interaction.

Thouless (1990) noted that, among red deer females, interactions at feeding sites had a relatively limited direct effect on individual's access to food, and concluded that, in this case, feeding competition was largely a passive process arising through avoidance of conflict by subordinates (see also Appleby 1983). While this may seem also to be true of the goats, our data also suggest that, while by no means all of the feeding interactions between the goats resulted in displacement from feeding places, most in fact did: in effect, feeding competition did occur, because the animal's feeding bout was disturbed and the recipient was forced to move a modest distance (about 3 m). Although an explanation in terms of different methodologies cannot be ruled out (Thouless 1990 defined an interaction as an approach within 5 m, whereas we used 2.5 m), this apparent difference between the two species may reflect a difference between grazers (deer) and intermediate feeders/browsers (goats) in the kinds of food resources typically exploited. Browsers may experience a resource sward that is more patchy than grazers because they are feeding on herbaceous plants (or, in the present case, small shrubs such as heathers) rather than just grasses like the deer; consequently, browsers may place a higher premium on successfully excluding competitors from feeding sites.

This study also found that the feeding interaction rates in feral goats varied with month: the rates and the proportion of feeding competition increased from August through November. Since the rut was over by the end of October, these variations probably reflect changes in the quality and distribution of forage in the various habitats as summer passes into autumn. Barton and Whiten (1993) found that the rate of supplanting from feeding sites (supplants/h) in female baboons was negatively correlated with vegetation biomass, and they attributed the increased level of competition to the fact that food was less abundant and more concentrated in discrete defendable patches during the dry season than during the wet season. Appleby (1980) showed that the frequency of feeding displacement and the proportion of total interactions between red deer stags were highest in winter when food availability was lowest. The present study indicated that, in feral goats, both the feeding interaction rate and the proportion of contests resulting in feeding competition were significantly higher in November (when forage availability was at its lowest) than in August/September (the impact of the rut on interactions notwithstanding).

In the present study, the majority of feeding contests (63%) were won by the initiator, with little overt aggression being exhibited. Such a pattern may be widespread: in female Roosevelt elk, for example, 72% of feeding interactions were won by the initiator, and involved little physical contact (Weckerly 1999), and similar findings have been reported from other ungulate species (Rutberg 1983; Bennett 1986; Thompson 1993; Veiberg et al. 2004). Thouless and Guinness (1986) argued that, if there is a high degree of social bonding among individuals, then it is reasonable to assume that individuals familiar with one another would resolve conflicts in a fashion that does not disrupt coexistence (e.g., the initiator of the aggression wins, and little physical contact occurs so that injury is less likely).

Competition may lead to intraspecific aggression within groups, and individuals may benefit from patterns of social behaviour that allow them to avoid the costs of aggression (Fournier and Festa-Bianchet 1995). Previous studies on grazing mammals indicate that direct intraspecific feeding competition may occur, but that the level of competition itself may not be important (Geist 1974; Appleby 1980; Berger 1986; Thouless and Guinness 1986; Rutberg and Greenberg 1990; Thouless 1990). Rutberg and Greenberg (1990) showed that food-related aggression is not important in grazers such as pony mares, and there is little evidence of grazing-related inter-band aggression among mares (Berger 1986).

An individual's competitive ability is likely to be affected by several factors, including body size and age. Age is very strongly related to social rank and fighting ability in ungulates (e.g., red deer: Appleby 1982; Hall 1983; Thouless and Guinness 1986; addax *Addax nasomaculatus*: Reason and Laird 1988; bighorn sheep *Ovis canadensis*: Festa-Bianchet 1991; chamois *Rupicapra rupicapra*: Locati and Lovari 1991; Nubian ibex *C. ibex*: Greenberg-Cohen et al. 1994; mountain goat *O. mericanus*: Côté 2000b), in most cases probably because age strongly influences body size and hence competitive ability. Although age (i.e., body size) also had an influence on the outcome of interactions between feral goats in this study, the ability to win feeding contests declined after 5 years of age in males and failed to increase after about 6 years of age in females. Sexual dimorphism in both body and horn size (both continue to grow each year) is likely to be the main reason why adult male goats are usually dominant over adult females. Similarly, within sexes, the main factor explaining the fact that older animals win more encounters is likely to be the fact that body size increases with age. However, failing body condition in older animals may begin to undermine an animal's capacity and willingness to compete, hence explaining the downturn among older animals. Dunbar et al. (1990) also noted that older males tended to lose (and hence avoid) contests with prime-age males over access to females during the rut, and Lloyd (2003) reported that there was an age- (and hence body size-) related dominance hierarchy among the males at the time of the present study.

Because most of the feeding interactions in the goats resulted in displacement of the subordinate by the dominant, this in turn may lead to frequent disruption of feeding activities for the subordinate. Feral goats are virtually diurnal (Shi et al. 2003), and their foraging time is largely constrained by day length, particularly in autumn/winter when the day length is considerably shorter. Although the goats' bite rates increase through the autumn (Shi 2002), they do not do so sufficiently to offset even the progressive constraint on feeding time as day length shortens through the autumn to its minimum in December (Dunbar et al., unpublished). Hence, any feeding time lost due to feeding interactions during the day cannot easily be compensated, and therefore the feeding efficiency (intake rate) of the subordinate is likely to be inversely affected.

This may have especially important consequences for the goats as the winter draws in. We can show (Dunbar et al., unpublished) that, in this population: (1) female goats live longer than males, (2) the overwinter mortality is very high for older adult males and (3) mortality in these older males is often associated with starvation (indicated by emaciated body condition). This study indicated that competitive ability decreases sharply for male goats over the age of 5 years. If feeding competition has a significant effect on males' access to the best food sources (as it is known to do in the case of mountain goats: Masteller and Bailey 1988), then older males may find it difficult to recover from weight loss after the summer rut when the weather conditions are harsh and biomass and quality of forage are lower. Intraspecific feeding competition may thus partly contribute to the high overwinter mortality experienced by older male goats on Rum (see also Pickering 1983).

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