# Foraging ecology of feral goats on the Isle of Rum, NW Scotland

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**Abstract**：We studied foraging ecology of feral goats (*Capra hircus*) on the Isle of Rum, Scotland, from June to November 2000. Grazing bout length varied greatly from 1 min to 460 min with mean duration being 103. 1 ± 15. 0 (SD) min. Adult males and females differed marginally significantly in feeding bout length with females having relatively longer feeding bouts ($P = 0.077$). The average bite rate for feral goats was 46. 3 ± 0. 6 bites/min with significant variations between sexes ($P = 0.023$) and among months ($P < 0.001$). Adult males had faster bite rates during pre- (June–July) and post-rutting (October–November) periods than during rutting period (August-September) ($P < 0.008$), but the bite rate of adult females during pre-rutting period was not different from that during rutting period ($P = 0.327$). Adult males also spent significantly less daytime feeding during rutting period. The differences in bite rates and feeding time between the two sexes might result in sexual differences in forage intake by feral goats：females had relatively stable intake, but males fluctuated greatly in their forage intake. The estimated forage intake decreased from June to November (although a slight increase from September to November), which means that feral goats on Rum may be in negative energy balance during autumn/winter period when the quality of forage is lower and the weather is beginning to deteriorate. There was no significant difference in step rate while feeding between sexes or among months.

**Key words**：Bite rate；Feral goats；Grazing bout length；Rum Island；Step frequency

# 苏格兰拉姆岛上野化山羊种群的取食生态学

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**摘要**：2000 年 6 ~ 11 月对苏格兰拉姆岛上野化山羊（*Capra hircus*）种群的取食生态学进行了研究。研究表明：山羊的觅食回合长度变化范围从 1min 到 460 min 不等，平均觅食回合长度是 103. 1 ± 15. 0（SD）min，雌性动物的觅食回合长度较雄性的长（$P = 0.077$）。野化山羊单位时间的取食频率平均为 46. 3 ± 0. 6 口/min，取食频率随性别（$P = 0.023$）和月份（$P < 0.001$）而显著变化。雄性山羊在繁殖交配之前（6 ~ 7 月）和之后（10 ~ 11 月）的取食频率比繁殖交配期中（9 ~ 10 月）的快（$P < 0.008$），但雌性动物并没有这样的变化（$P = 0.327$）。雄性动物在繁殖交配期中的取食时间显著减少。雌、雄两性动物在取食频次和取食时间方面的这些差异可能导致该山羊种群在食物摄入量上的性别差异：雌性山羊的食物摄入量相对比较稳定，而雄性山羊的摄入量则变动很大。估计的食物摄入量随月份而下降（尽管 9 月份以后有一微小幅度的上升），这意味着拉姆岛上的山羊种群在食物匮乏而天气寒冷潮湿的冬季可能面临着能量收支不平衡的威胁。

**关键词**：取食回合长度，取食频次，步移频次，野化山羊，拉姆岛

Foraging is the dominant activity of free-ranging ungulates, and they typically devote 40% – 60% of each day to finding and consuming food (Clutton–Brock *et al.*, 1982；Hanley, 1984). Although ungulate foraging behaviour has been studied in some detail, most of this has focused on the classic problems of optimal foraging theory, namely forage choice, patch choice and forage intake rate (see, for example, Leuthold, 1977；Novellie, 1978；Owen-Smith, 1979；Clutton–Brock *et al.*, 1982；Owen-Smith and Novellie, 1982；Collins and Urness, 1983；Arnold, 1987；Illius and Gordon, 1987；Hester *et al.*, 1996；Ruckstuhl and Festa-Bianchet, 1998；Langvatn and Hanley, 2000；Neuhaus and Ruckstuhl, 2002；Taweel *et al.*, 2004；Chilibroste *et al.*, 2008).

Within the framework of optimal foraging theory (Pyke *et al.*, 1977；Pyke, 1984), there has been a particular interest in the relationship between intake

rate and various extrinsic and intrinsic factors（including vegetation availability and quality，physical status，foraging apparatus，etc.）（Ungar and Noy–Meir，1988；Gordon and Illius，1992；Gordon，1995；Nellemann，1997）. However，the difficulty of studying the processes of foraging and ingestion in wild ungulates has meant that much of this work has been carried out on captive or domesticated animals（e. g. Gordon et al.，1996；Taweel et al.，2005；Chilibroste et al.，2008）. Studies of domesticated species grazing on simple，uniform pastures can give only a general guide as to how free–ranging animals behave because the relationship between food requirement，grazing behaviour and the availability of forage in natural habitat is more complex and multivariate（Arnold，1970；Hodgson，1977，1981；Stronge et al.，1997；Harvey et al.，2003；Rook and Tallowin，2003；Taweel et al.，2005；Chilibroste et al.，2008；Zhang et al.，2008）.

In many ungulate species，the adult females are considerably smaller than adult males and generally have a higher energy requirement than males（Owen–Smith，1988；Weckerly，1998）. Foraging behaviour，together with diet selection，determines the nutrient intake of the animals（Prache et al.，1998）. Forage intake can be described as the product of bite size，bite rate，and feeding time（Shipley et al.，1994）. Although bite size may have the greatest influences on short–term intake（Forbes，1989），the amount of food an individual ruminant ingests per day depends on the time spent feeding and the rate at which it can crop forage（Spalinger and Hobbs，1992）. In addition to measurements of bite size and total time spent feeding（Ruckstuhl et al.，2003；Shi et al.，2003），bite rates are also an important measure for determining intake rates of ungulates（Ruckstuhl et al.，2003；Harvey et al.，2003；Chilibroste et al.，2008）. The time available for foraging and the bite rate may limit an individual's daily forage intake and therefore affect its body condition and survival（Ruckstuhl et al.，2003）. In addition to satisfying its daily food requirements，ruminants in northern or mountain environments must accumulate enough fat during the growing season to reproduce and to survive the seasonal shortage of food during winter（Bruno and Lovari，1989）.

Feral goats in Rum start rutting mainly in August and September and females give births to kids mainly in late January and February（Gordon et al.，1987；Dunbar et al.，1990；Lloyd，2003）. The goats spend night time resting at sheltered places or caves on the beach（Shi et al.，2003），so the daylength available for feeding by goats may limit their forage intake.

The aim of this study was to investigate foraging ecology of feral goats（Capra hircus）on the Isle Rum with focus on measuring several key parameters（e. g. feeding bout length，bite rate，feeding time，etc.）which have important role in determining their forage intake. We predicted that there should be sexual differences in foraging ecology for goats and the adult females should have longer feeding bout length and higher bite rates，and the rutting behaivour may have impact on foraging behaivour and ecology.

## 1    Methods

This study was carried out on the Isle of Rum，northwest Scotland，from June to November 2000（inclusive）. Rum has been described in detail by Clutton–Brock et al.（1982）and Clutton–Brock and Ball（1987）. The vegetation of Rum was typical of westcoast of Scotland，and fell into four regions corresponding with the main geological formations. The lower ground was predominantly covered by moorland communities of the Calluna–Molinia，Calluna–Trichophorum，Eriophorum–Calluna，and Molinia flush types. Agrostis–Festuca grassland，important for feral goat grazing，was abundant in coastal and alluvial areas and on certain of the basic rocks. Molinia was overwhelmingly the dominant plant. Calluna and bogs were equally distributed（Clutton–Brock et al.，1982）. The production and quality in different plant communities on Rum changed greatly with the seasonal changes in climate and day length. The biomass of live materials of grasses，herbs，rushes（Juncus acutiflorus）and dwarf shrubs（predominantly Calluna vulgaris，Erica spp.，Vaccinium spp.）began to increase between April and May，and reached a peak around August. The biomass decreased until February and March（see Clutton–Brock et al.，1982；Gordon，1989）.

The population of feral goats on the Isle of Rum lives in a typical northern range with significantly seasonal variations in daylength，weather，and in biomass and nutrition of vegetation（Clutton–Block et al.，1982；Gordon，1989）. No one knows for sure when the goats were first brought to Rum，but they were probably brought as domestic stock some time before the clearances in 1828 because Pennant recorded the presence of wild goats on the Island（Rum）as early as 1770s（Gordon et al.，1987）. About 450 inhabitants on Rum were forced to leave for Canada in 1828，and they might have left their domestic goats behind them. These goats may be the ancestors of the current feral goat population on Rum today.

Feral goats are social animals and live in social units known as hefts，which are widely believed to be a matriarchal social organization（Dunbar et al.，1990；Lloyd，2003）. A heft consists of a group of closely associated females and their kids and a similar number of loosely associated males. Females are strongly hefted to

a particular area although goats are not territorial and therefore do not actively defend these areas. Male goats are also hefted although not as strongly as females and they are known to interact with individuals from other hefts especially during the rut (Dunbar et al., 1990; Lloyd, 2003). Males and females are sexually segregated for most of the year and stick to different areas within the heft range usually only coming together a few months in the year during the rut (Shi et al., 2005). Feral goat males usually use a tactic called tending, in which they defend oestrous females from other males. Males may also use a second mating tactic called coursing, in which they gain access to oestrous females by disturbing a tending pair (Saunders et al., 2005).

There have been unfortunately no accurate data on body mass of the feral goats on Rum, but it is believed that the adult males are about 10% – 20% heavier than females with other populations of feral goats across the Great Britain as a reference (Whitehead, 1972; Gordon et al., 1987).

The main study area was a section of cliffline on the west coast of Rum from Harris to Wrecker Bay that contained a relatively stable population of feral goats. However, the results reported here were based on a subset of this population whose ranging area was located within Harris bay (at the southern end of the main study area) where observation conditions were significantly better than other places and the animals could be approached to within 10 m (please see Shi et al., 2003 for details) (Fig. 1).
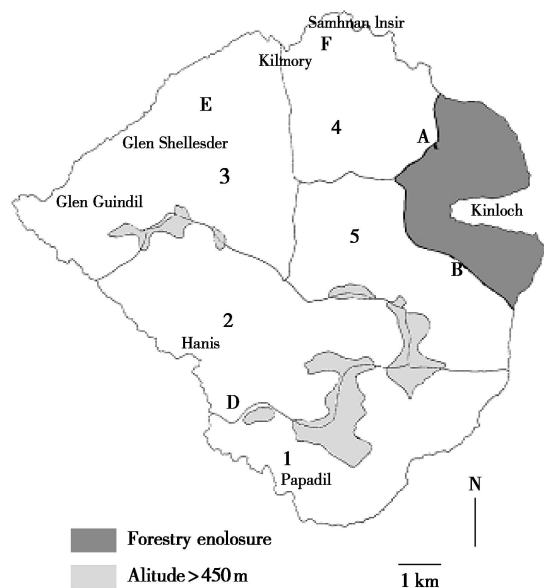


Fig. 1 Map of the Isle of Rum, Scotland to show the location of the study area along the western coastal line from Harris to Glen Guirdil. The main study area was at Harris. (Map was taken from Virtanen et al. (2002) with slight modification).

Because coat colour and horn shape are highly

variable (Gordon et al., 1987; Dunbar et al., 1990), all 189 goats within the study population were known individually. Age determination was made by horn ring counts with one ring being produced in each year of an animal's life (Greig, 1969; Bullock and Pickering, 1984). For present purposes, an individual was classified as an adult if it was older than 2 years of age. Individual animals could be sexed easily on the basis of horn shape and size.

Data on bite rate and step rate were collected using focal sampling method (Altmann, 1974; Martin and Bateson, 1993): individual feeding animals were randomly chosen from a group and observed for a period of 5 minutes. Records were made of the number of bites and steps taken during the 5 minutes. All the observations were made through a telescope in order to count the numbers as accurately as possible. A beeper-watch was used to keep the timing, and a portable counter was used to help record the number of bites while counting the number of steps.

Bite rate was indexed as bites per minute. Bites were recognized by a characteristic jerk of the head. Jaw movements alone were not considered bites because they were often used just to manoeuver food into position for the bite or just to chew food in mouth while feeding or ruminating. Step rate was indexed as steps per minute. A step was defined as an occasion when a goat moved either of its front legs forward during feeding. Step rate expressed the animal's rate of movement while feeding.

Although many studies of domestic ungulates species use bite rate and bite size (Stobbs, 1973a, 1973b; Forbes and Hodgson, 1985; Arnold, 1987; Armstrong et al., 1995) to measure food intake rate, estimating bite size is difficult for free-ranging ungulates. An attempt was made to estimate bite size for the feral goats by "hand-plucking" forage (Hudson and Watkin, 1986); however, since this seemed to produce very misleading values (see also Parker and Gillingham, 1993), we preferred to use estimates of bite size derived from studies of domesticated sheep and goats (Solanki, 1994; Pérez-Berbería and Gordon, 1999). Following the methods of Solanki (1994) and Pérez-Berbería and Gordon (1999), the daily forage intake was estimated by using the following formula (1):

Intake (g) = foraging time (min) × bite number/min × bite size (g/bite)

Instantaneous scan samples were taken at 10-minute intervals among groups (Altman, 1974; Martin and Bateson, 1993) to measure the percentage of daytime spent in feeding (see Shi et al., 2003 for details). The activities of all the group individuals were

instantaneously recorded by scan sampling at 10-min intervals. One behavioral sample was defined as an observation started when a group of feral goats was found until the group size changed or the group ran out of sight. The percentages of feeding were calculated for each behavioral sample and then averaged over individual months and sexes to acquire the percentage of daytime spent in feeding.

The values for daylength on the 15th day of each month were calculated from the equation available at http: //www. qpais. co. uk/modb-iec/dayleng. htm.

As with other ungulates (e. g. red deer *Cervus elephus*), the feeding behaviour of the feral goats occurs in temporal clusters (referred to as bouts) in which the same relatively brief feeding action is repeated several times in succession. In order to measure feeding bout length, a particular individual was watched continuously for as long as possible (mean observation duration: 108 ± 27 min, n = 179; the longest continuous observation was about eight hours). When an animal was selected for observation, its activity was recorded at 60-sec intervals by focal animal sampling with time-sampling (Martin and Bateson, 1993). Every effort was made to avoid allowing subjects to move out of sight. However, partly because the focal animal inevitably spent some time out of sight (or disappeared from sight altogether), and partly because the harsh weather (especially during the later stages of the study) made it unbearable to observe the subject for long time without moving, many watches were for incomplete days. Only those bouts longer than 20 minutes were included in our later analyses (n = 158 as shown in Results section) (see Clutton-Brock *et al*, 1982), and thus the feeding bout length may be overestimated.

Because feeding bouts are not always obviously discrete, a statistical criterion must be used to define a single bout of behaviour. One commonly used technique for identifying bout length is log survivorship analysis (see Slater, 1974; Clutton-Brock *et al.*, 1982; Martin and Bateson, 1993; Zhang, 1996). The minimum interval separating successive bouts is defined as the bout criterion interval (BCI); any gap between successive occurrences of the behaviour that is less than the BCI is treated as a within-bout interval, while all gaps greater than the BCI is treated as between-bout intervals.

All the observations were carried out during the daytime between 07: 00 and 20: 00, and we attempted to observe the goats evenly over the daytime hours and to sample equally between both sexes.

In order to minimize the risk of non-independent samples, the behavioural data were never recorded on more than two focal animals from the same group during the same day, nor was the same animal observed twice on the same day. Although a few individual animals were sampled more than once during the whole study period, it is unlikely that observations of the same animals on different days in different environments and behavioural contexts were strongly autocorrelated (Molvar and Bowyer, 1994).

We used ANOVA to analyze the variation in the foraging ecology of feral goats. All data were first examined for normality using one-sample Kolmogorov-Smirnov tests. If the data were not normally distributed, appropriate transformations were performed in order to meet the requirements of parametric tests. All the analyses and statistics were carried out with SPSS 10. 0 (Kinnear and Gray, 2000).

## 2  Results

The cumulative frequency of gap lengths (on a logarithmic scale) from 158 continuous observation sessions on adult goats was plotted against the corresponding gap length (on a linear scale), as shown in Fig. 2. The distribution of gap lengths was composed of two main parts. The first part decreased rapidly and represented the gaps within a feeding bout; the second decreased smoothly and represented the gaps between feeding bouts. The two parts met at a gap length of about 7 min, suggesting that all gaps between occurrences of feeding behaviour of less than this length should be included within the same feeding bout. A total of 307 feeding bouts was thus identified by this method and the mean duration of the feeding bouts was 103. 1 ± 15. 0 (SD) min, with bout lengths varying between 1 and 460 min.
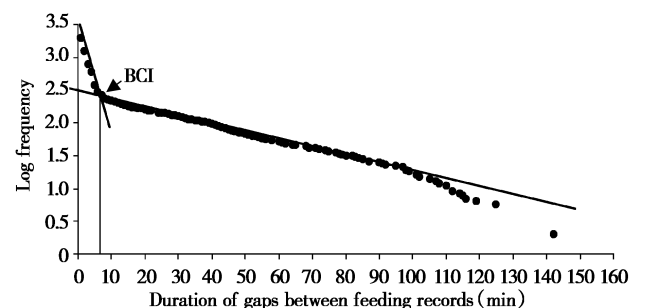


Fig. 2  Log survivorship of time intervals between successive feeding activities for feral goats. Log (N) is the logarithm of the frequency of intervals greater than the corresponding value of time interval. BCI is the bout criterion interval, an objective estimate of the minimum interval that distinguishes separate feeding bouts.

Fig. 3 shows that the duration of feeding bouts was shorter for adult males than for adult females in each month, and two-way ANOVA showed that there was marginally significant difference in the mean duration of feeding bouts between the two sexes (90. 3 ± 6. 4 SE

min for males vs. 111. 3 ± 7. 5 SE min for females. $n_1$ = 133, $n_2$ = 174) ($F_{1,306}$ = 3. 161, $P$ = 0. 077), and the mean duration varied significantly with month ($F_{5,306}$ = 5. 940, $P$ < 0. 001). There was no interactive effects between month and sex ($F_{5,306}$ = 1. 267, $P$ = 0. 278). Bouts increased in length from June to November for both males and females, except in September when feeding bout length decreased sharply for both sexes.
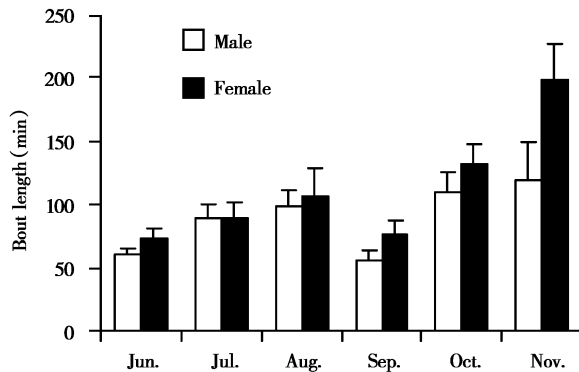


Fig. 3 Variation in feeding bout length for feral goats on Rum with respect to sex and month. Error bars show standard deviation of means.

The average bite rate for feral goats was 46. 3 ± 0. 6 bites/min (SD), based on a total of 346 samples from adults. Two-way ANOVA indicated that the average bite rate was faster in adult females than in adult males (47. 0 ± 0. 7 vs. 44. 9 ± 1. 1 bites/min, $n_1$ = 229, $n_2$ = 117. $F_{1,345}$ = 7. 665, $P$ = 0. 023), and bite rates were higher in October and November than in other months ($F_{5,345}$ = 7. 673, $P$ < 0. 001). There was only a marginally significant two-way interactions between sex and month ($F_{5,345}$ = 1. 823, $P$ = 0. 094). (Fig. 4).
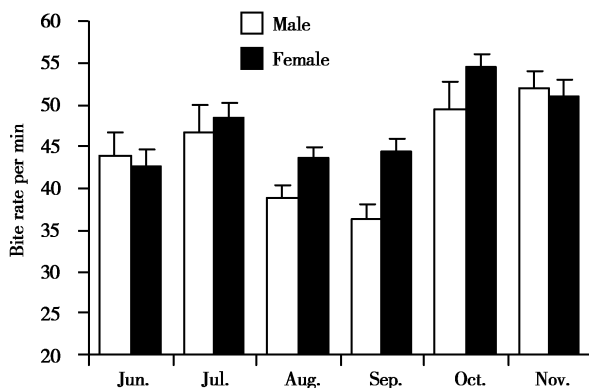


Fig. 4 Variation in feeding bite rate for feral goats on Rum with respect to sex and month. Error bars show standard deviation of means.

In a further analysis which re-grouped the months into pre-rutting (June-July), rutting (August-September) and post-rutting (October-November) periods,

we found that both males ($F_{2,116}$ = 17. 305, $P$ < 0. 001) and females ($F_{2,228}$ = 20. 958, $P$ < 0. 001) changed their bite rates greatly with these periods. The post-hoc tests showed that males fed markedly faster in both pre- and post-rutting periods than during the rutting period ($P$ < 0. 008), but females didn't feed faster during pre-rutting than during rutting ($P$ = 0. 327). Females fed faster during post-rutting period than during pre-rutting and rutting periods ($P$ < 0. 001).

We found no difference in step rates between the sexes (10. 6 ± 0. 5 steps/min for males vs. 10. 3 ± 0. 3 steps/min for females, $n_1$ = 117, $n_2$ = 229; ANOVA on arcsin-transformed data: $F_{1,345}$ = 0. 572, $P$ = 0. 452). Step rates differed significantly among months (Fig. 5: $F_{5,345}$ = 2. 409, $P$ = 0. 037). There were no significant interactions between the two factors ($F_{5,345}$ = 1. 421, $P$ = 0. 246).

The percentage of daytime spent feeding and the total amount of daytime spent feeding were calculated over the study period and were plotted in Fig. 6 (see also Shi et al., 2003; Shi et al., 2005).
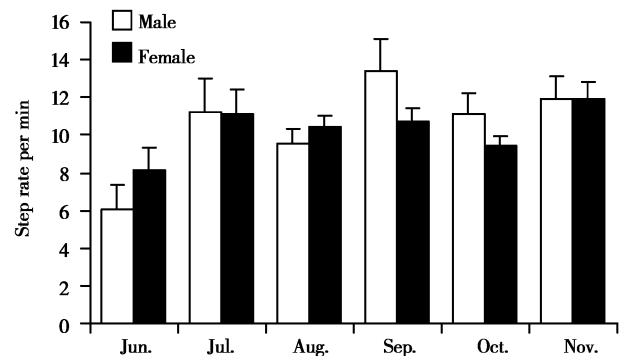


Fig. 5 Variation in step rate of feeding feral goats on Rum with respect to sex and month. Error bars show standard deviation of means.
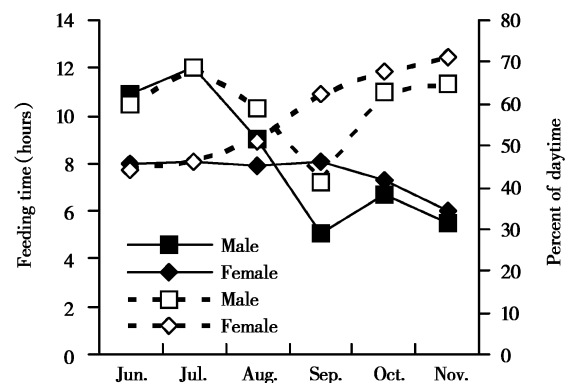


Fig. 6 Variations in mean monthly feeding time (solid lines) and percentage of daytime spent feeding (dashed lines) by adult male and female feral goats on Rum from June to November 2000.

Following the formula (1) described in Methods

and using estimates of the daytime spent feeding given in Fig. 6, the bite rates observed in this study (shown in Fig. 4), and values of bite size (weight of plant material removed per bite) available for caprines from the literature (males = 0.09 g/bite, females = 0.07 g/bite: Solanki, 1994; Pérez-Berbería and Gordon, 1999), we calculated the intake values as shown in Fig. 7. Daily forage intake varied significantly with both month ($F_{5,345}$ = 49.582, $P$ < 0.001) and sex ($F_{1,345}$ = 103.917, $P$ < 0.001). Adult female goats on Rum had relatively stable forage intakes from June to November, but males' forage intake fluctuated considerably. Across the period June–November, males had slightly higher average daily forage intake than females (1.72 ± 0.14 kg vs. 1.45 ± 0.08 kg, $n_1$ = 117, $n_2$ = 229, $F_{1,345}$ = 103.917, $P$ < 0.001), but this is principally because they had very much higher intakes during the pre-rut period in June and July. Male intake levels were lower than that for females during the rut (September in 2000).
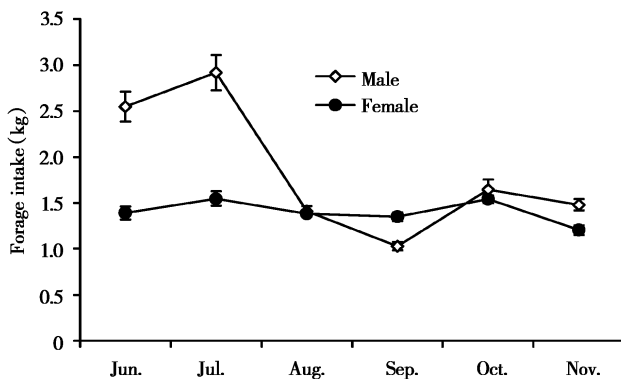


Fig. 7　Estimates of forage intake (kg/day) for male and female feral goats on Rum between June to November 2000. Intake was estimated by multiplying average feeding time, bite rate and bite size (see text for details). Error bars represent standard deviation of means.

## 3　Discussion

　　Like many other ungulate species (e. g. red deer: Clutton-Brock et al., 1982; bighorn sheep *Ovis canadensis*: Ruckstuhl and Festa-Bianchet, 1998; Chinese water deer *Hydropotes inermis*: Zhang, 1996; etc), the behaviour of feral goats on Rum was characterized by periods of grazing interrupted by other activities such as resting, moving, and rumination. In this study, grazing bout length increased steadily between June and November, presumably reflecting the combination of declining day length in which to feed, declining forage quality, and the increasing energy demands of thermoregulation (Gordon, 1989; Armstrong et al., 1995; Zhang, 1996). The only exception to this trend occurred during September, when feeding bouts of both males and females were shorter than at any oth-

er time during the study. This can be attributed to the rut, which began in late August and lasted until early October (Shi et al., 2003). During the rut, males frequently interrupted their grazing behaviour to engage in rutting activities (fighting with other males or tending females) (Pers. Observ. Lloyd, 2003). Although female goats were invariably disturbed by the males' attentions, it seems that the impact on their foraging patterns was much less. This is probably because individual females only suffer from the attentions of the males for the day or so when they are actually in oestrus, whereas the males are collectively engaged in rutting behaviour throughout the period of the rut (Dunbar et al., 1990; Lloyd, 2003).

　　The marginal difference in feeding bout leanth between the two sexes of Rum goats is mirrored in similar findings from another study with Chinese water deer by Zhang (1996). Zhang (1996) reported a significant difference in grazing bout length between sexes for Chinese water deer, which he attributed to the higher nutritional requirements of the male deer due to intensive territorial defense. Given the sex difference in body mass among the Rum goats (10% – 20%), we might have expected a similar effect. That we did not find a significant one suggests that the explanation may lie elsewhere (e. g. lack of territorial defense by males).

　　Feral goats on Rum had bite rates (46.6 bites/min pooled together) that were within the range reported for some other ungulates (red deer on Rum, 50 – 60 bites/min: Clutton-Brock et al., 1982; goats on semi-arid Indian pastures, 40.4 bites/min: Solanki, 1994). However, Chinese water deer at Whipsnade Zoo park had much higher bite rates (92.4 bites/min in males and 91.8 bites/min in females: Zhang, 1996), whereas Nubian ibex (*Capra ibex nubiana*) had much lower bite rates (19.1 bites/min in females and 13.9 bites/min in males: Gross et al., 1995). Goats on experimental swards had a much higher bite rate (81.9 bites/min: Gordon et al., 1996) than did feral goats on Rum, possibly because the experimental swards are sufficiently homogenous that goats do not need to spend much time selecting food items (Gordon and Illius, 1992).

　　A significant sex difference in bite rate was found in this study, with female goats having the faster one. Similar results have been observed in Soay sheep (*Ovis aries*) (67.3 bites/min vs. 55.6 bites/min for females and males, respectively: Pérez-Barbería and Gordon, 1999) and Nubian ibex (19.1 bites/min vs. 13.9 bites/min for females and males, respectively: Gross et al., 1995). Druzinsky (1993) suggested that animals with shorter jaws can chew faster than those with longer jaws, and Pérez-Barbería and Gordon (1999)

argue that this may explain the sex difference in bite rate in female Soay sheep. If this is the case, the shorter and smaller jaws of female goats may be partly responsible for the slightly higher bite rate in female feral goats than in males.

Although feral goats exhibit only limited sexual dimorphism in body mass ( males are only approximately 10% – 20% heavier than females as adults：Whitehead, 1972 ), there is a striking difference in the patterns of foraging by the two sexes. This study reveals that adult males notably tend to feed heavily during the early summer prior to the onset of the rut in August and September in terms of both bite rate and total time spent feeding. Since males' feeding rates plummet during the rut ( Lloyd, 2003 ), it seems as though males might be anticipating the energetic costs of the rut by trying to put on weight. During the rutting, adult males spend much time tendering esturous females and their feeding bouts are interrupted frequently by disruption by rutting behaviour ( pers. Observ. Shi et al. , 2003；Lloyd, 2003 ). Such interuption and disruption may have contributed to the sharp decrease in bite rates for adult males observed in this study.

Both males and females increased their bite rates greatly in October and November. This may be the combined result of several reasons. First, they need to feed faster to get more food in order to compensate the reduction of bite rate and to replenish the energy costs during the rut. Second, the decreasing daylength and temperature in October and November force them to forage faster to recover from the rut as soon as possible in order to save as much fat and energy as possible to survive the forthcoming winter ( Bruno and Lovari, 1989 ).

On Rum, there were no significant differences between the sexes in step rate. Ruckstuhl ( 1998 ), too, found no differences between adult bighorn rams and ewes, or between immature males ( aged 2 – 3 years), older males and adult females. However, Komers et al. ( 1993 ) found that, in bison, cows had a higher step rate than bulls, and they attributed this difference to higher food selectivity in cows. They concluded that a difference in step rate leads to temporal but not spatial segregation of the sexes. Ruckstuhl ( 1998 ) argued that, if step rate was a measure of selectivity, it could be concluded that bighorn rams and ewes did not differ in forage selectivity. The same conclusion presumably applies to the feral goats on Rum as there is no significant difference in habitat selectivity between the two sexes of goats on Rum ( Shi, 2002 ).

Herbage intake rate is a major determinant of animal nutrition and hence of weight change, lactation and reproductive performance ( Ungar and Noy-Meir,

1988；Gordon, 1995；Nellemann, 1997 ). The factors affecting intake rate include features of the environment, the animal itself and the vegetation. Most studies focus on the relationship between intake rate and vegetation characteristics ( including availability, structure and quality ) ( Wickstrom et al. , 1984；Goodson et al. , 1991；Nellemann, 1997 ), although some studies relate intake rate to animals' metabolic rate, body size and the anatomy of their digestive system ( Hanley, 1982；Gordon and Illius, 1992 ).

On Rum, the female goats had a relatively stable forage intake during the study period, whilst that for male goats fluctuated greatly. If forage intake is directly related to the energy intake level ( as is generally assumed ), the relatively stable forage intake for females may reflect their relatively stable energy requirement during the study period ( although this may increase for gestation and lactation, which occurs earlier in the year much before this study ). This could be a consequence of the fact that the costs of reproduction are low during those months covered by the study period ( most of the kids on Rum are born between January and March and kids start feeding for themselves about one or two weeks after birth [ Pickering, 1983 ] ). However, if we consider the low quality of forage in late autumn and winter ( which is out of our current study period ) ( Gordon, 1989 ), more work is still needed to evaluate the energy and nutrition intake by feral goats on Rum.

On the other hand, the higher forage intake for males in June and July may reflect their need to build up energy and fat stores ( to put on weight ) in preparation for the exhausting rut from late August to early October. During the rutting period, both time spent feeding and intake decreased sharply for males. It is worth noting that forage intake is at a low level for both females and males after rut, and particularly so for males even though adult males increase both bite rates and the percentage of daytime spent feeding ( Shi et al. , 2003 ). The daytime length available for feeding by goats on Rum thus seems to be a limiting factor for forage intake, and we expect that the similar pattern of forage intake will remain in winter. The low forage intake, coupled with the low quality of forage and the harsh weather at this time of the year, may mean that the feral goats are at negative energy balance and males may be prevented from rapid and complete recovery from exhausting rutting. This will in turn inevitably affect their survivorship over the forthcoming harsh winter and early spring during which the death rate of males is very high ( Boyd, 1981；Dunbar et al. , 1990 ).

The estimates of forage intake for the goats on Rum are, of course, based on the assumption that bite size is the same as that for Indian goats and does not

change significantly between seasons or vegetation communities. In fact, previous studies have shown that the bite size and bite rates are largely affected by such factors as the structure and biomass of forage (Hudson & Watkins, 1986; Hodgson *et al.*, 1991; Solanki, 1994; Pérez-Berbería and Gordon, 1999). However, the differences in both forage intake between the two sexes and between early and late summer (pre-rut versus rut) for males are sufficiently great that a near-doubling of bite rates would be required to equalize food intake levels. This seems implausibly large, and suggests instead that the estimates are likely to be at least within the right order of size.

In conclusion, male and female feral goats on Rum have different foraging behaviour as shown by our study. In this population of feral goats, the availability of daylength for feeding may be a key factor to determine the forage intake of goats, which has significant implication for their energy and nutrition balance in winter, and thus over-winter survival of the goats on Rum. More work is needed to investigate the foraging behaviour and forage intake, and thus energy requirement of feral goats on Rum over winter in order to better understand the mechanism under which the goats, an originally tropical species, cope with harsh winter weather in northern temperate region.

**References**:

Altmann J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**: 227 – 267.

Armstrong R H, Robertson E, Hunter E A. 1995. The effect of sward height and its direction of change on the herbage intake, diet selection and performance of weaned lambs grazing ryegrass swards. *Grass Forage Sci*, **50**, 389 – 398.

Arnold G W. 1970. Regulation of food intake in grazing ruminants. In: Phillipson A T ed. Physiology of Digestion and Metabolism in the Ruminant. Oriel Press: New-Castle upon Tyne, 262 – 276.

Arnold G W. 1987. Influence of the biomass, botanical composition and sward height of annual pastures on foraging behaviour by sheep. *J Appl Ecol*, **24**, 759 – 772.

Boyd I L. 1981. Population changes and the distribution of herd of feral goats (*Capra* spp.) on Rhum, Inner Herbides, 1960 – 1978. *J Zool Lond*, **193**, 287 – 304.

Bruno E, Lovari S. 1989. Foraging behaviour of adult *Apennine chamois* in relation to the seasonal variation in food supply. *Acta Therio*, **34**: 513 – 523.

Bullock D J, Pickering S P. 1984. The validity of horn ring counts to

determine the age of Scottish feral goats (*Capra* (domestic). *J Zool Lond*, **202**, 561 – 564.

Chilibroste P, Tamminga S, Boe H. 2008. Effects of length of grazing session, rumen fill and starvation time before grazing on dry-matter intake, ingestive behaviour and dry-matter rumen pool sizes of grazing lactating dairy cows. *Crass and Forage Science*, **52**: 249 – 257.

Clutton-Brock T H, Ball M E. 1987. Rhum: The Nature History of an Island. Edinburgh University Press.

Clutton-Brock T H, Guinness F E, Albon S D. 1982. Red deer: Behaviour and Ecology of Two Sexes. Chicago: University of Chicago Press.

Collins W B, Urness P J. 1983. Feeding behaviour and habitat selection of mule deer and elk on northern Utah summer range. *J Wildl Manage*, **47**: 646 – 663.

Druzinsky R E. 1993. The time allometry of mammalian chewing movement-chewing frequency scales with body-mass in mammals. *J Theor Biol*, **160**: 427 – 440.

Dunbar R I M, Buckland D, Miller D. 1990. Mating strategies of male feral goats: a problem in optimal foraging. *Anim Behav*, **40**: 653 – 667.

Forbes T D A. 1989. Researching the plant-animals interface: the investigation of ingestive behaviour in grazing animals. *J Anim Sci*, **66**: 2369 – 2379.

Forbes T DA, Hodgson J. 1985. Comparative studies of the influence of sward conditions on the ingestive behaviour of cows and sheep. *Grass and Forage Science*, **40**: 68 – 77.

Goodson N J, Stevens D R, Bailey J A. 1991. Winter-spring foraging ecology and nutrition of bighorn sheep on montane ranges. *J Wildl Manage*, **55**: 422 – 433.

Gordon I J. 1989. Vegetation community selection by ungulates on the Isle of Rhum. I: Food supply. *J Appl Ecol*, **26**: 35 – 51.

Gordon I J. 1995. Animal-based techniques for grazing ecology research. *Small Ruminant Research*, **16**: 203 – 214.

Gordon I, Dunbar R, Buckland D, Miller D. 1987. Ponies, cattle and goats. In Clutton-Brock T H, Ball M E eds. Rhum: The Natural History of an Island. Edinburgh University Press, 110 – 125.

Gordon I J, Illius A W. 1992. Foraging strategy: from monoculture to mosaic. In: Speedy A W ed. Progress in Sheep and Goat Research. CAB International. 153 – 177.

Gordon I J, Illius A W, Milne J D. 1996. Sources of variation in the foraging efficiency of grazing ruminants. *Func Ecol*, **10**: 219 – 226.

Greig J C. 1969. The Ecology of Feral Goats in Scotland. M. Sc. Degree thesis, University of Edinburgh.

Gross J E, Demment M W, Alkon P U, Kotzman M. 1995. Feeding and chewing behaviours of Nubian ibex: compensation for sex-related difference in body size. *Func Ecol*, **9**: 385 – 393.

Hanley T A. 1982. The nutritional basis of food selection by ungulates. *J Rang Manage*, **35**: 146 – 151.

Hanley T A. 1984. Habitat patches and their selection by wapiti and black-tailed deer in a coastal montane coniferous forest. *J Appl Ecol*, **21**: 423 – 436.

Harvey R A, Parsons A, Orr R, Rutter S. 2003. Bite dimensions and grazing movements by sheep and cattle grazing homogeneous perennial ryegrass swards. *Applied Animal Behaviour Science*, **88**: 227 – 242.

Hester A J, Mitchell F J G, Gordon I J, Baillie G J. 1996. Activity patterns and resource use by sheep and red deer grazing across a grass/heather boundary. *J Zool Lond*, **240**: 609 – 620.

Hodgson J. 1977. Factors limiting herbage intake by the grazing animals. In: Gilsenan B ed. Proc. Int. Meeting Anim. Prod. Temp. Grasslands. 70 – 75.

Hodgson J. 1981. Variations in the surface characteristics of the sward and the short term rate of herbage intake by calves and lambs. *Grass and Forage Science*, **36**: 49 – 57.

Hudson R J, Frank S. 1986. Foraging ecology of bison in aspen boreal

forests. *J Range Manage*, **40**: 71 – 75.

Hudson R J, Watkins W G. 1986. Foraging rates of wapiti on green and cured pastures. *Can J Zool*, **64**: 1705 – 1708.

Illius A W, Gordon I J. 1987. The allometry of food intake in grazing ruminants. *J Anim Ecol*, **56**: 989 – 999.

Kinnear P R, Gray C D. 2000. SPSS for Windows Made Simplec ( Releass 10). Psychology Press Ltd. HK.

Komers P E, Messier F, Gates C C. 1993. Group structure in wood bison: nutritional and reproductive determinants. *Can J Zool*, **71**: 1367 – 1371.

Langvatn R, Hanley T A. 2000. Feeding-patch choice by red deer in relation to foraging efficiency. *Oecologia*, **95**: 164 – 170.

Leuthold W. 1977. African Ungulates. A Comparative Review of Their Ethology and Behavioural Ecology. Springer Verlag, Berlin.

Lloyd K. 2003. Mating system and strategy of feral goats on the Isle of Rum, Scotland. University of Liverpool, PhD thesis.

Molvar E M, Bowyer R T. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *J Mammal*, **75**: 621 – 630.

Martin P, Bateson P. 1993. Measuring Behaviour, 2nd edition. Cambridge University Press.

Nellemann C. 1997. Grazing strategies of muskoxen ( *Ovibos moschatus* ) during winter in Angujaartorfiup Nunaa in western Greenland. *Can J Zool*, **75**: 1129 – 1134.

Neuhaus P, Ruckstuhl K E. 2002. Foraging behaviour in Alpine ibex ( *Capra ibex* ): consequences of reproductive status, body size, age and sex. *Ethology Ecology & Evolution*, **14**: 373 – 381.

Novellie P A. 1978. Comparison of the foraging strategies of blesbok and springbok on the Transval highveld. *S Afr J Wildl Res*, **8**: 137 – 144.

Owen-Smith N. 1979. Assessing the foraging efficiency of a large herbivore, the kudu. *S Afr J Wildl Res*, **9**: 102 – 110.

Owen-Smith N, Novellie P. 1982. What should a clever ungulate eat? *Am Nat*, **119**: 151 – 178.

Owen-Smith R N. 1988. Megaherbivores. Cambridge: University Press Cambridge.

Parker K L, Gillingham M P. 1993. An accurate technique for estimating forage intake of tractable animals. *Can J Zool*, **71**: 1462 – 1465.

Pickering S P. 1983. Aspects of behavioural ecology of feral goats ( *Capra* ( domestic ) ). PhD thesis. University of Durham.

Pérez-Barbería F J, Gordon I J. 1999. Body size dimorphism and sexual segregation in polygynous ungulates: an experimental test with Soay sheep. *Oecologia*, **120**, 258 – 267.

Pickering S. P. 1983. Aspects of behavioural ecology of feral goats ( *Capra* ( domestic ) ). Unpublished PhD thesis, University of Durham.

Prache S, Gordon I J, Rook A J. 1998. Foraging behaviour and diet selection in domestication herbivores. *Annales De Zootechnie*, **47**: 335 – 345.

Pyke G H, Pulliam H R., Charnov E L. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology*, **52**: 137 – 154.

Pyke G H. 1984. Optimal foraging theory: a critical review. *Ann Rev Ecol Syst*, **15**: 523 – 575.

Rook A J, Tallowin J R B. 2003. Grazing and pasture management for biodiversity benefit. *Animal Research*, **52**: 181 – 189.

Ruckstuhl K E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Anim Behav*, **56**: 99 – 106.

Ruckstuhl K E, Festa-Bianchet M. 1998. Do reproductive status and lamb gender affect foraging behaviour of bighorn ewes? *Ethology*, **104**: 941 – 954.

Ruckstuhl K E, Festa-Bianchet M, Jorgenson J T. 2003. Bite rates in Rocky Mountain bighorn sheep ( *Ovis Canadensis* ): effects of sea-

son, age, sex and reproductive status. *Behav Ecol & Sociobiol*, **54**: 167 – 173.

Saunders F C, McElligott A G, Safi K, Hayden T J. 2005. Mating tactics of male feral goats ( *Capra hircus* ): risks and benefits. *Acta Ethol*, **8**: 103 – 110.

Shi J. 2002. Habitat selection and foraging ecology of feral goats on the Isle of Rum, NW Scotland. PhD thesis. University of Liverpool.

Shi J, Dunbar R I M., Buckland D, Miller D. 2003. Daytime activity budgets in feral goats ( *Capra hircus* ) on the Isle of Rum: Influence of season, age and sex. *Can J Zool*, **81**: 803 – 815.

Shi J, Dunbar R I M, Buckland D, Miller D. 2005. Dynamics of grouping patterns and social segregation in feral goats on Rum Island. *Mammalia*, **69**: 185 – 199.

Shipley L A, Gross J E, Spalinger D E, Hobbs T N, Wunder B A. 1994. The scaling of intake rate in mammalian herbivores. *American Naturalist*, **143**, 1055 – 1082.

Slater P J B. 1974. Bouts and gaps in the behaviour of zebra finches, with special reference to preening. *Rev Comp Anim*, **8**: 47 – 71.

Solanki G S. 1994. Feeding-habits and grazing behaviour of goats in semi-arid region of India. *Small Ruminant Research*, **14**: 39 – 43.

Spalinger D E, Hobbs N T. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *Am Nat*, **140**: 325 – 348.

Stobbs T H. 1973a. The effects of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. *Austr J Agric Res*, **24**: 809 – 819.

Stobbs T H. 1973b. The effects of plant structure on the intake of tropical pastures. II. Differences in sward structure, nutritive value, and bite size of animals grazing *Setaria anceps* and *Chloris gayana* at various stages of growth. *Austr J Agric Res*, **24**: 821 – 829.

Stronge D C, Fordham R A, Minot E O. 1997. The foraging ecology of feral goats ( *Capra hircus* ) in the Mahoenui Giant Weta Reserve, Southern King country, New Zealand. *N Z J Ecol*, **21**: 81 – 88.

Taweel H Z, Tas B M, Dijkstra J, Tamminga S. 2004. Intake regulation and grazing behavior of dairy cows under continuous stocking. *J Dairy Science*, **87**: 3417 – 3427.

Taweel H, Tas B, Smit H, Tamminga S, Elgersma A. 2005. A note on eating behaviour of dairy cows at different stocking systems-diurnal rhythm and effects of ambient temperature. *Applied Animal Behaviour Science*, **98**: 315 – 322.

Ungar E D, Noy-Meir I. 1988. Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. *J Appl Ecol*, **25**: 1045 – 1062.

Virtanen R, Edwards G R, Crawley M J. 2002. Red deer management and vegetation on the Isle of Rum. *J Appl Ecol*, **39**: 572 – 583.

Wallis de Vries M F D. 1994. Foraging strategy of cattle in patchy grassland. *Oecologia*, **100**: 98 – 106.

Weckerly F W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J Mammal*, **79**: 33 – 53.

Whitehead G K. 1972. The Wild Goats of Great Britain and Ireland. David & Charles, Newton Abbot.

Wickstrom M L, Robbins C T, Hanley T A, Spalinger D E, Parish S P. 1984. Food intake and foraging energetics of elk and mule deer. *J Wildl Manage*, **48**: 1285 – 1301.

Zhang E. 1996. Behavioural ecology of the Chinese water deer at Whipsnade wild animal park, England. PhD thesis, University of Cambridge.

Zhang W H, Tao S L, Li J N, Liu J K. 2008. Effects of grazing time restriction on the grazing behavior of boer goat. *Pratacultural Science*, **125**: 85 – 90.