

Relationships between movement rate, agonistic displacements and forage availability in spanish ibexes (*Capra pyrenaica*)

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RESUME

Relations entre l'activité, l'agression et les disponibilités en aliment chez le bouquetin espagnol (*Capra pyrenaica*).

Le comportement de recherche de nourriture des IZARD espagnols dans les montagnes de Carzola et de Segura a été étudié durant l'hiver et le printemps 1985-1986. Des différences entre les différentes classes d'âge et de sexe en ce qui concerne le régime alimentaire ont été observées l'hiver.

Les jeunes animaux sont principalement des « grazers » et les mâles adultes du « browsers » ; les femelles adultes sont intermédiaires entre ces deux types. On observe des différences entre ces différentes classes en ce qui concerne le temps de recherche (nombre de pas par minute) ; les mâles sont plus mobiles que les femelles. Aucune différence n'a été observée en ce qui concerne le régime alimentaire des femelles au cours de deux années de l'étude.

Lorsque les ressources alimentaires sont faibles, en hiver, les bouquetins tendent à réduire leurs mouvements lors de la recherche de nourriture, mais redeviennent plus mobiles au printemps dès que les disponibilités en aliment augmentent. Un accroissement de la fréquence des interactions agonistiques est enregistré au printemps. Ceci est en partie dû à la plus grande disponibilité en plantes.

Mots clés : *Capra pyrenaica*. Comportement alimentaire. Sélectivité.

SUMMARY

The foraging behaviour of Spanish ibexes in the Cazorla and Segura Mountains was studied during the winter and spring of 1985-1986. Differences in the diet of different age and sex classes during winter were observed. Young

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animals were principally grazers, adult males browsers and adult females intermediates feeders. A difference in the searching time (steps per minute) of individuals in these classes was observed; with males being more mobile than females. No differences were found in the diets (grass/browsings (shoots and leaves)) of females during the two year study period. When food availability was low in winter, ibexes tended to reduce their rates of movement when foraging, but they become more mobile in the spring when profitable food items were more common. It is concluded in those seasons when little food is available, ibex tend to reduce their rates of movement when foraging, but become more mobile when profitable food items are common. An increase in the rate of agonistic interactions was recorded during the spring. This was in part due to the increased movement of females in response to the greater availability of food plants.

INTRODUCTION

Several factors influence forage quality, the most important of these is growth stage. Forage quality (measured in terms of nitrogen content, cell wall constituents and dry matter digestibility) is greatest in May and June when plant growth is greatest and thereafter declines steadily (Hanley, 1982a). When the diet has a high cellulose content, voluntary food intake has to be restricted since food has to be retained in the rumen for a long time to allow for the digestion of the cellulose (Hanley, 1982 b). Ruminants, in temperate climates thus face a difficult situation in winter when forage quality is low and voluntary food intake is limited by the food passage rate (Van Soest, 1965).

One of the earliest optimal foraging models (Veeder, 1983) concerned the trade-off between profitability of food items and searching time. Veeder (1983) suggested that, when availability of food items is low an animal should respond in one of two ways: (a) by including poorer-quality items in the diet, thereby decreasing search or travel time; or (b) by travelling further, at greater energetic cost, in order to obtain an adequate quantity of high quality food items.

Hanley (1982a) considers that the increase in travel distance results from increased selectivity of individual plant by the herbivore. Therefore, we hypothesised that ibexes should be more selective when profitable items are abundant (spring) but that, they should decrease searching time when the available food is of little nutritive value (winter). This hypothesis is in agreement with the fact that the number of species eaten by Spanish ibexes is lower in winter than in spring (Martínez *et al.*, 1985).

The potential costs of group foraging include increased competition for scarce resources as a consequence of agonistic displacements during dominance interactions (Alexander, 1974). Brown (1964) first introduced the idea of economic defendability. He pointed out that defence of a resource has a cost in terms of energy expenditure or risk of injury, as well as the benefits of priority of access to the resource. If resources are scarce, the gains excluding others may not be sufficient to compen-

sate for the cost of defence. In this study of the Ibex we tested hypothesis that the displacement rate (i.e. number of times displacing vs. number of times displaced) of a foraging individual is related to the season (winter vs. spring).

The feeding habits of ibexes have been studied by several authors (Couturier, 1962; Heptner *et al.*, 1966; Papageorgiou, 1974; Schaller, 1977; Palacios *et al.*, 1978; Martínez *et al.*, 1985), but, the adaptive behavioural strategies that enable ibex to exploit their physical environment are not well understood. This study investigated the relationship between rate of movement when feeding, food availability and agonistic displacements in Spanish ibexes.

METHODS

STUDY AREA

The study was conducted on the Cazorla and Segura Mountains, in area of 66,367 ha, situated between latitude 37°45' and 38°10' and longitudes 2°40' and 3°00'. These steep and rugged mountain ranges are limestone and the highest peak rises to 2,107 m. They have been artificially afforested with *Pinus nigra*, *P. pinaster* and *P. halepensis*, which, together with *Quercus ilex*, are the main tree species present. The Ibex population density in this area is 0.11 ha⁻¹ (Escòs and Alados, unpubl. data). Large mammals coexisting with the Spanish Ibex in the Cazorla and Segura Mountains, include *Dama dama*, *Cervus elaphus*, *Ovis musimon*, and domestic sheep and goat.

DATA RECORDED

The data were recorded by two observers. Each observer studied a different group of ibexes, but all observations were made at the same times on the same days. Each observation period lasted 4 hours. Observations were commenced approximately 4 hrs. before dusk because preliminary studies had shown that the ibexes most active at this time (Alados, 1986). During the period from December 1985 to February 1986 each observer made 11 such observations (i.e. one such 4 hrs. observation on each of 11 days). During May 1986, the ibexes were observed for 4 h per day (2 h at dawn and 2 h at dusk) on each of five days, because the animals were more active during these periods at this time of year. During the winter, both mixed groups and female/kid groups of foraging ibexes were studied, but during May, only female/kid groups were observed.

At the start of each observation the following Data were collected: date, hour, group size and composition and habitat density, index and locality. Focal animal scans (Altmann, 1974) were then made at 1-min intervals. The following parameters of the focal animals behaviour were recorded; the food items selected (grass or browse), steps per minute (measured from one of the legs), nearest neighbour distance (kids were excluded due to their close association with their mothers), and displacements made or received together with the age sex classes of the interacting animals. A displacement was defined as a withdrawal by a stationary individual in response to the approach of a second individual. Only those interactions during which the focal animal either displaced another ibex that was feeding or was itself displaced while feeding were included in the analysis. To qualify the displacer did not have to use the feeding site, only to interrupt the other's feeding.

The average number of steps per minute during feeding was used as an index of forage selectivity following Risenhoover & Bailey (1985).

The age and sex classes recognised were: adult females (older than 2 years), subadult females (1 to 2 years old), males (older than 2 years) and young (males and females less than 2 years old).

ANALYSIS OF DATA

In the analysis of displacement rates, a modified form of Altmann and Altmann's (1977) method for asymmetric interactions was used. This modification involved a correction for the use of focal sample data rather than all occurrences of a particular behaviour. The mean class-specific individual rate for any class (x) is the total number of acts by members of class x divided by the total observation time on members of that class.

The total frequency per individual-hour of observation is $\Sigma N_{xj} / \Sigma T_{xj}$: where $\Sigma_j N_{xj}$ is the number of times the behaviour (displacements made, received or the sum of both) was performed by the x^{th} individual during the period j. T_{xj} is the focal sample time on individual x during period j. When the subject was solitary, the data were excluded from the analysis.

In order to test our hypothesis that the displacement rate of a foraging animal is related to the time of year, we assumed that the displacements (made or received) follow a Poisson process (Altmann & Altmann, 1977). Thus, to compare the rates of displacements over the two year period, we assume that the observations for each follow independent Poisson processes and that it is necessary to compare the rates of occurrence within each period (Cox & Lewis, 1966, pp. 223).

RESULTS

During the winter there were significant differences between age and sex classes in the number of times that grass rather than browsings were eaten ($\chi^2 = 91.83$, $df = 2$, $P < 0.001$ (fig. 1). However, there was

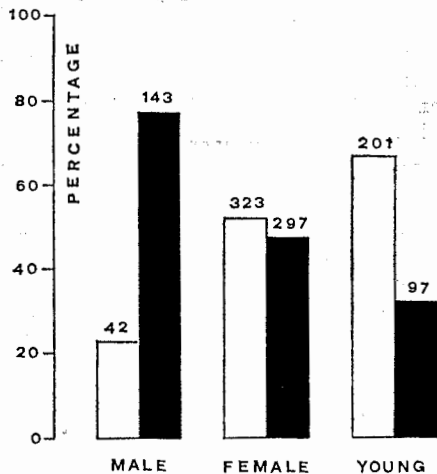


Fig. 1: Percentages of grass (in black) and browsing (in white) taken by focal animal Spanish ibexes during the winter. The figure above each column refers to the number of observations made.

Fig. 1: Pourcentages d'herbe (en blanc) et de fourrage (en noir) ingérés par les Bouquetins d'Espagne au cours de l'hiver. Le chiffre au-dessus de chaque colonne indique le nombre d'observations réalisées.

no significant difference in the amounts of grass and browsings eaten by females during the spring and winter ($\chi^2 = 1.38$, $df = 1$, N.S.).

A comparison of the mean number of steps taken per minute by ibexes, of all age and sex classes during the winter, showed a significant difference between age and sex classes when the ibex fed on grass ($F(2,565) = 4.7$, $P < 0.01$) but not when they fed on browsings ($F(2,534) = 1.2$, N.S.). While grazing, males were more mobile than females. During the winter, the rate of movement (steps per minute) of ibexes of all age and sex classes, was significantly greater when they fed on grasses than when they fed on browsings (Kolmogorov-Smirnov test, $\chi^2 = 65.35$, $df = 2$, $P < 0.001$ for females, $\chi^2 = 25.34$, $df = 2$, $P < 0.001$ for young, $\chi^2 = 30.88$, $df = 2$, $P < 0.001$ for males, one tailed tests). A similar difference was also significant in the spring for females, the only age and sex class studied (Kolmogorov-Smirnov test, $\chi^2 = 20.43$, $df = 2$, $P < 0.001$ one tailed test) (table 1). Since there food availability is higher in spring than in winter, ibexes might be expected to be more mobile in spring than in winter and this proved to be the case both for grazing (Kolmogorov-Smirnov test, $\chi^2 = 120.29$, $df = 2$, $P < 0.001$, one tailed test) and browsing animals (Kolmogorov-Smirnov test, $\chi^2 = 123.33$, $df = 2$, $P < 0.001$, one tailed test).

Since competition for food should affect the spatial distribution of individuals within the group, we analysed the relationships between mobility while foraging (steps per minute), group size and nearest

Table 1 : Steps taken per minute by different age and sex classes of Spanish ibexes during the winter and spring when feeding on grasses or browsings.

Tableau I : Nombre de pas par minute selon les différentes classes d'âge et selon le sexe des Bouquetins d'Espagne pendant leur alimentation d'hiver et de printemps en prairie ou en buisson.

| Winter | | | | | | | |
|---------------------------|--------|----------|--------|----------------------|-------|----------|--------|
| Grasses | | | | Browsings | | | |
| | Mean | Variance | Number | | Mean | Variance | Number |
| Female | 4.548 | 32.155 | 323 | Female | 2.795 | 21.981 | 297 |
| Male | 7.000 | 90.390 | 42 | Male | 2.364 | 29.360 | 143 |
| Young | 6.020 | 50.440 | 201 | Young | 3.443 | 44.478 | 97 |
| F(2,563) = 4.7, P = 0.009 | | | | F(2,534) = 1.2, N.S. | | | |
| Spring | | | | | | | |
| Grasses | | | | Browsings | | | |
| | Mean | Variance | Number | | Mean | Variance | Number |
| Female | 11.186 | 1.867 | 345 | Female | 8.970 | 1.844 | 361 |

neighbour distance for females during the spring, and for females, males and young animals during the winter, for both grazing and browsing (*table II*). We suggest that feeding competition and group size are conflicting variables in the spacing behaviour of ibexes. Competition for food resources but the protection from predation afforded by feeding in groups tends to draw them together. Therefore, in order to minimise agonistic actions during feeding but maximise protection from predators animals feeding in groups should vary their rates of movement in relation to the number of animals in the group and/or the nearest neighbour distances between the members of the group (i.e. animals in large groups with short nearest neighbour distances should move less than animals in small groups with large nearest neighbour distances). The results obtained support this hypothesis, there was a negative relationship observed between group size and nearest neighbour distance in most of the cases observed (r ranging from -0.53 to -0.31 , $P < 0.05$). The only exception to this was young animals in the winter, when the correlation was not significant for grazing animals but was significantly positive ($P < 0.001$) for browsing animals. The probable reason is that young animals in larger groups feel more secure and do not need to remain so close to their mothers. However, in general the larger the group, the shorter were nearest neighbour distances. *Table II* shows that, with the exception of grazing females during the winter, there was a negative relationship between the number of steps taken per minute and the group size and/or a positive relationship between number of steps per minute and nearest neighbour distances.

Since there is more food available in spring than in winter, we suggest that agonistic displacement rates should be greater in spring as a result of ibexes trying to improve the quality of their diet. Furthermore, agonistic displacements should be less likely in winter since the cost of fighting exceeds the benefit of extra food when food availability is low. In order to test these hypotheses we compared the rates of agonistic displacements in adult females (older than two years) in winter and spring. We found that the animals interacted significantly more in spring (5.93 displacements per focal hour of feeding) than in winter (1.41 displacements per focal hour of feeding) ($z = 6.18$ $P < 0.001$ one tailed test). A similar tendency was observed in subadult females, between 1 and 2 years old, although this difference was not significant (1.16 displacements per focal hour of feeding during the winter period, 3.21 displacements per focal hour of feeding during the spring period; $z = 1.21$, N.S. one tailed test) (*table III*).

The number of displacements, made and received, (*table III*) were significantly different in winter and in spring in both adult females and subadult females ($\chi^2 = 13.30$, $df = 1$, $P < 0.001$ for adult females; Fisher exact probability test $P = 0.04$, one tailed test for subadult females). During the spring but not the winter adult females tended to

Table II: *F-values and significance levels for analyses of variance. Differences in steps per minute (y) were analysed in relation to group size (x) and distance to nearest neighbour (z). R² is the proportion of variance explained.*

Tableau II: *Valeurs de F et niveau de significativité après analyses de variance. Les différences entre les nombre de pas par minute (y) ont été analysées en fonction de la taille du groupe (x) et de la distance par rapport au groupe voisin (z). R² indique la valeur de la variance expliquée.*

| Winter | | | | | | | |
|------------|---------------|--|-------|------------|---------------|--|-------|
| Food items | Age/sex class | F (v ₁ , v ₂) | P | Food items | Age/sex class | F (v ₁ , v ₂) | P |
| Browsings | Female | Total Regr. 3.4 (2,296) | 0.025 | Grass | Female | Total Regr. 6.2 (2,322) | 0.005 |
| " | " | Group size 5.9 (1,296) | 0.025 | " | " | Group size 1.1 (1,322) | N.S. |
| " | " | Distance 0.8 (1,296) | N.S. | " | " | Distance 11.4 (1,322) | 0.001 |
| | | R ² = 0.023 (y = 3.486 - 0.208x + 0.157z) | | | | R ² = 0.038 (y = 8.313 - 0.379x - 0.504z) | |
| Browsings | Male | Total Regr. 11.1 (2,142) | 0.001 | Grass | Male | Total Regr. 17.0 (2,42) | 0.001 |
| " | " | Group size 9.1 (1,142) | 0.005 | " | " | Group size 15.3 (1,42) | 0.001 |
| " | " | Distance 23.1 (1,142) | 0.001 | " | " | Distance 18.7 (1,42) | 0.001 |
| | | R ² = 0.187 (y = -0.964 + 0.009x + 0.953z) | | | | R ² = 0.466 (y = 6.387 - 1.060x + 2.016z) | |
| Browsings | Young | Total Regr. 4.1 (2,96) | 0.025 | Grass | Young | Total Regr. 1.2 (2,200) | N.S. |
| " | " | Group size 6.3 (1,96) | 0.005 | " | " | Group size 2.4 (1,200) | N.S. |
| " | " | Distance 1.9 (1,96) | N.S. | " | " | Distance 0.0 (1,200) | N.S. |
| | | R ² = 0.079 (y = 9.249 - 0.572x - 0.612z) | | | | R ² = 0.012 (y = 7.927 - 0.317x - 0.063z) | |
| Spring | | | | | | | |
| Browsings | Female | Total Regr. 4.6 (2,360) | 0.025 | Grass | Female | Total Regr. 2.5 (2,344) | N.S. |
| " | " | Group size 6.6 (1,360) | 0.025 | " | " | Group size 4.7 (1,344) | 0.05 |
| " | " | Distance 2.6 (1,360) | N.S. | " | " | Distance 0.4 (1,344) | N.S. |
| | | R ² = 0.025 (y = 9.195 - 0.455x + 0.281z) | | | | R ² = 0.014 (y = 12.662 - 0.740x + 0.175z) | |

Table III: Frequency of displacements made/received across age/sex classes during different periods of the year.

Tableau III: Rapport déplacements réalisés/déplacements imposés à l'intérieur des groupes âge/sexe durant différentes périodes de l'année.

| Year Period | Class | N° of Displacements | Displacements made | Displacements received | Time (minutes) |
|-------------|-----------------|---------------------|--------------------|------------------------|----------------|
| Winter | Adult Female | 23 | 12 | 11 | 976 |
| | Subadult Female | 2 | 2 | 0 | 103 |
| Spring | Adult Female | 56 | 50 | 6 | 567 |
| | Subadult Female | 16 | 2 | 14 | 299 |

make displacements and subadult females tended to be displaced (spring : $G = 34.89$, $df = 1$, $P < 0.001$; winter : $G = 2.45$, $df = 1$, N.S.).

DISCUSSION

The diet and activity patterns in many species of ungulates vary between age or sex classes (Geist, 1971 ; Shank, 1982 for *Ovis* ; Clutton-Brock *et al.*, 1982 for *Cervus* ; Holisová *et al.*, 1984 for *Capreolus*). One reason for this, proposed by Clutton-Brock *et al.* (1982), is that differences in body size give rise to differential nutritional requirements. Differences in diet may also be related to competition between individuals (Harrison, 1983).

In our study we observed differences in diets in the age/sex classes studied, with young animals being principally grazers, adult males browsers and females intermediate feeders. We suppose that one reason for this is that only the tallest individuals can reach the higher branches. Another reason is that dominant males can displace females from feeding points and consequently have access to areas of maximal food availability, such as the higher levels of bushes. Clutton-Brock *et al.* (1982) also observed a sex difference in the diets of *Cervus elaphus* with stags having a diet richer in fibre. Moreover, if the rate of movement (steps per minute) is influenced by feeding competition, we would expect higher mobility in males than females due to the wider ranging of males. This was found to be the case in our study.

Food selection by ungulates depends on the ratio of rumino-reticular volume to body weight as well as other morphological characteristics (Hanley, 1982a, b; Hanley and Hanley, 1982). An animal with a relative small rumen is adapted to a diet high in cellular content and/or lignin, typically a diet of young grasses, forbs and browse. Conversely, an animal with a relatively high rumino-reticular volume is adapted to a diet with high cellulose content, such as grasses. In our ibexes the diet of the females was a mixture of browsings and grasses both in winter and spring, probably due to the constraints imposed by the rumino-reticular volume.

Optimal foraging theory (MacArthur and Pianka, 1966; Schoener, 1971; Emlen, 1973) predicts that as the preferred diet becomes scarce and the searching time necessary to procure a sufficient amount of food becomes prohibitively large, an expansion of the diet to include less preferred items occurs. Since forage quality is greatest during the period of most active plant growth (i.e. spring) and least in winter (Hanley, 1982a), a higher rate of movement while foraging may be expected when food is abundant (spring) than when it is scarce (winter). This was observed to be the case for female Spanish ibexes whether they were grazing or browsing. Similarly, Hanley (1982a) observed that travel distance in *Cervus elaphus* and in *Odocoileus hemionus* increased in June when high quality forage was widely and abundantly distributed. Roby and Thing (1985) observed that caribou (*Rangifer*) on poor winter range showed very restricted movements but became more active when winter forage improved in quality.

The advantages of a large group size for predator detection and avoidance, have been demonstrated for ungulates (Berger, 1978; Underwood, 1982; Alados, 1985; Risenhoover & Bailey, 1985), but the tendency for group size to increase is limited by feeding competition, which increases with the group size (Hanley, 1982a; Risenhoover & Bailey, 1985; Stacey, 1986; Watts, 1985). An ibex in a large group is surrounded by competitors and is unable to defend all the high quality food item in its vicinity because confrontation with one competitor would allow a third to appropriate the disputed food. Such competition should also be costly. Hence one would expect the number of steps taken per minute to decrease as group size increases or as nearest neighbour distances to decrease. This trend occurred in our ibexes in most cases studied. However different results were found by Risenhoover & Bailey, 1985 with *Oreamnos americanus*.

We conclude that when food availability is low, due to the time of year, the ibexes tend to reduce their rates of movement when foraging, but when profitable food items are common, they become more mobile, this trend has been observed in monkeys (Harrison, 1983).

The weak social tendencies and low activity levels observed during periods of low food availability (e.g. winter) can be interpreted as

adaptations for reducing energy expenditure in response to low energy assimilation rates (Smith, 1974; Roby and Thing, 1985). Moreover, since the benefit from competition for food is higher when food is abundant than when it is scarce (Brown, 1964), a higher rate of competitive interactions can be expected in spring than in winter. This was the case in our ibexes. Finally we consider that the increase in agonistic displacements made by the adult females is responsible for the increase in competitive interactions recorded.

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