Huemul (*Hippocamelus bisulcus*) sociality at a periglacial site: sexual aggregation and habitat effects on group size

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Abstract: I studied social organisation of the huemul (*Hippocamelus bisulcus*), an Andean deer, during spring in coastal Chile. Analyses are based on individually recognised adults without young of the year. Deer that were not alone generally joined groups containing both sexes, and the proportion of time individuals spent in mixed-sex groups increased with the individual's mean group size. The absence of sexual segregation during spring is unusual among sexually dimorphic ungulates, and possibly reflected little variability in food distribution and (or) sex-specific predation pressure. Group sizes of individuals observed on multiple days increased strongly with distance from rocky slopes, and this relationship appeared to be unaffected by food distribution. These results suggest that the risk of predation, probably from cougars (*Felis concolor*) and (or) human hunters with dogs (*Canis familiaris*), is lower on rocky slopes than in valley-bottom habitats. Group sizes of individuals seen only once, however, were independent of distance from rocky slopes, possibly because these individuals were transients that did not integrate into the social structure of resident deer. The effect of rocky slopes on group sizes of individuals observed on multiple days is more characteristic of mountain Caprinae than of deer. The huemul is endangered, and its extinction could represent a substantial loss in the behavioural diversity of the Cervidae.

Résumé : J'ai étudié l'organisation sociale d'un cervidé des Andes, *Hippocamelus bisulcus*, au cours du printemps, le long de la côte chilienne, par des analyses effectuées sur des adultes reconnus individuellement, sans jeunes de l'année. Les cerfs non solitaires avaient l'habitude de se joindre à des groupes de mâles et de femelles et la proportion du temps que passaient les individus au sein des groupes mixtes augmentait en fonction de la taille moyenne du groupe. L'absence de ségrégation sexuelle au printemps est inhabituelle pour un ongulé à dimorphisme sexuel et reflète probablement la faible variabilité de la répartition de la nourriture et (ou) des pressions de prédation spécifiques au sexe. La taille des groupes d'individus observés durant plusieurs jours augmentait considérablement avec la distance des pentes rocheuses et cette relation semblait indépendante de la répartition de la nourriture. Ces résultats indiquent que les risques de prédation, probablement reliés au Couguar (*Felis concolor*) et (ou) aux chasseurs avec des chiens (*Canis familiaris*), sont moins élevés sur les pentes rocheuses qu'au fond des vallées. La taille des groupes d'individus aperçus une seule fois s'est cependant avérée indépendante de la distance des pentes rocheuses, probablement parce que les individus du groupe étaient de passage et ne se sont pas intégrés à la structure sociale des résidants. L'effet des pentes rocheuses sur la taille des groupes d'individus observés pendant plusieurs jours est plus caractéristique des Caprinae que des Cervidae. Ce cerf est une espèce menacée et sa disparition pourrait constituer une perte substantielle de diversité des comportements chez les cervidés.

[Traduit par la Rédaction]

Introduction

Spatial segregation between the sexes in adults is prevalent among polygynous, sexually dimorphic ungulates. These species generally live in environments where food quality and availability vary throughout the year, and have seasonally defined reproductive cycles. As adults, the sexes tend to associate extensively only during the rut, and segregation is most pronounced during the season of births and early development of the young (review in Main et al. 1996). Although other hypotheses have been proposed, recent field tests suggest that sexual segregation is driven largely by differences in antipredation behaviour and time budgets between the sexes in adults (review in Main et al. 1996; Bleich et al. 1997; Ruckstuhl 1998). Females mainly use habitats where the predation risk is lower because they and their young are more vulnerable to predators than males, and they often do so at the cost of reducing access to the best food. Meanwhile, males primarily use habitats with richer food resources, often at the cost of greater predation risk, so that they can maximise body and antler or horn growth, which ultimately leads to winning more fights and securing more mates during the rut (Berger 1991; review in Main et al.1996; Bleich et al. 1997). In addition, differences in body size between the sexes may cause females to spend more time foraging and walking in search of food than males, making it difficult for the sexes to synchronise their movements and form cohesive groups (Ruckstuhl 1998).

Another feature of the social organisation of ungulates is that group sizes vary with predation risk and habitat. Animals are under lower predation risk when in larger groups

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Fig. 1. An adult female huemul on a cliff at the study site in Fiordo Tempano (Frid 1994). Although the use of steep and continuous cliffs, like the one shown in this photograph, is not uncommon, most rocky slopes where I have seen huemuls consist of 5–10 m high bluffs interspersed with vegetated ledges.
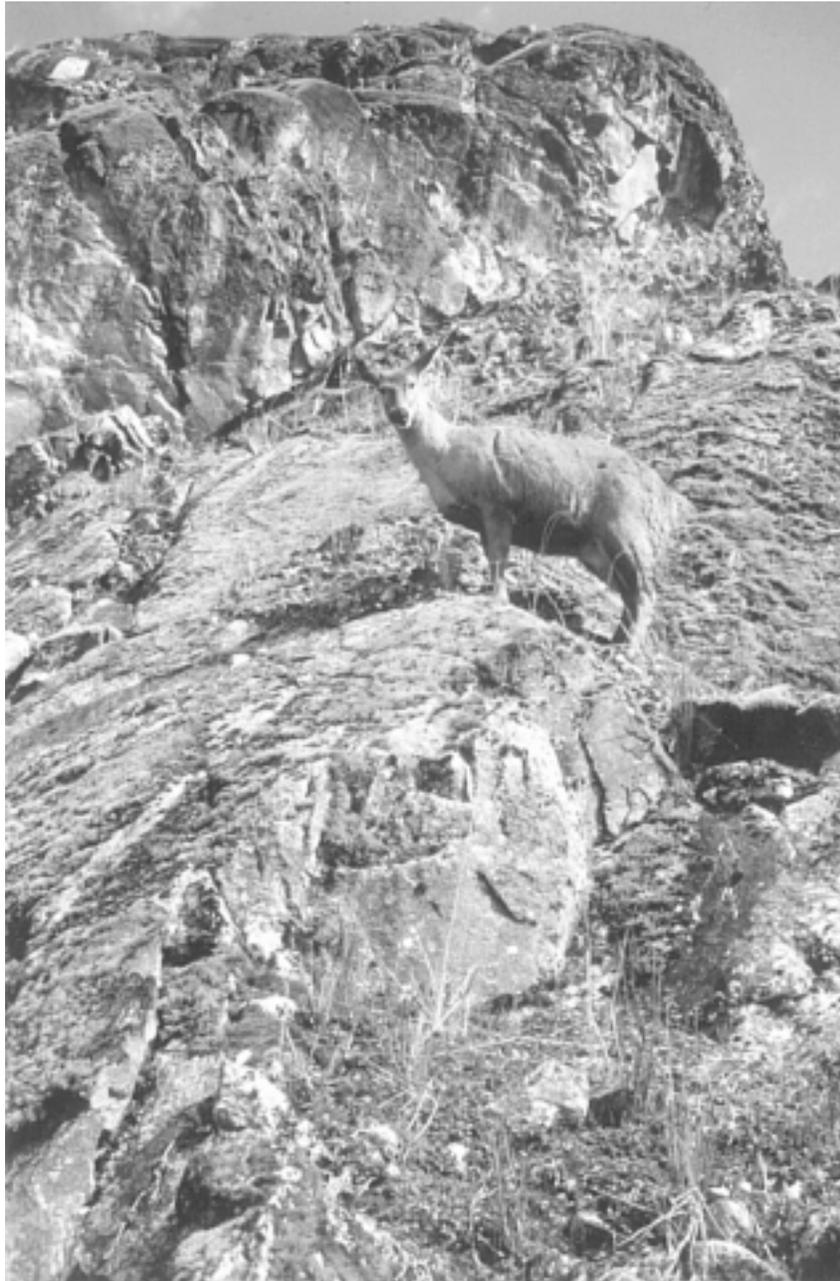
(review in Roberts 1996), and several studies suggest that ungulates in riskier habitats increase group size as an anti-predation strategy (Jarman 1974; Hirth 1977; Risenhoover and Bailey 1985; Warrick and Krausman 1987; Fox et al. 1992; Molvar and Bowyer 1994). Along with predation risk, the distribution of food and obstructive cover may affect variation in group size, and these factors are not mutually exclusive. Large, cohesive groups can form only where food is relatively abundant and (or) contiguous, and in open habitats where group members can maintain contact with each other (Jarman 1974).

Little is known about the social organisation of the huemul (*Hippocamelus bisulcus*), an endangered deer en-

demic to the southern Andes (Povilitis 1979, 1998; Groombridge 1993). Huemuls are medium-sized and sexually dimorphic (Figs. 1 and 2; see also photographs in Frid 1991, 1997*b*), live at temperate (Povilitis 1979, 1998) to subantarctic latitudes (Frid 1994), and appear to be serially polygynous (Povilitis 1985). Povilitis (1983) observed that adult males and females in interior parts of the species' distribution associated in the same groups during and outside the rut. In a previous study, however, I observed huemuls in coastal Chile and recorded sexual segregation by habitat (Frid 1994). Adult females in general, and two females with neonates in particular, spent most of the observation time on rocky slopes, while adult males spent most of the observation

Fig. 2. An adult male (left) and two adult female huemuls foraging about 200 m from rocky slopes (not visible in the photograph) at Estero Bernardo. As is portrayed in this photograph, mixed groups were common during spring, and most deer were very tolerant of observers. Photograph by Jasper Stephens.

time on flat grassland. I observed adult males and females in the same group only twice out of 104 observations of groups (Frid 1994).

Like mountain sheep (*Ovis* sp.), huemuls have short legs and stocky bodies, and are well adapted to climbing steep, rocky slopes (Fig. 1), where they spend substantial amounts of time. However, they also use flat habitats located far from rocky slopes that may or may not have dense vegetation (Fig. 2; Povilitis 1979, 1998; Frid 1994). Mountain sheep are under lower predation risk when on steep, rocky slopes (Murie 1944; Berger 1991; Frid 1997*a*), and it is plausible that huemuls are also safer from predators in this habitat. Predation pressure on adults in my study area likely results from a combination of cougars (*Felis concolor*) and hunters with dogs (*Canis familiaris*). Furthermore, during the Pleistocene, huemuls coexisted with carnivores that are now extinct, and past predation pressure could be influencing current antipredation behaviour (Byers 1997).

I studied huemul social organisation during early spring at a periglacial site on Chile's austral coast. I assessed whether as adults, the sexes were spatially segregated and whether group size increased with distance from rocky slopes. I expected the latter to occur if, like mountain Caprinae (Murie 1944; Berger 1991; Frid 1997*a*), huemuls experience lower predation risk on rocky slopes than in valley-bottom habitats (see Risenhoover and Bailey 1985; Warrick and Krausman 1987; Fox et al. 1992). To gain insight into food effects on group size (Jarman 1974), I analysed how the plant *Gunnera magellanica*, the main spring food at periglacial sites (Frid 1994; A. Frid, unpublished data), is distributed in relation to distance from rocky slopes.

Methods

Study animals, site, and season

Field data were collected from 25 October to 15 November 1995 in a periglacial valley (ca. 48°34–37′S, 73°36–32′W) located at the head of Estero Bernardo, a steep and roadless marine fjord in Bernardo O'Higgins National Park in southern Chile. The huemul is the only large herbivore native to the region. Puerto Edén, the nearest village, is ca. 135 km from the study site. Fieldwork included part of the fawning season (Frid 1994; this study).

The 10.6-km^2 study site is adjacent to the Southern Continental Icecap (one of the largest nonpolar glaciers in the world), and most of the valley bottom is at relatively early successional stages following deglaciation. Except for some fragments, old-growth forests dominated by southern beech (*Nothofagus* sp.) are found mainly on slopes along the valley sides. Except for a small isolated bluff area, all steep rocky slopes (≥30°) are also found along the valley sides. Some of these rocky slopes are covered by tall shrubs (mainly *Pernettya* sp.) and forest fragments, but slopes in the vicinity of the icecap have little shrub or tree cover. The valley bottom is a mixture of patches with tall shrubs (mainly *Pernettya* sp.) and areas with little or no shrub cover. *Gunnera magellanica* was present in all areas where we observed huemuls. Large sections of the valley bottom, however, are covered mainly by moss or cobbles, and *G. magellanica* is scarce or absent there. We rarely saw huemuls using these areas.

Although illegal hunting occurs at Estero Bernardo, this site appears to have the highest concentration of huemuls documented to date anywhere in the species' distribution. I recognised 60 individuals by their natural markings (antler shape in males, markings on the tail and adjacent areas in females). One of my assistants drew detailed sketches of each individual, which we used for reference during surveys (see below). I was still finding new individuals on the last day of the study, indicating that a complete count of deer

was not obtained. The percentage of new individuals identified during a daily survey, however, tended to decrease during the last 9 days of the study, which suggests that I identified most of the individuals using the area. Fawns were very cryptic and I may have missed several.

The population appears to be open, as 51% of individually recognised adults (23 of 45) were identified only once during the study. It is likely that some deer move regularly between Estero Bernardo and valleys at the head of other periglacial fjords, including Fiordo Tempano to the south, where I previously identified 22 huemuls (Frid 1994).

I classified deer by age–sex class following criteria described by Frid (1994) for subadult males and yearling females, and criteria described by Povilitis (1983) for all other age–sex classes. The known population included two neonates, five yearling females, three yearling males, five subadult males (2 years of age), 19 adult males (3 years of age or older), and 26 adult females (2 years of age or older). All data presented here are exclusively from adults without offspring.

Predators

Hunters with dogs were present shortly before I began field-work. Upon arriving at the site, we found recent tracks of humans with at least one dog. Although the Puerto Edén residents I interviewed could not estimate the hunting rate at Estero Bernardo, one hunter claimed that he kills 10–15 huemuls a year. He always uses dogs to corner them.

Cougars are cryptic animals that generally bury their scats (Murie 1954), and coming upon their sign is unlikely during a short-term study. I found no evidence of cougars within the study site, but they were present in the vicinity. According to the two Puerto Edén residents who assisted me with fieldwork (V.O. Muñoz and V.M. Zuñiga, personal communication), during the week prior to our arrival in Estero Bernardo, a cougar killed a domestic pig and a sheep at a homestead ca. 35 km from the edge of my study site. En route to Estero Bernardo I found a cougar scat on Isla Williams, a nearshore island 40 km from the study site. Furthermore, in 1990 I found two cougar scats within 15 km of Estero Bernardo. Thus, the risk from cougars was a plausible factor affecting the antipredation decisions of the deer I studied. Culpeo foxes (*Dusicyon culpaeus*) were also present at the study site, but these small canids are probably predators of fawns only.

Collection of data on grouping patterns

My assistants and I observed deer during daily surveys that followed standard routes. Surveys consisted of 1–3 observers walking in search of deer through all habitats except dense forest, where visibility is poor. Thus, my conclusions cannot be generalised to forests. Survey effort was also limited to ≤200 m above sea level.

We spread survey effort as evenly as possible between areas that were near or on rocky slopes and areas far from these slopes. We accomplished this by walking daily as much of the study area as possible, as well as scanning from vantage points with spotting scopes and (or) binoculars. While some habitats had tall shrubs, gullies, and (or) boulders that could conceal deer, the degree of visual obstruction far from and near to rocky slopes was similar. Thus, although observations may be somewhat biased against habitats with poorer visibility, this bias is likely consistent across distances from rocky slopes.

Upon locating a deer group, we mapped its location and recorded the age–sex class and identity of individuals, as well as the habitat that the group was using and its distance from rocky slopes (see below). In spite of a history of being hunted, most deer were tolerant of us (Fig. 2), and could be observed from <50 m away. A few individuals, however, fled if approached closer than about 200 m.

I considered huemuls to be in the same group if they shared an open space contained by the same bluffs or tall dense vegetation cover, and thus could maintain visual contact with each other (Frid 1997a). Although the definition may be problematic if individuals in the same purported group are widely spaced, this was not the case in my study. During almost all observations, groups consisted of remarkably tight clusters, with the nearest-neighbour distance rarely exceeding 10 m. This tight clustering was not caused by observer disturbance, as groups we observed with spotting scopes from ≥500 away also had very short nearest-neighbour distances. I will refer to groups containing adults of both sexes as mixed groups.

Mapping deer locations and measuring distances to rocky slopes

During surveys we recorded deer locations on maps that we sketched in the field using a 1 : 200 000 nautical chart for distance references. (I lacked aerial photographs and proper maps because I originally intended to work at Fiordo Tempano, but unexpected circumstances in the field forced me to switch study sites; Frid 1997b.) After fieldwork, I obtained a 1 : 60 000 aerial photograph and a 1 : 50 000 topographic map of the site. A cartographer used these and our field sketches to draw a 1 : 28 000 habitat map.

When in the field we used the body lengths of deer as reference points to visually estimate their distance from rocky slopes. If distances were <250 m, I used these estimates for analyses. Otherwise, I re-estimated distances using the 1 : 28 000 habitat map. Given the limited precision of distance estimates, I analysed distance to rocky slopes using the following categories: 0 = 0 m; 1 = 1–10 m; 2 = 11–25 m; 3 = 26–50 m; 4 = 51–100 m; 5 = 101–250 m; 6 = 251–500 m; 7 = 501–1000 m; and 8 = >1000 m.

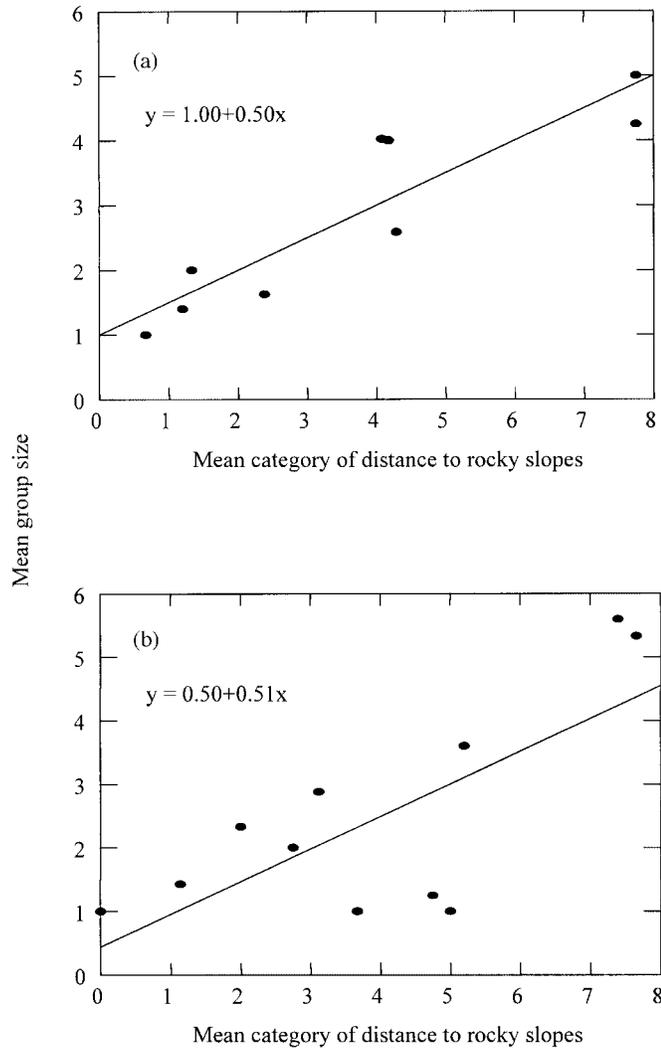### *Gunnera magellanica* measurements

I used an index to quantify the biomass of *G. magellanica* sampled inside 20-m^2 plots. We selected plot locations where we observed deer feeding at least twice, and spread these locations as evenly as possible over the range of distances from rocky slopes used by deer. Plots were divided into 20 subplots formed by a 50 × 20 cm Daubenmire quadrat. (The first two plots we used were an exception and had only 12 subplots.) Spacing between subplots was 5 m between rows and 4 m within rows. In each subplot we estimated the proportion of that ground that *G. magellanica* covered inside the Daubenmire quadrat, and measured the height above ground of the five tallest *G. magellanica* stems. (Exceptions were subplots in which <5 stems were available to be measured.) For each subplot I calculated a biomass index for *G. magellanica* by multiplying the proportion of cover by the average stem height.

Data analysis

Individual deer were the units of analysis. Thus, an observation of a given group provided as many data points as there were individuals that we could identify. For example, if we identified four individuals that were part of a group of six deer, then that observation yielded four data points. I considered observations of the same individuals to be separate repeated measures if they were recorded on different days.

I analysed two data subsets. *Individuals with multiple observations* (9 females, 11 males) included data on individually recognised deer observed on a minimum of 3 days (females: range = 3–17 days, median = 5 days, mean ± SD = 7.3 ± 4.8 days; males: range = 3–17 days, median = 4 days, mean ± SD = 5.9 ± 4.3 days). The second data subset, *individuals with single observations* (15 females, 8 males), included data on individually recognised deer observed on 1 or 2 days only. Eighteen of these deer were observed only once. The remaining five deer were observed on 2 different days, but I analysed only the first observation.
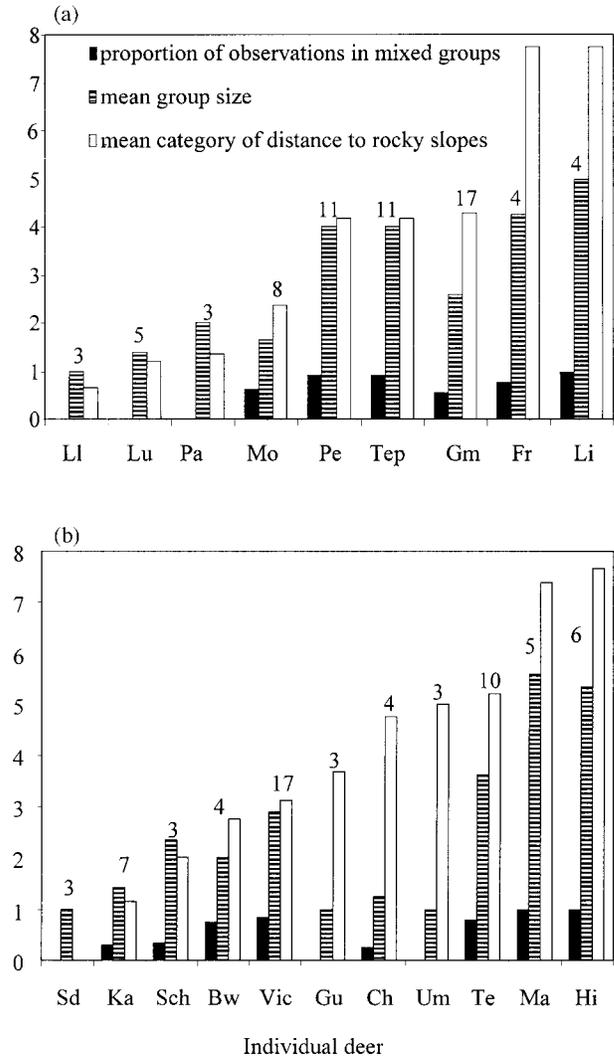
Fig. 3. Relationship between group size and distance to rocky slopes for individually recognised female (*a*) and male (*b*) huemuls observed multiple times. Values are the means of repeated measures for each individual. Distance categories are as follows: 0 = 0 m; 1 = 1–10 m; 2 = 11–25 m; 3 = 26–50 m; 4 = 51–100 m; 5 = 101–250 m; 6 = 251–500 m; 7 = 501–1000 m; and 8 = >1000 m.

Fig. 4. Grouping patterns of individually recognised female (*a*) and male (*b*) huemuls. Numbers above the bars indicate the number of days on which individuals were observed. Letters on the *x* axis identify individual deer. Values on the y axis are for the proportion or mean identified by the legend. For an explanation of distance categories see Fig. 3.

I analysed grouping patterns with linear regression. For these analyses I condensed data for deer with multiple observations into one data point per deer by using the mean value for each individual. Means were based on a wide range of sample sizes per individual (3–17), but sample size was not correlated with the individual's mean group size, mean distance to rocky slopes, or proportion of observations in mixed groups. This was the case for both females (all Pearson's $r \le 0.39$; Bonferroni-corrected P values for the three variable pairs = 1) and males (all Pearson's $r \le 0.52$; Bonferroni-corrected P values for the three variable pairs ≥ 0.6). Thus, variability in sample size did not introduce artifacts.

I used regression (linear or quadratic, depending on scatterplots; Zar 1984) to analyse the relationship between distance from rocky slopes and biomass index of *G. magellanica* at feeding sites chosen by huemuls. The 20-m² plots were my units of analysis, for which I condensed the 12–20 repeated measures into a single data point by averaging the values for subplots. I used the coefficient of vari-

ation (CV) of these means to index patchiness of *G. magellanica* at each 20-m² plot.
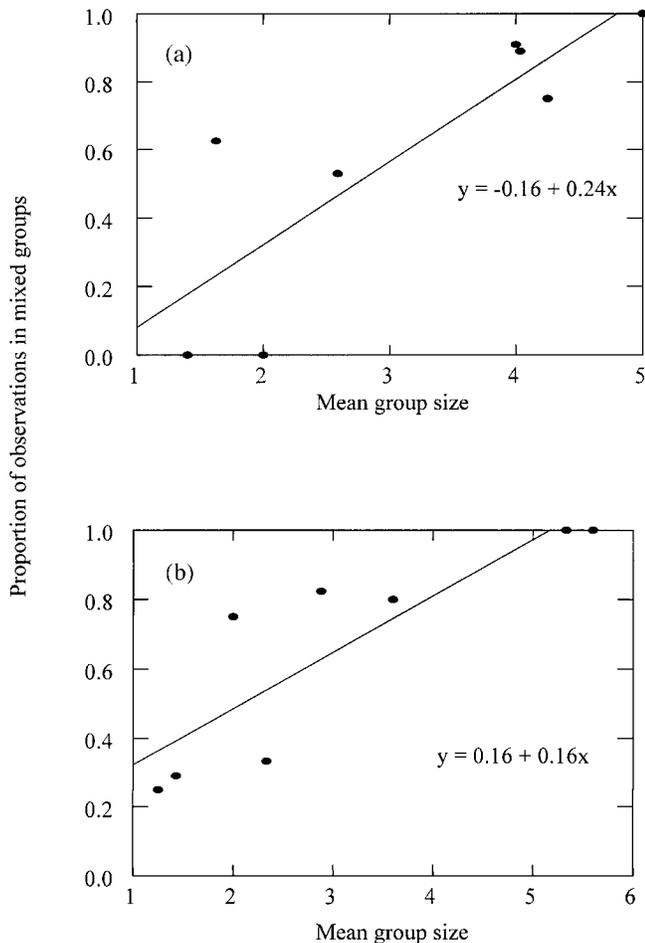
I used standard diagnostics to confirm that data met regression assumptions reasonably well, and log-transformed data when necessary (Zar 1984; Wilkinson et al. 1996). Analyses were performed with SYSTAT 6.0 (SPSS Inc. 1996).

Results

Grouping patterns of individuals with multiple observations

Both males and females were in groups ranging from one to eight deer. The mean group size of individuals observed multiple times did not differ ($t_{18} = 0.53$, $P = 0.6$) between males (2.5 ± 1.7 (mean ± SD); $N = 11$) and females (2.9 ± 1.5; $N = 9$). Groups were generally fluid. Although individuals sometimes remained in the same group for several days,

Fig. 5. Relationship between the proportion of observations of mixed groups (containing adults of both sexes) and mean group size of individually recognised female (*a*) and male (*b*) huemuls observed multiple times. Group sizes are given as the mean of repeated measures for each individual. Analyses exclude individuals with a mean group size of 1.
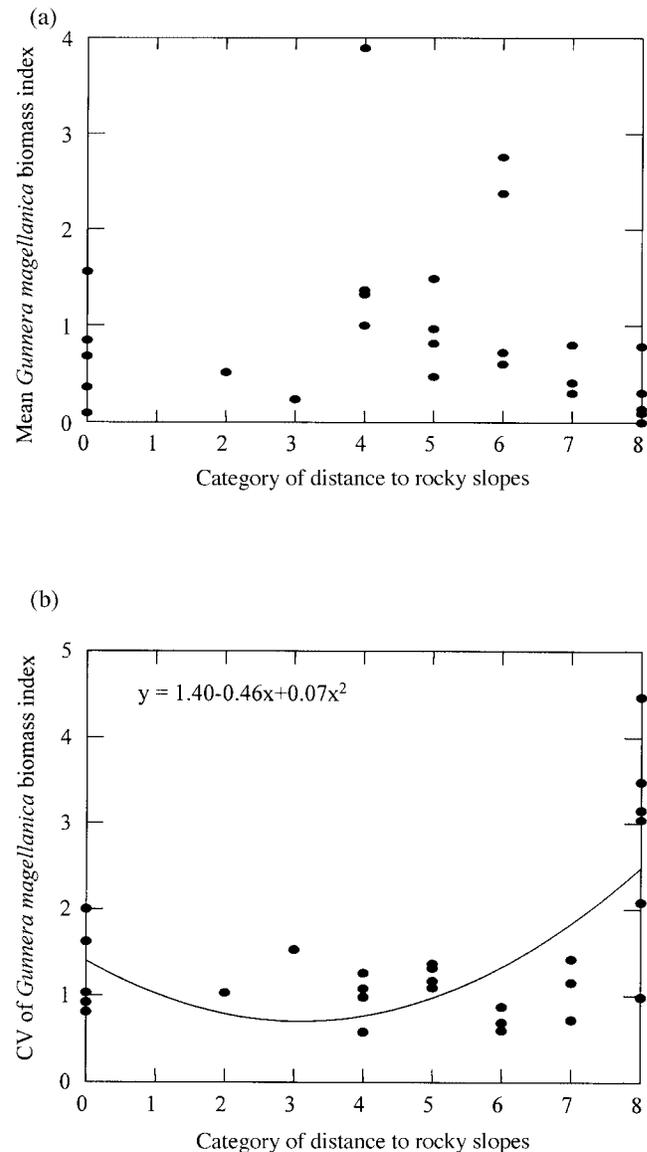
Fig. 6. Relationships between the biomass index of *Gunnera magellanica* and distance to rocky slopes. For an explanation of distance categories see Fig. 3.

almost all deer associated with a completely different set of individuals at some point during the study. The exception were two females who, though part of groups of three to five deer during 10 observations, were together during all of the 11 days on which I observed them.

The mean group size of individuals observed multiple times increased with the individual's mean distance to rocky slopes. This relationship was particularly strong for females ($N = 9$, $F_{[1,7]} = 33.36$, $P < 0.001$, $R^2 = 0.83$; Fig. 3a), but was also substantial for males ($N = 11$, $F_{[1,9]} = 10.35$, $P = 0.01$, $R^2 = 0.54$; Fig. 3b).

For both sexes, inter-individual differences were apparent in distance from rocky slopes and group size. In general, some individuals tended to be alone or in small groups and on or near rocky slopes, while others tended to be in larger groups and to be found at much greater distances from rocky slopes. However, this distinction was clearer for females than for males (Fig. 4).

Adult males and females associated frequently (Fig. 2), and there was a strong tendency for larger groups to be mixed. The proportion of observations in which individuals were seen in mixed groups increased with the mean group

size of individuals (females: $N = 8$, $F_{[1,6]} = 13.89$, $P = 0.01$, $R^2 = 0.70$; males: $N = 8$, $F_{[1,6]} = 16.92$, $P = 0.006$, $R^2 = 0.74$; Fig. 5. Individuals with a mean group size of 1 were excluded from both regressions). Thus, individual differences in group size implied that individuals with a tendency to be in larger groups spent more time with adults of the opposite sex, while individuals that tended to be in smaller groups did not (Fig. 4). This was particularly the case for males, as the only ones who did not form mixed groups were three individuals that were always alone (Fig. 4b). In the case of females that were not always alone, only two of eight individuals did not form mixed groups (Fig. 4a).

Grouping patterns of individuals with single observations

In contrast to individuals observed multiple times, there was no relationship between group size and distance from rocky slopes for individuals with single observations (fe-

males: $N = 15$, $F_{[1,13]} = 2.93$, $P = 0.11$, $R^2 = 0.18$; males: $N = 8$, $F_{[1,6]} = 0.03$, $P = 0.86$, $R^2 = 0.006$. Both regressions are on log-transformed data.). As with individuals observed multiple times, there was a strong tendency for the sexes to aggregate. Although they were alone in 65% of observations (15 out of 23), they were always in mixed groups when in groups of two to four deer ($N = 8$).

Gunnera magellanica in relation to distance from rocky slopes

I found no relationship between the mean biomass index of *G. magellanica* at feeding sites chosen by huemuls and distance from rocky slopes ($N = 28$, $F_{[1,26]} = 0.43$, $P = 0.52$, $R^2 = 0.02$; Fig. 6a). Patchiness of *G. magellanica* (as measured by the CV of the mean biomass index) was similar among feeding sites that were 0–1000 m from rocky slopes, but increased at feeding sites >1 km from rocky slopes ($N = 28$, $F_{[1,26]} = 9.43$, $P < 0.001$, $R^2 = 0.43$ Fig. 6b).

Discussion

Sexual aggregation

Results indicate that as adults, the sexes tended to aggregate during spring. Although sexual aggregation was not absolute, 22 of 24 individuals that were not always alone joined mixed groups at least once during the study (individuals with multiple and single observations were pooled). Furthermore, the proportion of time individuals spent in mixed groups increased with the individual's mean group size. This is unusual among sexually dimorphic ungulates during spring (see Main et al. 1996). Possible, non-mutually exclusive explanations for sexual aggregation include little variability in food distribution (see Oli and Rogers 1996) and perhaps similar predation pressures on males and females. Thus, there may have been no reason for adults without offspring to be sexually segregated.

In contrast, at Fiordo Tempano I found that adult males and females segregated by habitat during spring (Frid 1994). Although social organisation can differ between two populations of the same deer species (Hirth 1977), it is possible that my much smaller sample of adult females at Fiordo Tempano was biased towards pregnant females that were soon to enter the isolation period that typically precedes parturition in ungulates (Lent 1974).

Except for females in late pregnancy or with neonates, sexual aggregation outside the rut might be common among huemuls. Povilitis (1983) reported the occurrence of mixed groups during all seasons except spring in interior parts of the species' distribution. Furthermore, Merkt (1985, 1987) found that during the fawning season for the taruca (*Hippocamelus antisensis*, the only close relative of the huemul), females with neonates or near parturition segregated themselves away from males, but otherwise groups containing adults of both sexes were common year-round.

Predation risk in relation to distance from rocky slopes

For deer of both sexes observed multiple times, there was a strong positive relationship between group size and distance from rocky slopes. This is consistent with observations of bighorn sheep (*Ovis canadensis*; Risenhoover and Bailey 1985; Warrick and Krausman 1987) and ibex (*Capra ibex*

sibirica; Fox et al. 1992), and suggests that huemuls are safer from predators while on rocky slopes.

Predation pressures affecting huemuls are likely to be from a combination of cougars, hunters using dogs to corner deer, and possibly the ghosts of predators past (Byers 1997). Canids are cursorial predators. Given that mountain sheep are under lower predation risk from wolves (*Canis lupus*) or coyotes (*Canis latrans*) while on rocky slopes (Murie 1944; Berger 1991), huemuls are probably safer from dogs while in or near mountainous habitat. The risk from dogs is not new; it preceded European colonisation and the use of rifles, as Kaweshkar natives hunted with dogs (Vega Delgado 1995). Furthermore, during the Pleistocene, huemuls may have been under predation risk from canids now extinct, including the dire wolf (*C. dirus*; Anderson 1984), and past predation pressures could be influencing current anti-predation behaviours (Byers 1997).

I suggest that the risk from cougars was also lower when huemuls were on or near rocky slopes. Cougars are stalking predators and, as Ross et al. (1997, p. 774) argue, "Their most vulnerable prey, therefore, should be solitary animals in habitats that provide stalking cover yet are not dangerous areas in which to engage in a struggle." Ross et al. (1997, p. 774) also argue that "Predation in the precipitous terrain used by bighorn sheep is dangerous to the predator," and have documented a radio-collared cougar falling to his death while attempting to kill a bighorn sheep (Ross et al. 1995). Furthermore, Hornocker (1970) found that bighorn sheep were preyed on by cougars less than other ungulates, such as mule deer and elk, which spend less time on rocky slopes. Areas of the valley bottom that were farthest from rocky slopes and that were used by huemuls met the criteria of Ross et al. (1997) for good places for cougars to hunt. These areas had gullies, boulders, and clumps of tall shrubs that could conceal stalking cougars. When I disturbed huemuls using these areas, the fleeing deer quickly became obscured by habitat features. Not surprisingly, those where the only places where I saw the largest huemul groups.

The possibility that huemuls perceive the predation risk on rocky slopes to be lower is supported by my observations of deer that I disturbed. In 9 out of 12 records in which I disturbed huemuls using the valley bottom, the deer did not stop running until they had climbed a rocky slope. In the remaining three records, the deer stopped running once they entered tall shrubs, which were much closer than the nearest rocky slope.

Although food distribution can also affect group size (Jarman 1974), I found no relationship between distance from rocky slopes and mean biomass index of *G. magellanica* at feeding sites chosen by huemuls. During spring, huemuls ate *G. magellanica* almost exclusively at Estero Bernardo and Fiordo Tempano (Frid 1994; A. Frid, unpublished data). I believe it is unlikely that the distribution of other plants affected group size. The possibility that food distribution did not have a major effect is supported by the maximum group size that I observed, which was only eight deer. It is not uncommon to see mountain sheep groups of that size using food-poor rocky slopes (A. Frid, unpublished data). Furthermore, *G. magellanica* was most patchy at feeding sites located more than 1 km from rocky slopes, where the largest huemul groups were located. Had food distribution been the

main factor driving group size, then the largest huemul groups would have formed where food was most contiguous (Jarman 1974), and this was not the case.

In contrast to individuals observed multiple times, there was no relationship between group size and distance from rocky slopes for individuals with single observations. When in groups of two or more, deer with single observations associated with deer observed multiple times in only two out of eight sightings, suggesting that deer with single observations were only briefly at the study site. Perhaps these individuals were transients that did not integrate into the social structure of the resident deer.

Behavioural diversity and conservation

The strength of my study is that it is based on a reasonably large sample of known individuals living in a relatively undisturbed environment. Its weakness is that it encompasses a short window of time for one population during one season. Still, this represents a major advance in our understanding of huemul behaviour and ecology. The species is little known, and surviving populations could well be impacted substantially by humans before we get a chance to learn much more about huemul social organisation under relatively undisturbed conditions (Frid 1997b; Povilitis 1998).

My results do suggest that long-term studies of huemuls could provide important insights into the evolution of sociality in ungulates. While not unique (e.g., Fox et al. 1992; Oli and Rogers 1996), the species appears to be unusual among sexually dimorphic, polygynous ungulates in not exhibiting spatial segregation between the sexes outside the rut (see Main et al. 1996). My data also suggest that the distribution of rocky slopes affected grouping patterns and likely predation risk, which is more characteristic of mountain Caprinae than of deer (see Risenhoover and Bailey 1985; Warrick and Krausman 1987; Fox et al. 1992). Huemuls, however, also inhabit large islands in the south Chilean archipelago, such as Wellington Island near Puerto Edén (A. Frid, unpublished data), where forest cover is much more extensive and rocky slopes are less common. Social organisation could be driven by very different factors in island populations, which have never been studied. The huemul is endangered (Groombridge 1993), and its extinction could represent a substantial loss in the behavioural diversity of Cervidae.

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