Spacing Patterns within Groups in Vicuñas, in Relation to Sex and Behaviour

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The inter-individual distances between vicuña (Vicugna vicugna) group members were studied in Abrapampa Field Station, Northwestern Argentina. Vicuña social organization is based on family (one male, 3-4 females and calves) and bachelor groups. Spacing patterns between members of family and bachelor groups were studied. Distances between females were usually constant, ranging from two to three meters. Distance between territorial males and their nearest female were always greater than those between females. Males were furthest from their females when they walked and ran, closer when they were alert, and were closest to their females during maintenance activities (grazing and lying down). Distances between bachelors were the shortest. Bachelors stayed closer together when moving and alert than during other activities, reflecting their response to harassment by territorial males. Calves formed "clubs" in which the distances between calves were shorter than the distance between them and the nearest adult.

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Introduction

The spatial relationships and interactions between individuals are two important factors in describing the social organization of wild mammal populations (Crook et al., 1976; Bekoff & Wells, 1986; Berger, 1988). Frequently, female ungulates aggregate to minimize the predation risk to themselves and their offspring (Gosling, 1986).

Ungulates in a social group maintain inter-individual spacing at an intermediate point between an "individual distance", which is the distance that can be maintained without hostility, and a "social distance", which is the maximum distance between individuals to keep group cohesion (Walther, 1977). Space maintenance has been described in a diverse range of species and different interpretations of its selective advantages have been offered, including the minimization of disturbance while feeding, reduction of interference while fleeing from danger, and avoidance of transmission of infectious diseases (Wilson, 1975; Broom, 1981).

In ungulates the distance between the mother and young is often recorded as it is accepted as an indicator of mother-offspring bonding (e.g. Espmark 1971; Clutton-Brock et al., 1982; Crowell-Davis, 1986; Ralls et al., 1987; Alados & Escos, 1988; Richard & Pepin, 1990; Vilá, 1992b). Calves have been classified in accordance with their distance from their mothers as "hiders" or "followers" (Lent, 1974; Leuthold, 1977; Ralls et al., 1986, 1987).

In contrast, little information is available on distances between adult ungulates in groups, especially in relation to different behaviours. Studies have been carried out on gazelles, *Gazella thomsoni*, (Walther, 1977); white tailed deer, *Odocoileus virginianus*, (LaGory et al., 1981) and isards, *Rupicapra pyrenaica*, (Richard & Pepin 1990). Such studies suggest that the mean distance between two animals varies in relation to sex, individual activity and climatic factors (Estes, 1967, 1969; Walther, 1977; LaGory et al., 1981) with the general pattern being that females stay closer together than males. In the red deer, *Cervus elaphus*, on Rhum, unrelated animals remained closer together than related ones and interindividual distances increase with age and density (Albon et al., 1992).

Vicuñas are South American camelids (average weight 45 kg) that inhabit the high grasslands and scrublands of the "Puna" or "Altiplano" region (3200-4900 meters above sea level) of Bolivia, Chile, Peru and Argentina (Koford, 1957; Franklin, 1974). They lack sexual dimorphism, and are obligate drinkers and sedentaries (Franklin, 1974, 1983).

Vicuñas' social organization includes stable family groups with one male, 3-4 females and offspring, and more variably sized groups of bachelor animals (Koford, 1957; Franklin, 1974, 1983; Cajal, 1985; Vilá & Roig, 1992). The males in family groups defend areas all year round, where females and calves live (Koford 1957; Franklin, 1974, 1983). Within one or two weeks of parturition (one calf per partum) females come into oestrus and may copulate. Females nurse while pregnant, and have a gestation period of 350 days and a nursing period of about 6-8 months (Franklin, 1983). Calves tend to form groups that can include animals from neighbouring families (Koford, 1957).

The mating system of the vicuña in Abrapampa includes territoriality as well as female defence (Vilá & Cassini, in press). Territorial males are more aggressive than any other member of the population and males with small families (1-2 females) are less aggressive than males with bigger ones (Vilá, 1992a). Although there is some overlap at the boundaries, most of the territory is used exclusively by the family while the family is present (Vilá, 1990).

Females graze during most of the daylight period and feed significantly more than males (Vilá & Cassini, in press). In summer they feed principally early in the morning and late in the afternoon, and drink at midday (Vilá & Cassini, 1993).

The objective of this work is to describe the inter-individual spatial relationships in the vicuña and to test the following predictions: (1) females maintain cohesion and stay closer together while carrying out activities that increase susceptibility to predation (e.g. lying down); (2) females maintain greater interindividual distances while grazing than not grazing, and in bigger than smaller groups due to competition for food; (3) bachelors have the tightest groups due to harassment by territorial males; (4) family males are more distant from females in bigger family groups and in "territorial behaviours" (walking, running and

Table 1. General mean distances (and SE) between vicuñas. Distance is measured in "Vicuñas length" of an adult female, approximately one meter. The statistical treatment (with the calculation of distances/day) is in the text.

		mean		
		distance	SE	n
FAMILY	female-female	2.62	0.045	3085
GROUPS	male-female	8.63	0.21	1269
	calf-adult (single calf in group)	2.93	0.21	469
	calf-adult (calves in "club")	6.72	0.77	114
BACHELOR				
GROUPS	bachelor-bachelor	1.73	0.02	3646

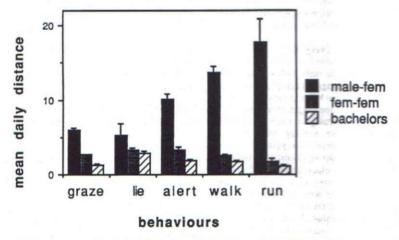


Fig. 1. Mean daily distances (female-female, male-female and between bachelors) (and SE) in relation with activities.

nificant results (with a 95 % significance value): (a) The distance between females was smaller while they were running, (b) the distance between the male and his females was smallest when he was grazing or lying down, intermediate when he was standing alert and greatest when he walked and ran (i.e., they ran and walked alone), (c) The bachelors were closer together when moving, at an intermediate distance while grazing or standing alert and, furthest apart when they were lying down. There were differences depending on the presence of one or several calves in the group. In groups with more than one calf, in 62 % of the scans the calves formed "clubs" and in 90.1 % of the scans they were performing the same activity. The distance between the calves in a "club" and the nearest adult was greater than the calf-adult distance in groups with only one calf (t = 4.77, df = 81, p < 0.001).

Discussion

Distances between individuals varied in relation to sex and behaviour. Female vicuñas formed stable groups that maintained a spatial structure and only when running females were closer together. The average distance between females in vicuñas (2.6 m) is similar to that found between Thomson's gazelles where more than 75 % of the recordings were 0-3 m (Walther, 1977), the white tailed deer where 70 % of the recording were less than 5 meters (Lagory et al., 1981) and smaller than the median distance in female isards (between 4-10 m) (Richard & Pepin, 1990). The female-female distance was not affected by feeding. Although there are advantages to grazing in a group, for example the "enhanced sward quality due to the facilitatory effects of prior grazing" (Gosling, 1986), several studies have found competition among ungulate females grazing (Clutton-Brock et al., 1976; Wells & Goldschmidt, 1979; Rutberg, 1986; Rutberg & Greenberg, 1990; Thouless, 1990). Aggression occurs between female vicuñas (Vilá, 1992), but could not be detected in the spacing pattern of the whole group while feeding. In Thomson's gazelles, however, females were more distant while grazing than resting or moving (Walther, 1977).

Although the natural predator of adult vicuñas, the puma Felis concolor, is extinct in the area, calves can be killed by the "zorro" Dusicyon culpaeus and adults and calves may be attacked by feral dogs. The well known antipredator advantage of forming groups in the plains antelopes (Gosling 1986) is therefore also valid in this species.

Males were always peripheral to their group of females: when they grazed or laid down, they were approximately six meters from their females, but when they were standing alert they were further apart. Males walked and ran alone to the periphery of the area.

As in most of the gregarious ungulates, bachelors form fission-fusion groups with a variable structure of age, which split and reform rapidly (Estes, 1974, Gosling, 1986). Vicuñas have been compared with equids as they share the lack of sexual dimorphism and live year round in small family groups. However in most of the equids, the dominant male tolerates bachelors and satellite males [zebras and wild asses (Klingel, 1974), and wild horses (Berger, 1986)]. In comparison, male vicuñas exhibit a strong intolerance which forces bachelors to form very tight groups, staying less than two meters apart. Bachelors in the observation area were often chased by territorial males. They could remain in the territory of a family group only when the family had left the area to drink. Only in those places (and in marginal areas out of sight) could bachelors perform grazing and lying down with more distance between them.

In African antelopes, members of bachelor herds maintain greater inter-individual distances than do females. This has been interpreted as a consequence of the greater male aggressiveness (Estes, 1974; Monfort-Braharn, 1975). This may also be the case when bachelor groups of vicuñas are in the marginal areas where there is less harassment.

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