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DO ISARD FEMALES ASSOCIATE IN WINTER ON THE BASIS OF SUMMER BONDS?

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Abstract

In the Cauterets Valley (Pyrenees National Park), isard (*Rupicapra pyrenaica*) females winter in small spatial units where they live in groups of changing composition. These winter spatial units, however, can include both all-year round resident females and migrant females summering in distant higher-elevation ranges to which they are faithful year after year. We measured the level of association between marked females within winter units. Similar level of association was found among both resident and migrant females using the same summer range. In contrast, association indexes of females inhabiting the same winter unit but distinct summer ranges were lower. These results suggest that association in isard females involves a mechanism of discrimination of familiar companions or of individual recognition. It is proposed that avoidance of unfamiliar conspecifics and/or attraction to a familiar individual may contribute to fine-scale spatial organisation in social ungulates.

Key words: Isard, winter, Pyrenees National Park, social organization, ungulates.

Resumen

¿Se asocian las hembras de rebeco en invierno en fucnción de los vínculos estivales?

En el Valle de Cauterets (Parque Nacional de los Pirineos) las hembras de rebeco (*Rupicapra pyrenaica*) pasan el invierno en pequeños territorios donde viven en grupos de composición variada. Estos territorios invernales, sin embargo, suelen ser ocupados por hembras que viven en él todo el año, así como por hembras emigrantes que ocupan en verano territorios más elevados, y a los que son fieles año tras año. En este trabajo, se ha medido el nivel de asociación entre hembras, usando animales marcados. El nivel de asociación es similar entre aquellas hembras residentes o migrantes que usan el mismo territorio de verano. Sin embargo, la asociación es menor entre aquellas hembras que utilizan un mismo territorio de invierno pero que pasan el verano en zonas diferentes. Estos resultados sugieren que las hembras de rebeco muestran mecanismos para discriminar a los compañeros o mecanismos de reconocimiento individual. Se propone que evitar acercarse a desconocidos y/o la atracción de familiares, puede contribuir a una organización a fina escala en ungulados sociales.

Palabras clave: Rebeco, invierno, Parque Nacional de los Pirineos, organización social ungulados.

Introduction

Numerous species of large mammalian herbivores live in short-lasting groups that often merge and split up over the course of the day (Murray 1981, Clutton-Brock *et al*. 1982, Schaal 1982, Lott & Minta 1983, Southwell 1984, Fichter 1987, Barrette 1991, Estes 1991, Bekenov *et al*. 1998, Pays *et al*. 2007, Pépin & Gerard 2008). It was concluded that animals associate at random (Hillman 1987, Lott & Minta 1983). On the other hand, gregarious species with complex intra-specific communication patterns are likely to have the ability to discriminate between or to categorize conspecifics (Veissier *et al.* 1998), as proved by recent studies on social networks in mammals (*e.g*. Wey *et al*. 2008). However, there is growing evidence that preferential associations occur between mother and daughters (Green *et al.* 1989, Le Pendu *et al.* 1995) or relatives (Halpin 1991, Cassinello & Calabuig 2008), which may lead to fine-scale structuring of the population (Nituch *et al.* 2008, Gerard & Richard-Hansen 1992, Le Pendu *et al.* 1995, Miller *et al*. 2010). Individuals from distinct home ranges or raised separately avoid mixing or form labile groups (Lawrence 1990), which also suggests that familiarity contributes to group formation (Stookey & Gonyou 1998, Komdeur *et al*. 2004, Cheetham *et al*. 2008). In the ibex (*Capra ibex*), individuals have also been shown to associate more than expected at random (Villaret & Bon 1998).

We already found that isard (*Rupicapra pyrenaica*) females are faithful over the years to their seasonal ranges in one population of the French Pyrenees (Crampe *et al*. 2007). This species lives in flexible groups but females' philopatry could lead them to associate more with related than unrelated conspecifics. Long-term monitoring of marked individuals revealed two patterns of space use. Part of the females (sedentary) use summer and winter ranges close together whereas the other part (migrant) emigrate from the winter range to join more distant summer ranges at higher elevations. Because winter grounds are limited, sedentary and migrant animals may co-occur in the same range from autumn to spring (Crampe *et al.* 2007). By using the values of dyadic association recorded inside seven winter spatial units, we assessed the level of association between

females according to their space use patterns. We expected (i) association to be lower among females summering in separate grounds than among animals summering in the same range. Because associations are flexible and migration movements increase the probability of group fission (Fancy *et al.* 1990), we also hypothesized that ii) the bonds should be less perennial among migrant than among sedentary females. Accordingly, the association indices should be higher among sedentary than among migrant females.

Study Area and Population

The study was carried out in the Cauterets valley (42°53' N, 0°06' W; Figure 1) in an area encompassing *ca*. 10,000 ha, with elevation ranging from 890 to 3,298 m and *ca*. 50% of the area above 2,000 m. Climate is oceanic and mountainous with annual temperatures averaging 7.5°C and annual precipitation 1,340 mm at 1,000 m (the snow layer can reach 600 cm at 1,850 m in winter). Vegetation consisted mainly of meadows (*Festuca eskia* Ramond ex DC, *Nardus stricta* L.) on slopes with interspersed cliffs and screes. Forests were mainly composed of pines (*Pinus sylvestris* L., *P. uncinata* Ramond ex DC) and firs (*Abies alba* Mill.) locally mixed with beech (*Fagus sylvatica* L.) with a timberline occurring at *ca*. 2,200 m.

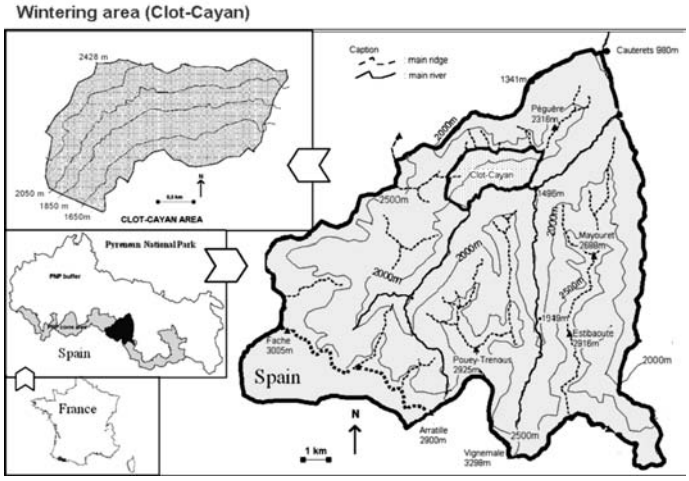

Figure 1. Study area.

The isard population studied has been protected since 1967. During the study, population density reached about 10 animals/km² in summer, and 80 animals/km² in winter in the main wintering area, 'Clot Cayan', a south-facing slope extending over *ca*. 370 ha, where the data were collected.

No large predators were present, although golden eagle (*Aquila chrysaetos* L., 1758) and red fox (*Vulpes vulpes* L., 1758) could opportunistically kill neonates or adults "crawling" in heavy snow (J.-P. Crampe, pers. obs.).

Methods

From 1992 to 2002, 119 females (<1-23 years old at capture) were fitted with coloured collars and ear tags. Individual age was estimated through horn rings and tooth wear for animals ≤4 years (Schröder & von Elsner-Schack 1985). The mean age at capture was 6 years (range 1-17) and the period of monitoring averaged 4.8 ± 2.7 years (± SD; range <1-11).

Field surveys were performed along standardized transects from 1993 to 2002 using binoculars (10×40) and telescopes (30×75) to locate and identify the marked isards. One of us (J.-P.C.) collected winter observations during 1–2 weekly ground surveys in Clot Cayan where all marked females wintered. The protocol was devised in order to avoid multiple counts of the same groups at a daily scale. Noticeably, all females captured in the wintering area used this same area during the whole study period whatever their spatial status, resident or migrant. Also no females were found to change spatial status (Crampe *et al.* 2007).

We identified two periods defined by the movement schedule of migrant females. The summer (May to October) begins when females leave the winter range (Clot Cayan, Figure 1), and the winter (November to April, i.e. the snowy period) when females return to it. The birth period extends from mid-May through June.

Among the 119 marked females, 62 were frequently observed from 1993 to 2002. The mean (±SD) number of groups observed annually was 1048 ± 523 groups. The mean group size recorded (±SD) was 3.8 ± 3.98 individuals, including alone animals. Groups were structured by stable associations among specific individuals, possibly indicating long-lasting relationships among female

kin, as the persistent association between some marked grand mother, mother and daughter triads along years suggests.

Arithmetic centres of females' locations in winter allowed seven spatial units to be distinguished in Clot Cayan (Crampe *et al.* 2007) (Figure 2). The units may include only one (i.e. Uw5, Uw7, Uw9) or the two spatial phenotypes (i.e. Uw2, Uw3, Uw4).

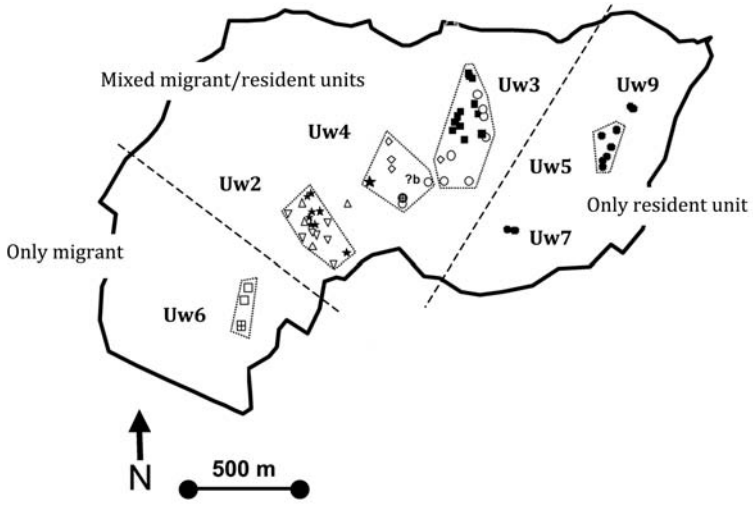

Figure 2. Delimitation of winter units (Uw2 to Uw7) including the position of arithmetic mean of winter locations of 62 marked females (black symbols: resident females; empty symbols: migrant females) (adapted from Crampe *et al.* 2007). Some winter units were inhabited only by resident or by migrant females whereas others were used by females of both spatial statuses.

We considered all the possible dyads of contemporaneous females inside each unit during the nine winters, and quantified their levels of association. The data were restricted to females ≥ 1 year in order to avoid the close link between females and their offspring, which would have biased the data toward high values. We used a modification of the simple ratio association index (Aycrigg & Porter 1997),

$$AI = 2N_{AB} / (N_A + N_B)$$

where N_{AB} is the total number of times individuals A and B were seen in the same group, and N_A (N_B) the total number of times A (B) was seen in the course of the winters during which both individuals were contemporaneous.

Four basic dyad types were distinguished within units: resident - resident (RR); migrant - resident (MR); migrants using the same summer range (sMM); migrants using different summer ranges (dMM).

Association indexes are not independent within a given unit: two animals that are often together necessarily exhibit similar patterns of association with other individuals. Accordingly, statistical analyses were only performed using mean association index per dyad type and unit. The means obtained were logit-transformed before computing ANOVA models (Table 1). The logit-transformed mean association index was considered as the dependent variable, and the winter unit (Uw2 to Uw7, Uw9), the dyad type (RR, RM, sMM, dMM), and the summer range (same or different), as independent/fixed factors. In models m1, m2, and m3, all winter units were considered (five levels); in models m4, m5, and m6, winter units were pooled except Uw3 (two levels); in models m7, m8 and m9, all the winter units were pooled. In models m1, m4, and m7, the four dyad types were considered. In models m2, m5, and m8, we only distinguished the dyads of females that used the same summer range from those for which it was untrue (i.e. RR and MM dyads vs MR and dMM dyads). In models m3, m6, and m9, dyad types were not considered. The relevancy of the models was assessed using the Akaike information criterion (AIC), an estimate for the relative information loss from the original data set and the parsimony rule, i.e. preference for the simplest model, the one with the lowest number of variables (Burnham & Anderson 2002). Statistical computations were performed using R software (R Development Core Team 2005).

Results

Association indices varied substantially when considering all pairwise values. The most parsimonious model (m5) is the one for which winter units Uw3 were considered apart from others, and two types of dyads were included, those that used the same summer ranges and those that did not (Table 1). Females within

winter unit Uw3 tended to associate less frequently than within the other units. Females using the same summer range (MM and RR dyads) tended to associate in winter units more often than females using different summer ranges (RM and dMM dyads; Figure 3). Moreover, dyads of residents (RR), and dyads of migrants using the same summer high-elevation range (MM), exhibited similar association levels (model m4: t= 1.18; P> 0.2) although most of the higher values of association index were exhibited by MM dyads in all units (Figure 3).

TABLE 1
AIC values of the fitted ANOVA models. Selected model is given in bold. Model m9 is the null model (no difference between dyad types and no difference between units).

Models	df	AIC	ΔAIC
m1: logit(mean index) ~ basic dyad type + unit	11	15.92	0.95
m2: logit(mean index) ~ same (vs diff) summer range + unit	9	13.98	-0.99
m3: logit(mean index) ~ unit	8	28.03	13.06
m4: logit(mean index) ~ basic dyad type + unit Uw3 (vs other)	6	16.99	2.02
m5: logit(mean index) ~ same (vs diff) summer range + unit Uw3 (vs other)	4	14.97	0.00
m6: logit(mean index) ~ unit Uw3 (vs other)	3	24.62	9.65
m7: logit(mean index) ~ basic dyad type	5	37.67	22.70
m8: logit(mean index) ~ same (vs diff) summer range	3	33.95	18.98
m9: logit(mean index) ~ 1	2	37.24	22.27

DISCUSSION

The level of association between females inside each winter unit was low to moderate for most of the pairs, and characteristic of open societies with numerous fission/fusion events (Murray 1982, Cross *et al.* 2005). However, as expected (prediction i), the strength of the bond depends on summer space use: females sharing the same summer range tended to associate more frequently than those summering in distinct ranges. It is unlikely that simple attraction to a common range explains these results, because we would expect similar levels of association among females irrespective of their summer origin. Preferential

association among females summering together when wintering with females coming from distinct summer ranges potentially reflects avoidance of unfamiliar individuals. Alternatively, social affinity may result from early social experience in life or recurrent meeting promoting familiarity and association (Millspaugh *et al.* 2004). In this latter case, females would be capable of social or/and individual recognition. Moreover, agonistic interactions exchanged between females just after coming from distinct summer ranges when they meet on winter grounds (J.P. Crampe, pers. obs.) could strengthen the cohesion, at least spatial, among familiar females (Geffen *et al.* 1999, Lesage *et al.* 2000).

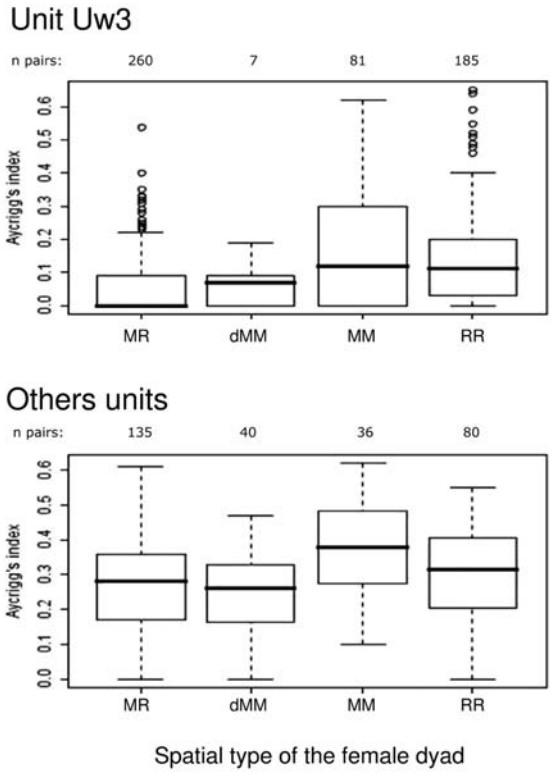

Figure 3. Box plot of the distribution of the association index according the type of female dyad. MR: migrant - resident; dMM: migrants using different summer ranges; MM: migrants using the same summer range; RR: resident - resident. The plain diamonds correspond to values predicted by the ANOVA model m5 (see Table 1).

In contrast to our second prediction (ii), association values within winter units were not significantly influenced by the spatial status (resident vs. migrant) of isard females. Instead, migrant females (MM) tended to associate more than residents, and expressed most of the highest values of association index. Contrary to what was expected, social familiarity and cohesion might be reinforced during coordinated movements as reported for immigrant dolphins (Karezmarski *et al.* 2009) and white-tailed deer (Comer *et al*. 2005). In our study, females using the same summer unit were occasionally seen to migrate as a single group (J.-P.C.).

The most parsimonious model (i.e. m5) revealed lower association indices in Uw3 winter unit than in the others. As observed by Comer *et al.* (2005) and Mathews & Porter (1993) for white-tailed deer, when many matriarchal social groups are present and not geographically independent, i.e. in groups with overlapping home-ranges, the probability that in the same spatial unit, females show a temporal shift between neighbouring groups is increased. This mixing could explain the low values of the median association index in this spatial unit, whatever the type of dyad. Although this is somewhat contradictory with the existence of agonistic interactions between members of neighbouring groups, the latter trend could be restricted to the first meetings, allowing further temporal mixing.

Faithfulness to seasonal range clearly contributes to the non-random spatial distribution of female isards (Crampe *et al.* 2007). Our results additionally suggest that avoidance of unfamiliar conspecifics and/or attraction to familiar individuals may contribute to a fine-scale spatial organisation as found in the Sea lion (Wolf & Trillmich 2007). Such structuring could even appear at a genetic level as proved in red deer (*Cervus elaphus*) (Nussey *et al*. 2005) and captive aoudad (*Ammotragus lervia*) at rest (Casinnello & Calabuig 2008).

Indeed, social bonding among animals of the same sex is known to act against dispersal of that sex. Individuals could benefit from kin cooperation to acquire resources (Silk 2007), to limit predation risks (Lawson *et al.* 2007) and even to favour acclimatization in the case of translocation (Pinter-Wollman *et al.* 2009). While a number of studies have focused on age or sex in dispersal behaviour, comprehensive treatment is still lacking for the behavioural traits

that characterize the different spatial phenotypes present in a population. Growing evidence that social experience has a significant influence on the spatial dynamics of populations should promote individual-based studies of social ungulates.

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