



REVIEW

Mountain ungulate mating systems: patterns and processes

Luca CORLATTI*  *Chair of Wildlife Ecology and Management, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany and Stelvio National Park, Via De Simoni 42, 23032 Bormio, Italy. Email: luca.corlatti@wildlife.uni-freiburg.de*

Sandro LOVARI  *Department of Life Sciences, University of Siena, Via P.A. Mattioli 4, 53100 Siena, Italy and Maremma Natural History Museum, Strada Corsini 5, 58100 Grosseto, Italy. Email: sandro.lovari@gmail.com*

Keywords

alternative reproductive tactics, Caprinae, habitat, reproductive behaviour, sexual dimorphism, sexual selection, social behaviour

*Correspondence

Received: 2 March 2023
Accepted: 26 April 2023
Editor: DR

doi: 10.1111/mam.12319

ABSTRACT

1. Mountain ungulates of the subfamily Caprinae, including wild sheep, goats and goat-antelopes, show remarkable interspecific diversity in habitat preferences, social organisation and morphological features. We review how this diversity relates to their mating behaviour.
2. After introducing the ecology of mating systems and the evolution of the Caprinae, we investigate the pairwise, sequential relationships between habitat preferences, social behaviour, level of polygyny, and morphological features, and discuss the ecological processes underlying the patterns of mate monopolisation and acquisition.
3. From forest-dwelling, solitary, monogamous and monomorphic goat-antelopes, to highly dimorphic, polygynous and social wild sheep and goats inhabiting open landscapes, mountain ungulates reveal a close relationship between habitat openness and sexual dimorphism, through the level of sociality and that of mate monopolisation.
4. Although over the last few decades some information has been collected on the biology of Caprinae, our understanding of determinants of their mating systems is still hampered by limited data to estimate opportunities for sexual selection, as well as uncertainties over the occurrence and maintenance of alternative reproductive tactics, and lack of information on female mate choice.
5. The study of mating systems and that of the factors influencing them play a key role from an evolutionary and conservation standpoint. This is relevant to the Caprinae, whose main habitat is expected to be strongly affected by the ongoing climatic change, with potential effects on the phenology of their mating systems, and whose economic value is relevant for consumptive and nonconsumptive uses. A better understanding of the diversity and ecology of mating systems will require a wealth of additional field observations on male and female behaviour, as well as genetic assessments of reproductive success.

INTRODUCTION

Krebs and Davies (1987) wrote that “A powerful method for studying adaptation is to compare groups of related species and attempt to find out exactly how differences in their behaviour reflect differences in ecology”. In fact, a number of studies have been published based on applying the so-called comparative approach to groups ranging from amphibians (Sullivan et al. 1995)

and birds (Crook 1964, Owens & Bennett 1997) to primates (Clutton-Brock & Harvey 1977, Goldizen 1988). Most of these studies have dealt with species from the Tropics, for which seasonality of resources is relatively modest compared to that for species living at greater latitudes, especially on mountains. As for bovids (Mammalia: Bovidae), also the seminal work by Jarman (1974) concerned mainly the African antelopes

of plains and hills, in the Tropical belt. With the partial exception of Jarman (1983), to our knowledge, no comparative paper has been published yet on a group of species characterised by occurring in highly seasonal habitats, with strong fluctuations of resources, such as mountains, which should exacerbate interspecific competition and promote adaptations.

Mountain ungulates are defined as a group of Artiodactyl species showing behavioural, physiological and morphologic adaptations to life on strongly seasonal, steep, rocky habitats, such as those present on mountains. They mainly include wild sheep, wild goats and goat-antelopes (Bovidae: Caprinae, a monophyletic subfamily; Lovari et al. 2020). Mountain ungulates may be forest resource-defenders that monopolise a small, food-rich area against conspecifics (e.g. *Capricornis* spp.). Other taxa (e.g. *Pseudois nayaur*, *Capra* spp., *Ovis* spp.) group together into herds and roam freely over larger, relatively less nutritious areas (Schaller 1977). Mountain ungulates, especially Caprinae, show a remarkable diversity of social organisation and morphological adaptations, thus offering the opportunity to compare and test the insights into sociality and mating systems developed by Jarman (1974) from Tropical antelopes. Furthermore, within mountain ungulates, some Caprinae are prized 'trophy' game animals for human hunters, because of the often spectacular male horns, which have evolved to assess dominance in ritualised fights and achieve mating rights (Coltman et al. 2002, Bro-Jørgensen 2007). In fact, insights into the behavioural mechanisms acting on male sexual dimorphism can provide important information to avoid anti-Darwinian effects of hunting regimes on hunted populations (e.g. Festa-Bianchet et al. 2014, Festa-Bianchet 2017).

Over the past few decades, the number of publications on Caprinae has sharply increased (cf. Corlatti et al. 2022a), providing new data on habitat preferences, social behaviour, reproduction and morphology. Building on the ideas of Schaller, Geist and Jarman, we provide an updated synthesis on the patterns and processes of Caprinae mating systems. We first introduce mating systems, their classification, ecology and diversity, then we outline the evolutionary history of Caprinae. Next, we provide the methods and results of our synthesis of species-specific patterns in terms of habitat preferences, social behaviour, mating systems and morphology, investigate their relationships, and discuss the ecological processes underlying the diversity in the number of mates and in the form of mate acquisition within the Caprinae.

Mating systems: classification, ecology and diversity

Mating systems describe who mates with whom, and when (Davies et al. 2012, Snook 2017). In animals, this entails the description of the social relationships between sexual partners in a given time period (i.e. the mating season), including both the number of mates acquired and the form of mate acquisition (cf. Emlen & Oring 1977), so a more complete definition of mating system may be "the description of who mates with whom, how, and when". These relationships can be complex and, over time, a number of classifications have been proposed, often lacking a common terminology (Shuster & Wade 2003, Snook 2017). Unambiguous definitions are nonetheless necessary to avoid misinterpretations, and we will follow the classification proposed in Table 1 based on number

Table 1. Classification of the Caprinae mating systems used in this review, in terms of number of mates (level of mate monopolisation), form of mate acquisition, and time period (number of breeding seasons)

Level of mate monopolisation	
Monogamy	An individual restricts matings to one partner
Polygamy	Males mate with several females (polygyny), or females mate with several males (polyandry)
Promiscuity	Both males and females mate with multiple partners and there is no pair-bond
Form of mate acquisition	
Female-guarding polygyny	A male seeks, associates with or guards individual females, but he does not defend ranges, or groups, or a territory; this may be realised through: 'tending', which entails the formation of consort pairs, where a male courts and defends one oestrous female at a time; 'coursing', which entails temporary association to individual females by disruption of existing pairs; 'blocking', which entails temporary association to individual females by preventing them to move away (cf. Bowyer et al. 2020); or 'sneaking', which entails temporary association with individual females by kleptogamy, i.e., stealing mates when the consort male is distracted (Dawkins & Krebs 1978)
Group-guarding polygyny	A male defends a group of females from intruding males
Range-guarding polygyny	A male defends a territory or a range that is larger than female ranges
Site-guarding polygyny	A male defends a mating territory that is smaller than female ranges and that contains resources attractive to females (resource-based territories), or males defend small, clustered territories which do not contain resources (leks)
Number of breeding seasons	
One breeding season	Relationships between sexual partners are considered within one breeding season only, not over multiple seasons

of mates, or level of mate monopolisation ('who mates with whom'), form of mate acquisition ('how') and number of breeding seasons ('when'). Other classifications exist (cf. Shuster & Wade 2003, Clutton-Brock 2016), but the one employed here is widely accepted and appears well-suited to mountain ungulates.

Mating systems are not fixed characteristics of species (Clutton-Brock 1989) and, despite the practical value of the simple framework proposed in Table 1, they may vary within and between populations in response to social and environmental factors (Lott 1991). Multiple indices have been developed to quantify variation in mate monopolisation, including operational sex ratio (the ratio of the number of mating males to the number of sexually receptive females), Bateman gradient (the slope of the least-squares regression of reproductive success on mating success), and the opportunity for sexual selection index I_{mates} (the variance in number of mates per male divided by the squared average number of mates per male, a dimensionless index that reflects the potential strength of sexual selection proposed by Crow 1958, Jones 2009). Shuster and Wade (2003) showed that I_{mates} is related to the spatial and temporal mean crowding of receptive females, in line with Emlen and Oring (1977), who provided a general scheme where the degree of mate monopolisation is governed by the spatial distribution of resources and the temporal availability of mates. Accordingly, as mating systems are related to the intensity of sexual selection (Shuster 2009), I_{mates} can be used to provide a quantitative description of mating systems (Shuster & Wade 2003, Snook 2017). With values of I_{mates} close to 0, males will have similar mating success, typical of monogamous mating systems; with large values of I_{mates} , only a few males will actually mate, thereby leading to highly polygynous mating systems. Although I_{mates} , as such, does not provide direct information on the form of mate acquisition, it offers advantages over verbal descriptions, as it allows a quantitative assessment of mating system variations in response to different factors.

Notably, skew in mating success (increasing value of I_{mates}) is expected to favour the emergence of different mating phenotypes (Shuster & Wade 2003, Shuster et al. 2019). Such discrete variations, known as alternative reproductive tactics (ARTs), reflect alternative forms of mate acquisition (Taborsky et al. 2008). In the attempt to achieve reproductive success, mating systems may thus vary widely, both within and between populations, and several forms of mate acquisition can coexist within the same species. For example, individuals of a given species may adopt different forms of polygyny, or of female-guarding polygyny. ARTs can occur simultaneously or sequentially, so that in a population different tactics can be adopted by different individuals, or the same individual

can switch between tactics over time, or both (Taborsky et al. 2008). The maintenance of alternative phenotypes can be favoured by frequency-dependent selection, or be conditional upon changes in internal factors such as health, energy reserves (Gross 1996), age or dominance status (Hogg & Forbes 1997), or upon external factors such as weather, predation (Isvaran 2005), population density (Kokko & Rankin 2006) and female distribution (Clutton-Brock 1989).

The evolution of the Caprinae

Geist (1974a) and particularly Schaller (1977) have ably outlined the patterns of evolution of goat-antelopes, wild goats and wild sheep, with special reference to their social behaviour and associated morphology. Ancestral forms of Caprinae are known from as early as the Miocene (e.g. Gentry 2000), but the group did not reach its greatest diversity until the recent ice ages. Apparently, Caprinae had two major spurts in evolution, both when mountains were rising up: in the Late Miocene-Early Pliocene, with Caprinae spreading over Eurasia and probably North Africa, and in the Late Pliocene-Early Pleistocene (Schaller 1977). Schaller (1977) and Geist (1985, 1987) suggested that the early Caprinae may have been morphologically less differentiated than later forms, thus closer to the extant genera *Capricornis* and *Naemorhedus*, although the actual picture remains unclear (Gentry 2000). Schaller (1977) also stated that: "The Caprinae become progressively more dimorphic starting with the goral and serow and continuing through the chamois and mountain goat to the two Ovisovini [i.e. muskox *Ovibos moschatus* and takin *Budorcas taxicolor*] and finally the Caprini, and this cline can be correlated with emphasis on dominance, the caprids [i.e. Caprinae] having marked hierarchies". If so, ancestral Caprinae have been assumed to be forest-dwellers, solitary or pair-living, monogamous and sexually monomorphic; the colonisation of open habitats by some forms favoured gregariousness, which could have led to increased polygyny and sexual dimorphism (Geist 1974b, Jarman 1974). Over the past few decades, this hypothesis has received increasing support (Pérez-Barbería et al. 2002, Szemán et al. 2021). Species from extreme environments seem to have evolved later than those from warmer climates, for example goat-antelopes (Geist 1985). However, while we expect 'simpler' forms to be older, we have to accept that current knowledge on Caprinae evolution and phylogeny is fuzzy. In some cases, phylogenetic relationships remain uncertain even when molecular data are used (Hassanin et al. 1998). In fact, it has been remarked that "environmental change places such a premium on adaptability that speciation may have proceeded so rapidly that no recognizable intermediate forms were left behind" (Schaller 1977).

Furthermore, because of the high rate of erosion in mountain areas, fossil deposits are known mainly from recent periods, as older ones are likely to have been lost (Masini & Lovari 1988), thus making phylogenetic reconstructions of mountain-dwelling ungulates a somewhat tricky matter.

METHODS

For all species of Caprinae, we collected information on habitat preferences, social behaviour, sexual dimorphism, and on mating system in terms of mate monopolisation, forms of mate acquisition and quantitative measures. Information on habitat type, social behaviour (group size) and sexual dimorphism was mostly retrieved from Damm and Franco (2014) and Castelló (2016). Information on species-specific mating behaviour was compiled from the literature as described in Appendix S1.

The information we collected was classified using categorically distinct labels. Specifically, the primary habitat type was classified into four different classes reflecting different degrees of habitat openness: 'forest' (if a species is mostly found in forested habitats), 'forest-open' (if a species uses both forests and open areas), 'shrubland-open' (if a species is rarely found in forests and mainly inhabits shrublands and open lands) and 'open' (if the species mostly lives in open areas). The level of sociality, based on average group size outside of the rut, was placed in four classes: 'low' (1–2 individuals), 'medium-low' (2–10 individuals), 'medium-high' (10–20 individuals) and 'high' (>20 individuals). The level of mate monopolisation, based on the terms used in the relevant literature, was divided into three classes: 'monogamy', 'weak polygyny' and 'polygyny'. The terms used to describe the form of mate acquisition were not consistent in the literature, and were aligned using the categories previously described in Table 1. The quantification of mating system was based on available information on I_{mates} (or one of its components, such as the opportunity for selection on males I_{males} , the variance in male reproductive success divided by the squared averaged male reproductive success; Shuster & Wade 2003). The level of mate monopolisation can be linked to various forms of sexual dimorphism, such as difference in body size, colouring, shape and size of weaponry (Andersson 1994). In bovids, body mass and horn size are targets of sexual selection (Bro-Jørgensen 2007, Tidière et al. 2020); horn size, however, may also depend on combat style, so horn dimorphism is less likely to be related to polygyny than body mass. Therefore, sexual dimorphism in the Caprinae was categorised primarily on the basis of body mass dimorphism, into four classes: 'low' (<10%), 'medium-low' (10–30%), 'medium-high' (30–50%) and 'high' (>50%). Level of dimorphism was secondarily adjusted

for horn size dimorphism in chiru *Pantholops hodgsonii* and bharal *Pseudois nayaur*; in these species, male body mass is about 40–50% greater than that of females, suggesting a 'medium-high' dimorphism, but since horns are a male-only trait in chiru, and much larger in males than in females in bharal, the overall sexual dimorphism was classified as 'high'. For each category (habitat, sociality, mate monopolisation, sexual dimorphism), a numerical value from one to four was assigned to the labels, following the order presented above. For some species, it was not possible to retrieve any information on the mating system; when data were not available, we assumed the same numerical value of mate monopolisation as the taxonomically closest species. Numerical values were used to inspect graphically the pairwise, sequential relationships between habitat, level of sociality, patterns of mate monopolisation and development of sexual dimorphism, following the hypothesis proposed by Jarman (1974); relationships were quantitatively evaluated through two-tailed Spearman's rank order correlation tests.

RESULTS

We screened about 160 literature sources (journal articles, books) on Caprinae mating systems and social and ecological correlates. The full list of literature used is reported in Appendix S2. Caprinae inhabit many habitat types and vary substantially in their level of sociality and sexual dimorphism (Table 2). Most species are polygynous, although the degree of female monopolisation remains unclear, as a quantitative assessment is available only for Alpine ibex *Capra ibex* and bighorn sheep *Ovis canadensis* through I_{males} (Table 2). Direct comparisons between these species, however, require some caution, as I_{males} was calculated over one single season in the former (values between 4.6 and 5.6; Willisch et al. 2012), and over multiple seasons in the latter (mean value = 4.5, between 2.5 and 8.3; Coltman et al. 2002). The most widespread form of mate acquisition is female guarding, used by about 78% of the species for which at least one tactic is known, and tending appears to be the primary tactic for most species (63%; Table 2); range and group guarding are less frequent, about 16%, and site guarding, found in about 19% of the Caprinae, is mostly limited to 'primitive' species (sensu Schaller 1977, Geist 1985).

The pairwise, sequential relationships between habitat type, sociality, mating system and sexual dimorphism shown in Fig. 1 are not formal analyses, which would ideally require a phylogenetic structural equation modelling approach to support causal pathways and quantify indirect effects (cf. Szemán et al. 2021). In fact, the lack and the questionable quality of some data on mating systems, and the intrinsically small sample size ($n = 32$

Table 2. Summary of the main characteristics of the Caprinae in terms of: habitat type, degree of sociality, degree of sexual dimorphism (SexDim), main mating system (level of mate monopolisation, form of mate acquisition), presence of male alternative reproductive tactics (ARTs); n.a. = information not available in the literature. The last column shows the reference(s) with the most complete set of information about mating behaviour

Genus	Species	Common name	Habitat	Sociality	SexDim	Mating system		Male ARTs	Main reference
						Mate monopolisation	Mate acquisition		
<i>Naemorhedus</i>	<i>baileyi</i>	Red goral	Forest-open	Low	Low	n.a.	n.a.	n.a.	Myslenkov and Voloshina (1978, 1998)
	<i>caudatus</i>	Long-tailed goral	Forest-open	Low	Low	Weak polygyny	a) Range-guarding/site-guarding?	n.a.	
<i>Capricornis</i>	<i>goral</i>	Brown goral	Forest-open	Low	Low	Weak polygyny	a) Female guarding: tending	n.a.	Lovari and Apollonio (1994)
	<i>swinhoei</i>	Formosan serow	Forest-open	Low	Low	n.a.	n.a.	n.a.	
<i>Capricornis</i>	<i>rubidus</i>	Red serow	Forest	Low	Low	n.a.	n.a.	n.a.	Akasaka and Maruyama (1977), Kishimoto (2003)
	<i>crispus</i>	Japanese serow	Forest-open	Low	Low	Monogamy	a) Site-guarding: resource-based territoriality b) Female guarding?	Yes?	
<i>Rupicapra</i>	<i>sumatraensis</i>	Sumatran serow	Forest-open	Low	Low	n.a.	a) Site guarding	n.a.	Lovari and Locati (1994)
	<i>pyrenaica</i>	Southern chamois	Forest-open	Medium-low	Medium-low	Weak polygyny	a) Site guarding (resource-based territoriality) b) 'Non-territoriality' (female and group guarding?)	Yes	
<i>Rupicapra</i>	<i>rupicapra</i>	Northern chamois	Forest-open	Medium-low	Medium-low	Weak polygyny	a) Site-guarding: resource-based territoriality b) 'Non-territoriality' (female and group guarding?)	Yes ²	Krämer (1969), Corlatti et al. (2013, 2015)
	<i>americanus</i>	Mountain goat	Forest-open	Medium-low	Medium-high	Polygyny	a) Female guarding: tending b) Female guarding: courting/sneaking	Yes	
<i>Ammotragus</i>	<i>lervia</i>	Aoudad	Forest-open	Medium-high	High	Polygyny	a) Female guarding: tending b) Female guarding: courting/sneaking?	Yes	Habibi (1987)
<i>Arabitragus</i>	<i>jayakari</i>	Arabian tahr	Shrubland-open	Medium-low	High	n.a.	n.a.	n.a.	Munton (1985)
<i>Hemitragus</i>	<i>jemlahicus</i>	Himalayan tahr	Shrubland-open	Medium-high	High	Polygyny	a) Female guarding: tending b) Female guarding: sneaking	Yes	Lovari et al. (2009)
<i>Nilgiritragus</i>	<i>hylocrius</i>	Nilgiri tahr	Open	Medium-high	Medium-high	Polygyny	a) Female guarding: tending b) Female guarding: sneaking?	Yes?	
<i>Capra</i>	<i>aegagrus</i>	Wild goat	Forest-open	Medium-low	High	Polygyny	a) Female guarding: tending b) female guarding: courting?	Yes?	Schaller and Laurie (1974)

(Continues)

Table 2. (Continued)

Genus	Species	Common name	Habitat	Sociality	SexDim	Mating system		Male ARTs	Main reference
						Mate monopolisa- tion	Mate acquisition		
	<i>caucasica</i>	Tur	Forest-open	Medium-high	High	Polygyny	a) Female guarding: tending b) Female guarding: coursing	Yes	Weinberg and Lortkipanidze (2022)
	<i>falconeri</i>	Markhor	Forest-open	Medium-low	High	Polygyny	a) Female guarding: tending	n.a.	Schaller and Mirza (1971)
	<i>ibex</i>	Alpine ibex	Open	Medium-high	High	Polygyny ³	a) Female guarding: tending b) Female guarding: coursing/sneaking?	Yes ²	Willisch et al. (2012)
	<i>nubiana</i>	Nubian ibex	Open	Medium-high	High	Polygyny	a) Female guarding: tending b) Female guarding: sneaking?	Yes	Habibi (1994)
	<i>pyrenaica</i>	Iberian wild goat	Forest-open	Medium-low	High	Polygyny	a) Female guarding: tending	Yes?	Alados (1986)
	<i>sibirica</i>	Siberian ibex	Open	Medium-high	High	Polygyny	a) Female guarding: tending	n.a.	Fedosenko and Blank (2001)
	<i>waliae</i>	Walia ibex	Open	Medium-low	High	Polygyny	a) Female guarding: tending b) Female guarding: sneaking?	Yes?	Nievergelt (1981)
<i>Ovis</i>	<i>ammon</i>	Argali	Open	High	High	Polygyny	a) Female guarding: tending b) Female guarding: coursing	Yes	Fedosenko and Blank (2005)
	<i>canadensis</i>	Bighorn sheep	Open	High	High	Polygyny ³	a) Female guarding: tending b) Female guarding: coursing c) Female guarding: blocking	Yes ²	Hogg (1984), Hogg and Forbes (1997)
	<i>dalli</i>	Dall’s sheep	Shrubland-open	Medium-high	High	Polygyny	a) Female guarding: tending b) Female guarding: coursing	Yes	Geist (1971)
	<i>aries</i>	Mouflon	Forest-open	Medium-high	High	Polygyny	a) Female guarding: tending b) Female guarding: coursing c) Female guarding: blocking	Yes	Bon et al. (1992)
	<i>nivicola</i>	Snow sheep	Open	Medium-high	High	Polygyny	n.a.	n.a.	
	<i>vignei</i>	Urial	Open	High	High	Polygyny	a) Female guarding: tending b) Female guarding: coursing	Yes	Schaller and Mirza (1974)
<i>Pseudois</i>	<i>nayaur</i>	Bharal	Shrubland-open	High	High	Polygyny	a) Female guarding: tending b) Female guarding: coursing c) Female guarding: blocking	yes	Schaller (1977), Lovari and Ale (2001)

(Continues)

Table 2. (Continued)

Genus	Species	Common name	Habitat	Sociality	SexDim	Mating system			
						Mate monopolisation	Mate acquisition	Male ARTs	Main reference
<i>Budorcas</i>	<i>taxicolor</i>	Takin	Forest-open	Medium-high	Medium-high	Polygyny	a) Female guarding: tending b) Female guarding: coursing	Yes	Powell et al. (2013)
<i>Ovibos</i>	<i>moschatus</i>	Muskox	Open	High	Medium-high	Polygyny	a) Group guarding b) Female guarding: sneaking	Yes	Smith (1976)
<i>Pantholops</i>	<i>hodgsonii</i>	Chiru	Open	High	High	Polygyny	a) Site guarding: lek b) Female guarding: coursing c) Group guarding	Yes	Buzzard et al. (2012)

¹The behaviour of males was originally defined as 'harem defence'.

²Genetically confirmed breeding.

³Genetically confirmed through I_{males} .

species), make this assessment a coarse-grained description of potential patterns emerging from the data at hand. With these caveats in mind, Fig. 1 shows clear positive correlations between variables within each panel plot, thereby supporting the existence of relationships between spatial, social and reproductive behaviour and morphology of mountain ungulates (cf. Geist 1974b, Jarman 1974, Schaller 1977). Spearman's rank order correlation tests also support these relationships (habitat ~ sociality: $\rho = 0.72$, d.f. = 30, $P < 0.001$; sociality ~ mate monopolisation: $\rho = 0.77$, d.f. = 30, $P < 0.001$; mate monopolisation ~ sexual dimorphism: $\rho = 0.88$, d.f. = 30, $P < 0.001$). Correlations remain statistically significant also when species with no information on mating system are excluded (sociality ~ mate monopolisation: $\rho = 0.65$, d.f. = 25, $P < 0.001$; mating system ~ sexual dimorphism: $\rho = 0.80$, d.f. = 25, $P < 0.001$).

DISCUSSION

The eco-evolutionary history of mountain ungulates sets the scene for the remarkable diversity of spatial and social behaviours and of morphological features observable in extant Caprinae species. From the forest-dwelling, solitary, monogamous and monomorphic serows *Capricornis* spp., through the mountain-dwelling, social, weakly polygynous and seasonally size dimorphic chamois *Rupicapra* spp., to the highly dimorphic, polygynous and social wild sheep and goats of open habitats, mountain ungulates broadly support the eco-evolutionary scenario linking habitat use, sociality, reproductive behaviour and morphology (Fig. 2) suggested by Jarman (1974) for African bovids and further confirmed by Pérez-Barbería et al. (2002) and Szemán et al. (2021).

Even today, Schaller's book '*Mountain Monarchs*' (Schaller 1977) remains the most authoritative, informed and compelling account of such diversity. Since then, much has been learned of the male reproductive behaviour of a few species, such as chamois (Corlatti et al. 2015), mountain goats *Oreamnos americanus* (Mainguy et al. 2008), Alpine ibex (Willisch et al. 2012) and bighorn sheep (Coltman et al. 2002), but much remains to be learned for the large majority of Caprinae species, which exerts some constraints on our conclusions. Perhaps the most innovative advancement in our knowledge on mountain ungulate mating systems was the discovery of different forms of mate acquisition and the mechanisms that maintain them within populations (Hogg 1984, Taborsky et al. 2008). Our understanding, however, remains open to several doubts, and much work is still to be done to fill the gaps. Below, we attempt a synthesis of our understanding of the ecology of Caprinae mating systems, in terms of mate monopolisation and forms of mate acquisition, we discuss the limitations of our review, and present the research that is still ahead of us.

The ecology of mate monopolisation

Pair-living is expected to be the most ancestral form of social organisation in Artiodactyla, mostly owing to anti-predator behaviour (Jaeggi et al. 2020). Similarly, Lukas and Clutton-Brock (2013) showed that "the ancestral condition for all mammalian groups is of solitary individuals and (...) social monogamy is derived almost exclusively from this social system". This type of social behaviour is found in forest-dwelling and resource-defending African bovids, where antipredator behaviour and the patchy distribution of poorly shareable food items such as browse

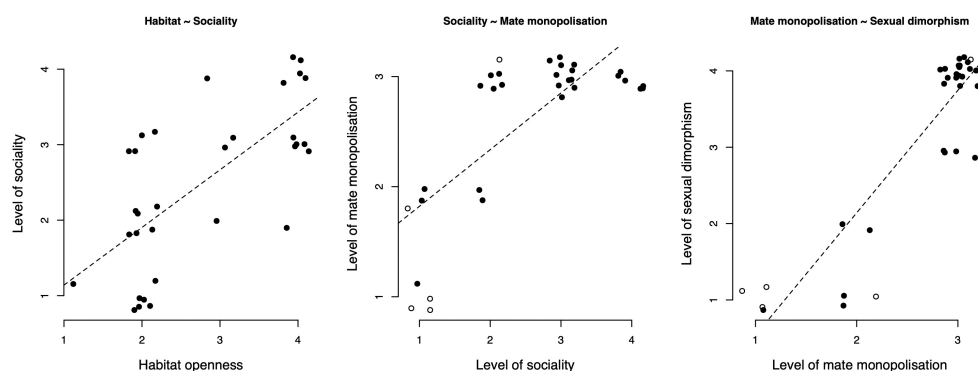


Fig. 1. Pairwise relationships in the Caprinae between habitat openness and level of sociality, level of sociality and level of mate monopolisation, and level of mate monopolisation and level of sexual dimorphism (see text for details on categorisation). Dashed lines represent least-squares lines. Open circles indicate species with no data on mating system, that were assumed to have the same system as the taxonomically closest species. Points have been jittered to improve visualisation.



Fig. 2. From the forest-dwelling, solitary, monogamous and monomorphic Japanese serow, through the mountain-dwelling, social, weakly polygynous and seasonally size dimorphic northern chamois, to the highly dimorphic, polygynous and social bighorn sheep inhabiting open habitats, mountain ungulates broadly support the eco-evolutionary scenario linking ecology and social behaviour suggested by Jarman (1974) for African antelopes and further confirmed by Pérez-Barbería et al. (2002) and Szemán et al. (2021) (Drawing: Lucrezia Lorenzetti).

and forbs promote intolerance among individual females, hence their spatial separation, thereby forcing males to patrol a shared territory, favouring monogamy (Jarman 1974). Among the Caprinae, the Japanese serow *Capricornis crispus* (Akasaka & Maruyama 1977, Kishimoto & Kawamichi 1996, Brotherton & Komers 2003) and possibly gorals *Naemorhedus* spp. fit this scenario (Schaller 1977,

but see Lovari & Apollonio 1994). Conversely, when food supply or antipredator strategy do not impose upper limits on group size, males are free to pursue alternative strategies to maximise reproductive success (Andersson 1994). In open habitats, antipredator behaviour and, possibly, more evenly dispersed, nondefensible food items (e.g. grasses) favour the onset of large social groups (Jarman

1974). This process has been observed in Pyrenean chamois *Rupicapra pyrenaica pyrenaica* (Herrero et al. 2002) and, more recently, in the Japanese serow, where open habitats promote spatial group formation (Takada & Minami 2021). In turn, the patchy distribution of serow females should favour the monopolisation of mating opportunities and the transition between monogamy and polygyny (Kishimoto 2003, Takada et al. 2023). In other words, the degree of polygyny is largely influenced by the spatiotemporal crowding of females (Emlen & Oring 1977, Shuster & Wade 2003). In fact, for a species living between forest and open habitat and with moderate spatial crowding such as the chamois, a moderately skewed reproductive success among males, hence a weakly polygynous mating system, has been suggested (Corlatti et al. 2015). With increasing use of open habitats and female spatial clumping, as in many wild sheep and goats, tahr, bharal, takin, muskox and chiru, the degree of polygyny is expected to increase and be constrained by the efficiency of mate guarding (Carranza 2000), although taxon-specific variations are difficult to assess quantitatively, as I_{males} is available only for Alpine ibex (Willisch et al. 2012) and bighorn sheep (Coltman et al. 2002).

In turn, the intensity of sexual selection is expected to be related to sex-specific phenotypic differences that enhance reproductive success (Andersson 1994). The level of polygyny, for example, seems to be a good predictor of sexual size dimorphism in ungulates (Loison et al. 1999a), although actual data are not available for most species. This pattern appears to be broadly supported also in the Caprinae (Table 2, Fig. 1). Competition over mates is generally limited in monogamous species, and a weak pressure of sexual selection is unlikely to favour extreme phenotypic differences between sexes (Andersson 1994), as in serows or gorals (Table 2, Fig. 1). A limited, seasonal body mass dimorphism is observed in chamois (Rugghetti & Festa-Bianchet 2011); this fits the presumed weakly polygynous mating system, although extreme dimorphism in *Rupicapra* may be also counter-selected by the form of combat, which may favour skills other than body mass, such as speed or agility (cf. Blanckenhorn 2000). Ferretti et al. (2014) showed that in the warm months, female chamois prioritise fine-scale selection of vegetation and the safety of offspring, while males gain body weight by increasing their food intake rate, thus preparing to meet the high costs of the mating season (Garel et al. 2011, Rugghetti & Festa-Bianchet 2011) and the winter rigours. Achieving dominance for mating through increased body size could have primed this foraging adaptation (Ferretti et al. 2014). However, in polygynous Caprinae, body mass dimorphism is not seasonal and it is often extreme, with the partial exception of takin and muskox (Damm & Franco 2014, Castelló 2016). Sexual dimorphism in mountain ungulates is not limited to body mass, but may extend to other features such as horn size and shape; as opposed to

monogamy, which favours short and straight horns (e.g. in serows and gorals), polygyny creates a selective environment that in turn generates a great variety of horn shape, from smooth and straight (e.g. chiru), to crenulated and twisted (e.g. wild goats), or smooth and curled (e.g. wild sheep; Caro et al. 2003). In polygynous species, because of the costs related to intrasexual competition and larger body masses and weaponry, higher mortality rates of males than that of females may be expected (cf. Clutton-Brock et al. 1982). Although reliable information on age- and sex-specific survival is limited to very few species, the data at hand suggest that neither sexual dimorphism nor the level of polygyny are good predictors of sex-specific differences in survival probabilities of mountain ungulates (see Cransac et al. 1997 for mouflon, Toigo et al. 2007 for Alpine ibex, van de Kerk et al. 2020 for Dall's sheep *Ovis dalli*). As noted by Loison et al. (1999b), copulations are not costly *per se*; thus, polygyny in itself may be a poor measure of the energetic costs sustained by males; other factors such as the intensity of male–male contests during the rut may better explain variation in sex-specific survival patterns.

Although the mating system of most wild sheep has been described here as polygynous, some authors used the term ‘promiscuous’ (cf. Bon et al. 1992, Michel & Ghoddousi 2020b for mouflon *Ovis aries*, or Michel & Ghoddousi 2020a for urial *Ovis vignei*). Enforced copulations by several males in bighorn sheep (Hogg 1988), multimale copulations in feral sheep (Coltman et al. 1999), alongside the large size of testes and retaliatory copulations displayed by tending rams actually suggest the occurrence of promiscuity and sperm competition in wild sheep species (Hogg 1984). Bergeron et al. (2012) stated that “the definition of promiscuity (...) is not categorical about the extent of multiple mating required to be described as a promiscuous mating system”; as such, the extent of species-specific promiscuity still needs to be quantified. This information is important, because an increased level of promiscuity may affect precopulatory sexual selection on male mating success, and promote postcopulatory sexual selection on male traits that increase and defend paternity share, such as retaliatory copulations (Morimoto et al. 2019).

The ecology of mate acquisition

Although increasing levels of polygyny should favour the emergence of several mating phenotypes (Shuster et al. 2019), most Caprinae species display different forms of mate acquisition (Table 2). The most widespread mate acquisition tactic adopted by mountain ungulate males is female guarding through tending. This pattern largely owes to the prevalence, in the Caprinae subfamily, of wild sheep and goat species which, despite their wide distribution, have maintained conservative behaviour with

little interspecific variation (Geist 1971, Schaller & Laurie 1974), as opposed to the greater diversity that occurs in goat-antelopes (Table 2).

Overall, female guarding appears to be beneficial when the chance of a receptive female occurring in any one location is low (Gosling 1986). The prevalence of this form of mate acquisition in the Caprinae may be related to the climatic and topographic characteristics of mountainous habitats, where discontinuous food supply and terrain ruggedness could force females to forage over large areas (Gosling 1986), hence favouring the adoption of a more flexible tactic over static tactics such as site guarding or group guarding. As noted by Schaller (1977), “if both food and females are likely to vanish, a male’s most sensible strategy is to stay with the herd”. Indeed, site guarding is found in a limited number of species for which mating tactics are known. Geist (1974b) noted that, because of poor and discontinuous food supply, “we cannot expect northern ungulates to be territorial if they rut in fall and early winter”; accordingly, this form of mate acquisition is found in species that restrict their ranges to areas with a relatively constant food supply (Schaller 1977), such as the forest-dwelling serow (Lovari & Locati 1994, Kishimoto 2003). Yet, relatively great and continuous plant diversity and productivity may not be a necessary condition for territoriality, as long as some predictability in spatio-temporal resource availability occurs: for example, although Geist (1974b) suggested that chamois territoriality may be an artefact of high population density, it is likely to represent an example of seasonal resource-based territoriality owing to predictable snow-dependent movements of females in search of food (von Hardenberg et al. 2000, Corlatti et al. 2020). Predictability in mating opportunities, rather than in food supply, might be at the core of another form of site-guarding behaviour, lekking, in chiru males (Buzzard et al. 2008). This behaviour is favoured when local population density is high, leading to increased male–male competition (Lott 1991, McLain 1992), although it remains unclear what kind of lekking model (Davies et al. 2012) is the catalyst for the clustering of chiru males (Buzzard et al. 2008). Group guarding is also rare in wild Caprinae: as noted by Bowyer et al. (2020): “harem mating for species inhabiting steep and rugged terrain is uncommon, likely because effective herding of females by dominant males would be challenging” (see also Schaller 1977). Accordingly, this form of mate acquisition is only found in muskox (Smith 1976) and perhaps as an alternative tactic in chiru (Buzzard et al. 2008), possibly because of the gentler topographical features of the Arctic tundra and of the Tibetan plateau.

Some inconsistencies in the ecology of Caprinae mate acquisition nonetheless remain: species such as Alpine ibex and Alpine chamois *Rupicapra rupicapra rupicapra*, for

example, share most of their geographic range, yet display radically different mating systems (Brambilla et al. 2022, Corlatti et al. 2022b). We speculate that phylogenetic constraints must have imposed some limits on mating system plasticity. The possibility to detect relationships between habitat features and forms of mate acquisition is further challenged by the co-occurrence of different male tactics within the same species and population. Female guarding, for example, co-exists with territoriality in serow, chamois and chiru, and with group guarding in muskox (Table 2). This is probably because, besides distribution of food supply, terrain ruggedness and predictability of food or mates, the maintenance of ARTs within and between populations depends on many other endogenous and exogenous variables such as age, weather conditions and population density (Gosling 1986, Taborsky et al. 2008). For example, in most wild sheep and goats, as well as in bharal and mountain goat, different tactics are associated with age and physical correlates such as body mass and horn size (Alados 1986, Habibi 1987, Lovari & Ale 2001, Mainguy et al. 2008), suggesting maintenance of ARTs through individual status-dependent selection. Another form of condition-dependent selection, mediated through variations in environmental conditions, co-occurs in Alpine ibex, where males can switch tactics depending on snow abundance during the rut (Apollonio et al. 2013). Snow conditions also affect the maintenance of ARTs in northern chamois, but mainly through long-term stochastic variations that impact female spatial behaviour and hence the reproductive success of territorial and non-territorial males (Corlatti et al. 2020), as tactics used by this species appear to be stable over an individual’s lifetime (Cotza et al. 2023). In the Japanese serow, adult density negatively correlates with territory size (Ochiai & Susaki 2002), suggesting that population abundance may affect the ability of males and females to defend territories, and hence the form of mate acquisition (territoriality vs. female guarding).

More work is needed to understand the coexistence of ARTs in the Caprinae. There is increasing evidence that a few mechanisms may concur in maintaining alternative phenotypes (Brockmann 2001), such as age and snow cover conditions in Alpine ibex (Apollonio et al. 2013), or age and population density in muskox (Smith 1989), and the study of ARTs may benefit from combining them and solving for their joint equilibrium (Gross 1996). In wild Caprinae, this is challenged by the fact that, in species such as Alpine ibex, bighorn sheep and muskox, ARTs do not appear to be a fixed trait of individuals, and males can switch between tactics (Smith 1976, Hogg & Forbes 1997, Willis & Neuhaus 2010, but see Cotza et al. 2023 for the northern chamois). Furthermore, for many species, the occurrence of alternative reproductive behaviour patterns still needs to be assessed, as in gorals,

serows, Arabian tahr *Arabitragus jayakari* and snow sheep *Ovis nivicola* (Table 2), and while categorisation into the main forms of mate acquisition reflects distinct behaviours (e.g. female guarding vs. group guarding vs. site guarding), at times different tactics may simply reflect terminological artefacts. The classification of female-guarding behaviour into coursing or sneaking, for example, depends on how loosely we define coursing (cf. Mainguy et al. 2008, Bowyer et al. 2020). A genetic assessment of different behaviour patterns will help us to improve the categorisation of ARTs in mountain ungulates, and to understand the mechanism of their maintenance within and between populations.

Caveats

Our taxonomic account is intrinsically limited by how mating systems were defined and classified, as well as by the number of ecological variables that may influence their variations. For example, verbal classifications of mating systems are severely limited in their ability to assess variations in the number of mates, not only because of intrinsic descriptive vagueness, but also because assessing mate monopolisation through behavioural observations may be inaccurate (Coltman et al. 1999). The adoption of quantitative measures such as the opportunity for sexual selection would be necessary to shed light on the diversity of mating behaviour (Shuster & Wade 2003). Furthermore, although we decided to limit our investigation to a given breeding season, it should be noted that, when bond duration is considered not within the timeframe of a single breeding season, but over multiple seasons, mating systems may be classified differently. Monogamy, for example, may be redefined as serial polygamy if individuals pair with different partners in different years (Wickler & Seibt 1983). The definition of pair bond duration may also impact the opportunity for sexual selection: differences in the relative variance of male success between monogamous and polygynous species, for example, may be smaller than expected, as long as the variance in lifetime reproductive success and offspring survival to adulthood are included in the measure of success (Clutton-Brock 1988).

Additionally, mating systems may be influenced by many more variables than those included in this review. Jarman's (1974) scenario was recently refined by Bowyer et al. (2020), by incorporating quality and defensibility of resources, terrain ruggedness, as well as population density as major drivers of ungulate mating systems. The conceptual model of Bowyer et al. (2020) is an important step towards an improved understanding of the determinants of ungulate mating system, although, as pointed out by the authors, assessing parameters such as quality and defensibility of resources may be problematic. We suggest that, when applied to mountain ungulates, seasonal

variation in the quality and availability of resources could also be included in the conceptual model of Bowyer et al. (2020), as temporary availability of forage appears to play a major role, for example, in shaping territorial behaviour (Jarman 1974), and hence in the mating system of some Caprinae species such as the chamois (von Hardenberg et al. 2000, Lovari et al. 2006).

Finally, we acknowledge that the generalisations used to evaluate the pairwise, sequential relationships between habitat use, sociality, polygyny and morphology, inevitably oversimplify reality. For example, flexibility in habitat preferences occurs in populations of the same species; grouping patterns may change with sex, season and population density; in the absence of genetic data it is difficult to define the degree of mate monopolisation; for most Caprinae species, mass dimorphism is paralleled by horn size dimorphism, but there are exceptions (e.g. chamois, tahr, chiru, muskox) for which the overall level of dimorphism is difficult to define. Small deviations from the proposed labelling, however, do not change the overall picture. A compelling analysis of the sequential relationships between habitat openness, sociality, polygyny and morphology should ideally be based on the use of continuous, raw data (e.g. weighted averages across populations and seasons) rather than on a priori defined classes, which may possibly introduce subjective bias. Representative raw data on habitat types, grouping patterns, mate monopolisation and body and horn size may be available for a limited number of species, but are lacking for the majority of the Caprinae species.

CONCLUSION: THE ERA OF FIELDWORK IS NOT OVER!

Although our review broadly supports the eco-evolutionary scenario of Jarman (1974) linking ecology, sociality, reproduction and morphology, the hypothesis remains somehow speculative when applied to mountain ungulates, as information on their mating systems is poor. For example, we found no published information about the level of mate monopolisation or the form of mate acquisition for about 18% of species (Table 2). Quantitative assessments of mating system are virtually absent in Caprinae, with the exception of two species for which we have data on I_{males} . We acknowledge that the genetic approach to estimating I_{males} is challenging, as it requires not only paternity data, but also data on the operational sex ratio (Shuster & Wade 2003), information that is hard to collect in mountain ungulates. For example, beside the technical difficulties of collecting genetic samples of species living in steep and rugged terrain, in species such as the bighorn sheep two-year-old rams can mate and occasionally sire lambs, but cannot be considered the same as mature males in establishing the operational sex ratio (Ritchot et al. 2021). The alternative

approach to estimate I_{mates} , namely from count data on the spatial and temporal distribution of receptive females during the rut (Shuster & Wade 2003), has never been tested in Caprinae, but it proved a poor predictor of genetic I_{mates} in pronghorn *Antilocapra americana*, owing to the difficulty of collecting accurate behavioural data (Dunn et al. 2012). Furthermore, not all males have the same probability of access to females in a population, for example because of differences in spatiotemporal and competitive factors, as well as timeliness, making the estimates of I_{mates} challenging (Montana et al. 2020). More generally, “no current specific measure or combination of measures used to quantify sexual selection, and thus mating systems, satisfies everyone” (Snook 2017). However, assessing the opportunity for selection on males I_{males} would be important to explore how the relative intensity of selection varies over different populations or across time (Wade & Arnold 1980), hence how ecological and social factors may influence the mating system and its associated evolutionary effects such as sexual dimorphism and ornamentation (Krakauer et al. 2011). Since I_{males} does not take into account variation in female reproductive success, the ratio between I_{males} and I_{females} (Wade & Arnold 1980) may also be calculated, as it appears to be positively correlated with the intensity of sexual selection (Clutton-Brock 1988).

Indeed, the study of mating systems and of the factors affecting their variations plays a key role from an evolutionary perspective. Our analyses suggest a positive correlation between habitat openness and sexual dimorphism, through the level of sociality and that of mate monopolisation. The realisation that mating behaviour is conditional upon ecological factors suggests that environmental changes may have major impacts on the pressure of sexual selection, and this may be particularly true for the Caprinae, whose habitats are expected to be largely affected by global changes (Root et al. 2003, Lovari et al. 2020). Because of the ongoing climatic change, habitat openness, as well as plant phenology and plant associations, have been and will continue to be altered (e.g. Gottfried et al. 2012, Pauli et al. 2012, Telwala et al. 2013). These changes will lead to local landscape modification, herbivore population dispersion and different species composition of animal guilds, which may lead to increasing species competition (Lovari et al. 2020). Especially in strongly seasonal environments such as those on mountains, in the long run these effects could influence the phenology of mating systems in species which will adapt to life in closed habitats favoured by increased temperature, with the decrease of meadows triggered by an elevational shift of the forest habitat. Furthermore, the warming climate will continue to cause declines in snow cover in mountainous environments (Matiu et al. 2021), possibly releasing constraints on female movements during the mating season. In turn,

a change in female spatial clumping can hamper the opportunity for sexual selection, possibly also changing forms of mate acquisition through variations in reproductive success of males adopting different tactics. Finally, recent studies have highlighted that climate change is likely to affect the viability of mountain ungulates by lowering the quantity and quality of food resources available on mountains, possibly altering intraspecific competition (Lovari et al. 2020) and investment in sexually related traits, such as body mass and horn size (cf. Geist 1978). These, and other types of environmental variations such as land use change may have different consequences on the pressure of sexual selection and on the form of mate acquisition (Lane et al. 2011), which still need investigation. Mating systems can also influence effective population size (Nunney 1993), and hence the ability of a population to maintain its genetic diversity and respond to natural and anthropogenic environmental pressures (Lane et al. 2011). This is particularly relevant to the Caprinae, whose economic value is important for both consumptive use (e.g. hunting) and non-consumptive use (e.g. tourism; Shackleton 1997). Trophy hunting of mature, large males, for example, may disrupt dominance hierarchies and impact young male survival in Dall's sheep (Singer & Zeigenfuss 2002). In bighorn sheep, rams of high breeding value shot at an early age cannot achieve high reproductive success, eventually causing a decline in male body mass and horn size (Coltman et al. 2003). More information on the short- and long-term consequences of different hunting regimes on Caprinae mating behaviour is needed.

Finally, behavioural research has been focused on males, possibly because in many species males are larger and stronger than females, and display their competitive behaviours more overtly than females (Wasser & Waterhouse 1983). This has generated an ‘androcentric’ view on mating systems, and the widespread belief that the reproductive strategy of a species can be explained solely by looking at it from a male perspective (Blaffer Hrdy & Williams 1983). However, the two sexes have co-evolved throughout the evolutionary history of sex (Wasser & Waterhouse 1983), and female behaviour is likely to play an important active role in shaping mating systems (Bowyer et al. 2020). For example, females may influence male behaviour during the rut by encouraging male–male contests (Byers et al. 1994), they may alter male reproductive success through their spatial behaviour during the rut (Lovari et al. 2008) and, for some species, they may affect postcopulatory sperm selection, hence paternity share, through their mate choice (Firman et al. 2017). Thus far, little information is available on how female behaviour may influence mating systems in mountain ungulates: in bighorn sheep, the tending tactic implies, at least

superficially, a cooperative mating relationship between males and females, while coursing and blocking “reveal clear conflicts between the sexes over the circumstances of mating” as females attempt to resist copulation (Hogg 1987). In other species of mountain ungulates, however, the role of females in deciding who mates with whom, how and when, still remains obscure.

Paraphrasing Schaller (1977), science proceeds by asking questions that have never been asked before but, at times, as we reach for the stars, we may neglect the flowers at our feet. The intricate relationship between natural and sexual selection still requires precious time to be spent in the field (Geist 1971), collecting data on spatial behaviour, outcome of male–male interactions during the rut, age-specific courtship behaviour patterns and female choice behaviour, combined with genetic assessment of paternity. It cannot be emphasised enough that improved knowledge on the evolutionary history of mountain ungulates will ultimately help their conservation.

ACKNOWLEDGEMENTS

We are grateful to Marco Festa-Bianchet for his comments on an earlier draft of this manuscript and for revising our English. We are also grateful to Rita Lorenzini for a discussion on the molecular evolution of Caprinae, to Francesco Ferretti for his comments on an earlier draft of this manuscript, and to Lucrezia Lorenzetti for preparing Fig. 2. We thank the EIC and the ME of *Mammal Review*, Luca Montana and an anonymous reviewer for their helpful comments. Open Access funding enabled and organized by Projekt DEAL.

FUNDING

The article processing charge was funded by the funding program DEAL.

REFERENCES

- Akasaka T, Maruyama N (1977) Social organization and habitat use of Japanese serow in Kasabori. *Journal of the Mammalogical Society of Japan* 7: 87–102.
- Alados CL (1986) Aggressive behaviour, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenaica*). *Behavioural Processes* 12: 145–158.
- Andersson M (1994) *Sexual Selection*. Princeton University Press, Princeton, New Jersey, USA.
- Apollonio M, Brivio F, Rossi I, Bassano B, Grignolio S (2013) Consequences of snowy winters on male mating strategies and reproduction in a mountain ungulate. *Behavioural Processes* 98: 44–50.
- Bergeron P, Montiglio P-O, Réale D, Humphries MM, Garant D (2012) Bateman gradients in a promiscuous mating system. *Behavioral Ecology and Sociobiology* 66: 1125–1130.
- Blaffer Hrdy S, Williams GC (1983) Behavioral biology and the double standard. In: Wasser SK (ed) *Social Behavior of Female Vertebrates*, 3–17. Academic Press, New York, New York, USA.
- Blanckenhorn WU (2000) The evolution of body size: what keeps organisms small? *Quarterly Review of Biology* 75: 385–407.
- Bon R, Gonzalez G, Bosch M, Cugnasse JM (1992) Ram rut-involvement in a hunted population of mouflons. *Acta Theriologica* 37: 63–71.
- Bowyer RT, McCullough DR, Rachlow JL, Ciuti S, Whiting JC (2020) Evolution of ungulate mating systems: integrating social and environmental factors. *Ecology and Evolution* 10: 5160–5178.
- Brambilla A, Bassano B, Biebach I, Bollmann K, Keller L, Toïgo C, von Hardenberg A (2022) Alpine ibex *Capra ibex* Linnaeus, 1758. In: Corlatti L, Zachos F (eds) *Handbook of the Mammals of Europe – Terrestrial Cetartiodactyla*, 383–408. Springer Nature, Heidelberg, Germany.
- Brockmann HJ (2001) The evolution of alternative strategies and tactics. *Advances in the Study of Behavior* 30: 1–51.
- Bro-Jørgensen J (2007) The intensity of sexual selection predicts weapon size in male bovids. *Evolution* 61: 1316–1326.
- Brotherton NM, Komers PE (2003) Mate guarding and the evolution of social monogamy in mammals. In: Reichard UH, Boesch C (eds) *Monogamy – Mating Strategies and Partnerships in Birds, Humans and Other Mammals*, 42–58. Cambridge University Press, Cambridge, UK.
- Buzzard PJ, Bleisch WV, Xü D, Zhang H (2008) Evidence of lekking in chiru. *Journal of Zoology* 276: 330–335.
- Buzzard PJ, Bleisch WV, Xü D, Zhang H (2012) Evidence of lekking in chiru. *Journal of Zoology* 276: 330–335.
- Byers JA, Moodie JD, Hall N (1994) Pronghorn females choose vigorous mates. *Animal Behaviour* 47: 33–43.
- Caro TM, Graham CM, Stoner CJ, Flores MM (2003) Correlates of horn and antler shape in bovids and cervids. *Behavioral Ecology and Sociobiology* 55: 32–41.
- Carranza J (2000) Environmental effects on the evolution of mating systems in endotherms. In: Apollonio M, Festa-Bianchet M, Mainardi D (eds) *Vertebrate Mating Systems*, 106–139. World Scientific, Singapore City, Singapore.
- Castelló JR (2016) *Bovids of the World*. Princeton University Press, Princeton, New Jersey, USA and Oxford, UK.
- Clutton-Brock TH (1988) Reproductive success. In: Clutton-Brock TH (ed) *Reproductive Success*, 472–485. University of Chicago Press, Chicago, Illinois, USA.

- Clutton-Brock TH (1989) Mammalian mating systems. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 236: 339–372.
- Clutton-Brock TH (2016) *Mammal Society*. John Wiley & Sons, Chichester, UK.
- Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organisation. *Journal of Zoology London* 183: 1–39.
- Clutton-Brock TH, Guinness FE, Albon SD (1982) *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago, Illinois, USA.
- Coltman DW, Bancroft DR, Robertson A, Smith JA, Clutton-Brock TH (1999) Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Molecular Ecology* 8: 1199–1209.
- Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C (2002) Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269: 165–172.
- Coltman DW, O'Donoghue P, Jorgenson JT, Hogg JT, Strobeck C, Festa-Bianchet M (2003) Undesirable evolutionary consequences of trophy hunting. *Nature* 426: 655–658.
- Corlatti L, Caroli M, Pietrocini V, Lovari S (2013) Rutting behaviour of territorial and nonterritorial male chamois: is there a home advantage? *Behavioural Processes* 92: 118–124.
- Corlatti L, Bassano B, Polakova R, Fattorini L, Pagliarella M, Lovari S (2015) Preliminary analysis of reproductive success in a large mammal with alternative mating tactics, the Alpine chamois, *Rupicapra r. rupicapra*. *Biological Journal of the Linnean Society* 116: 117–123.
- Corlatti L, Bassano B, Lovari S (2020) Weather stochasticity and alternative reproductive tactics in northern chamois. *Biological Journal of the Linnean Society* 130: 359–364.
- Corlatti L, Iacolina L, Safner T, Apollonio M, Buzan E, Ferretti F et al. (2022a) Past, present and future of chamois science. *Wildlife Biology* 4: e01025.
- Corlatti L, Herrero J, Ferretti F, Anderwald P, García-González R, Hammer S, Nores C, Rossi L, Lovari S (2022b) Northern chamois *Rupicapra rupicapra* (Linnaeus, 1758) and southern chamois *Rupicapra pyrenaica* Bonaparte, 1845. In: Corlatti L, Zachos F (eds) *Handbook of the Mammals of Europe – Terrestrial Cetartiodactyla*, 325–366. Springer Nature, Heidelberg, Germany.
- Cotza A, Corlatti L, Ferretti F, Tomassini O, Santoro J, Bassano B, Lovari S (2023) Alternative reproductive tactics: a fixed trait in a large mammal? *Animal Behaviour* 196: 165–181.
- Cransac N, Hewison AJM, Gaillard JM, Cugnasse JM, Maublanc ML (1997) Patterns of mouflon (*Ovis gmelini*) survival under moderate environmental conditions: effects of sex, age, and epizootics. *Canadian Journal of Zoology* 75: 1867–1875.
- Crook JH (1964) The evolution of social organisation and visual communication in the weaver birds (Ploceinae). *Behaviour Supplement* 10: 1–178.
- Crow JF (1958) Some possibilities for measuring selection intensities in man. *Human Biology* 30: 1–13.
- Damm GR, Franco N (2014) *CIC Caprinae Atlas of the World*. CIC International Council for Game and Wildlife Conservation, Budakeszi, Hungary, in cooperation with Rowland Ward Publications, Johannesburg, South Africa.
- Davies NB, Krebs JR, West SA (2012) *An Introduction to Behavioural Ecology*. Wiley-Blackwell, Oxford, UK.
- Dawkins R, Krebs JR (1978) Animal signals: information or manipulation. In: Krebs JR, Davies NB (eds) *Behavioural Ecology: an Evolutionary Approach*, 282–309. Blackwell, Oxford, UK.
- Dunn SJ, Waits LP, Byers JA (2012) Genetic versus census estimators of the opportunity for sexual selection in the wild. *American Naturalist* 179: 451–462.
- Emlen ST, Oring LW (1977) Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215–223.
- Fedosenko AK, Blank DA (2001) *Capra sibirica*. *Mammalian Species* 675: 1–13.
- Fedosenko AK, Blank DA (2005) *Ovis ammon*. *Mammalian Species* 773: 1–15.
- Ferretti F, Costa A, Corazza M, Pietrocini V, Cesaretti G, Lovari S (2014) Males are faster foragers than females: intersexual differences of foraging behaviour in the Apennine chamois. *Behavioural Ecology and Sociobiology* 68: 1335–1344.
- Festa-Bianchet M (2017) When does selective hunting select, how can we tell, and what should we do about it? *Mammal Review* 47: 76–81.
- Festa-Bianchet M, Pelletier F, Jorgenson JT, Feder C, Hubbs A (2014) Decrease in horn size and increase in age of trophy sheep in Alberta over 37 years. *Journal of Wildlife Management* 78: 133–141.
- Firman RC, Gasparini C, Manier MK, Pizzari T (2017) Postmating female control: 20 years of cryptic female choice. *Trends in Ecology and Evolution* 32: 368–382.
- Garel M, Forsyth DM, Loison A, Dubray D, Jullien JM, Tustin KG, Maillard D, Gaillard JM (2011) Age-related male reproductive effort in two mountain ungulates of contrasting sexual size dimorphism. *Canadian Journal of Zoology* 89: 929–937.
- Geist V (1971) *Mountain Sheep: a Study in Behavior and Evolution*. University of Chicago Press, Chicago, Illinois, USA.
- Geist V (1974a) On the relationship of ecology and behaviour in the evolution of ungulates: theoretical considerations. In: Geist V, Walther F (eds) *The Behaviour of Ungulates and Its Relation to Management*, 235–246. IUCN Publications, Unwin Brothers Limited, Morges, Switzerland.

- Geist V (1974b) On the relationship of social evolution and ecology in ungulates. *Annual Review of Ecology and Systematics* 8: 193–207.
- Geist V (1978) *Life Strategies, Human Evolution, Environmental Design*. Springer-Verlag, New York, New York, USA.
- Geist V (1985) On evolutionary patterns in the Caprinae with comments on the punctuated mode of evolution, gradualism and a general model of mammalian evolution. In: Lovari S (ed) *The Biology and Management of Mountain Ungulates*, 15–30. Croom Helm, London, UK.
- Geist V (1987) On the evolution of the Caprinae. In: Soma H (ed) *The Biology and Management of Capricornis and Related Mountain Antelopes*, 3–40. Croom Helm, London, UK.
- Gentry AW (2000) Caprinae and Hippotragini (Bovidae, Mammalia) in the Upper Miocene. In: Vrba ES, Schaller GB (eds) *Antelopes, Deer and Relatives: Fossil Record, Behavioural Ecology, Systematics and Conservation*, 65–83. Yale University Press, New Haven, Connecticut, USA and London, UK.
- Goldizen AW (1988) Tamarin and marmoset mating systems: unusual flexibility. *Trends in Ecology and Evolution* 3: 36–40.
- Gosling LM (1986) The evolution of mating strategies in male antelopes. In: Rubenstein DI, Wrangham RW (eds) *Ecological Aspects of Social Evolution*, 133–160. Princeton University Press, Princeton, New Jersey, USA.
- Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barančok P, Alonso JLB et al. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change* 2: 111–115.
- Gross MR (1996) Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* 11: 92–98.
- Habibi K (1987) Behavior of aoudad (*Ammotragus lervia*) during the rutting season. *Mammalia* 51: 497–513.
- Habibi K (1994) *The Desert Ibex: Life History, Ecology and Behaviour of the Nubian Ibex in Saudi Arabia*. Immel, London, UK.
- von Hardenberg A, Bassano B, Peracino A, Lovari S (2000) Male Alpine chamois occupy territories at hotspots before the mating season. *Ethology* 106: 617–630.
- Hassanin A, Pasquet E, Vigne JD (1998) Molecular systematics of the subfamily Caprinae (Artiodactyla: Bovidae) as determined from cytochrome *b* sequences. *Journal of Mammalian Evolution* 5: 217–236.
- Herrero J, Garín I, García-Serrano A, García-González R, Aldezabal A (2002) Grouping patterns in a forest dwelling population of Pyrenean chamois. *Pirineos* 157: 89–101.
- Hogg JT (1984) Mating in bighorn sheep: multiple creative male strategies. *Science* 225: 526–529.
- Hogg JT (1987) Intrasexual competition and mate choice in Rocky Mountain bighorn sheep. *Ethology* 75: 119–144.
- Hogg JT (1988) Copulatory tactics in relation to sperm competition in Rocky Mountain sheep. *Behavioral Ecology and Sociobiology* 22: 49–59.
- Hogg JT, Forbes SH (1997) Mating in bighorn sheep: frequent male reproduction via a high-risk ‘unconventional’ tactic. *Behavioral Ecology and Sociobiology* 41: 33–48.
- Isvaran K (2005) Variation in male mating behaviour within ungulate populations: patterns and processes. *Current Science* 89: 1192–1199.
- Jaeggi AV, Miles MI, Festa-Bianchet M, Schradin C, Hayes LD (2020) Variable social organisation is ubiquitous in Artiodactyla and probably evolved from pair-living ancestors. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 287: 20200035.
- Jarman PJ (1974) Social organisation of antelopes in relation to their ecology. *Behaviour* 48: 215–267.
- Jarman PJ (1983) Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biological Reviews* 58: 485–520.
- Jones AG (2009) On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution* 63: 1673–1684.
- van de Kerk M, Arthur S, Bertram M, Borg B, Herriges J, Lawler J, Mangipane B, Lambert Koizumi C, Wendling B, Prugh L (2020) Environmental influences on Dall’s sheep survival. *Journal of Wildlife Management* 84: 1127–1138.
- Kishimoto R (2003) Social monogamy and social polygyny in a solitary ungulate, the Japanese serow (*Capricornis crispus*). In: Reichard UH, Boesch C (eds) *Monogamy – Mating Strategies and Partnerships in Birds, Humans and Other Mammals*, 147–160. Cambridge University Press, Cambridge, UK.
- Kishimoto R, Kawamichi T (1996) Territoriality and monogamous pairs in a solitary ungulate, the Japanese serow, *Capricornis crispus*. *Animal Behaviour* 52: 673–682.
- Kokko H, Rankin DJ (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361: 319–334.
- Krakauer AH, Webster MS, Duval EH, Jones AG, Shuster SM (2011) The opportunity for sexual selection: not mismeasured, just misunderstood. *Journal of Evolutionary Biology* 24: 2064–2071.
- Krämer A (1969) Soziale Organisation und Sozialverhalten einer Gemspopulation *Rupicapra rupicapra* der Alpen. *Zeitschrift für Tierpsychologie* 26: 889–964.
- Krebs JR, Davies NB (1987) *An Introduction to Behavioural Ecology*. Blackwell, Oxford and London, UK.
- Lane JE, Forrest MNK, Willis CKR (2011) Anthropogenic influences on natural animal mating systems. *Animal Behaviour* 81: 909–917.
- Loison A, Gaillard J-M, Pélabon C, Yoccoz NG (1999a) What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research* 1: 611–633.

- Loison A, Festa-Bianchet M, Gaillard J-M, Jorgenson JT, Jullier J-M (1999b) Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80: 2539–2554.
- Lott DF (1991) *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge University Press, Cambridge, UK.
- Lovari S (1984) Herding strategies of male Abruzzo chamois on the rut. *Acta Zoologica Fennica* 172: 91–92.
- Lovari S, Apollonio M (1994) On the rutting behaviour of the Himalayan goral *Nemorhaedus goral* (Hardwicke, 1825). *Journal of Ethology* 12: 25–34.
- Lovari S, Locati M (1994) Site features of territorial dung-marking in mainland serow. *Mammalia* 58: 153–156.
- Lovari S, Ale SB (2001) Are there multiple mating strategies in blue sheep? *Behavioural Processes* 53: 131–135.
- Lovari S, Sacconi F, Trivellini G (2006) Do alternative strategies of space use occur in male Alpine chamois? *Ethology Ecology and Evolution* 18: 221–231.
- Lovari S, Bartolommei P, Meschi F, Pezzo F (2008) Going out to mate: excursion behaviour of female roe deer. *Ethology* 114: 886–896.
- Lovari S, Pellizzi B, Boesi R, Fusani L (2009) Mating dominance amongst male Himalayan tahr: blonds do better. *Behavioural Processes* 81: 20–25.
- Lovari S, Franceschi S, Chiatante G, Fattorini L, Fattorini N, Ferretti F (2020) Climatic changes and the fate of mountain herbivores. *Climatic Change* 162: 2319–2337.
- Lukas D, Clutton-Brock TH (2013) The evolution of social monogamy in mammals. *Science* 341: 526–530.
- Mainguy J, Côté SD, Cardinal E, Houle M (2008) Mating tactics and mate choice in relation to age and social rank in male mountain goats. *Journal of Mammalogy* 89: 626–635.
- Masini F, Lovari S (1988) Systematics, phylogenetic relationships and dispersal of the chamois (*Rupicapra* spp). *Quaternary Research* 30: 339–349.
- Matiu M, Crespi A, Bertoldi G, Carmagnola CM, Marty C, Morin S et al. (2021) Observed snow depth trends in the European Alps: 1971 to 2019. *The Cryosphere* 15: 1343–1382.
- McLain DK (1992) Population density and the intensity of sexual selection on body length in spatially or temporally restricted natural populations of a seed bug. *Behavioral Ecology and Sociobiology* 30: 347–356.
- Michel S, Ghoddousi A (2020a) *Ovis vignei* (errata version published in 2021). The IUCN Red List of Threatened Species 2020: e.T54940655A195296049. <https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T54940655A195296049.en>
- Michel S, Ghoddousi A (2020b) *Ovis gmelini*. The IUCN Red List of Threatened Species 2020: e.T54940218A22147055. <https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T54940218A22147055.en>
- Montana L, Rousseu F, Garant D, Festa-Bianchet M (2020) Siring success in kangaroos: size matters for those in the right place at the right time. *Behavioral Ecology* 31: 750–760.
- Morimoto J, McDonald GC, Smith E, Smith DT, Perry JC, Chapman T, Pizzari T, Wigby S (2019) *Sex peptide receptor*-regulated polyandry modulates the balance of pre- and post-copulatory sexual selection in *Drosophila*. *Nature Communications* 10: 283.
- Munton PN (1985) The ecology of the Arabian tahr (*Hemitragus jayakari* Thomas 1894) and a strategy for the conservation of the species. *Journal of Oman Studies* 8: 11–48.
- Myslenkov AI, Voloshina IV (1978) Mating behavior of *Nemorhaedus goral caudatus* Milne-Edwards. *Bulletin of the Moscow Society of Naturalists* 1: 30–39.
- Myslenkov AI, Voloshina IV (1998) Sexual behavior of Amur goral. Proceedings of the Second World Conference on Mountain Ungulates. *Collana Scientifica Parco Nazionale Gran Paradiso* 1/98: 75–80.
- Nievergelt B (1981) *Ibexes in an African Environment*. Springer, Berlin, Germany.
- Nunney L (1993) The influence of mating system and overlapping generations on effective population size. *Evolution* 47: 1329–1341.
- Ochiai K, Susaki K (2002) Effects of territoriality on population density in the Japanese serow (*Capricornis crispus*). *Journal of Mammalogy* 83: 964–972.
- Owens IPF, Bennett PM (1997) Variation in mating system among birds: ecological basis revealed by hierarchical comparative analysis of mate desertion. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 264: 1103–1110.
- Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Alonso JLB et al. (2012) Recent plant diversity changes on Europe's mountain summits. *Science* 336: 353–355.
- Pérez-Barbería FJ, Gordon IJ, Pagel M (2002) The origins of sexual dimorphism in body size in ungulates. *Evolution* 56: 1276–1285.
- Powell D, Speeg B, Li S, Blumer E, McShea W (2013) An ethogram and activity budget of captive Sichuan takin (*Budorcas taxicolor tibetana*) with comparisons to other Bovidae. *Mammalia* 77: 391–401.
- Rice CG (1988) Reproductive biology of Nilgiri tahr, *Hemitragus hylocrius* (Mammalia: Bovidae). *Journal of Zoology* 214: 269–284.
- Ritchot Y, Coltman DW, Festa-Bianchet M, Pelletier F (2021) Determinants and long-term costs of early reproduction in males of a polygynous mammal. *Ecology and Evolution* 11: 6829–6845.
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.
- Rugheiti M, Festa-Bianchet M (2011) Seasonal changes in sexual-size dimorphism in northern chamois. *Journal of Zoology* 284: 257–264.

- Schaller GB (1977) *Mountain Monarchs. Wild Sheep and Goats of the Himalaya*. University of Chicago Press, Chicago, Illinois, USA.
- Schaller GB, Mirza ZB (1971) On the behavior of Kashmir markhor (*Capra falconeri cashmiriensis*). *Mammalia* 35: 548–565.
- Schaller GB, Laurie A (1974) Courtship behaviour of the wild goat. *Zeitschrift für Säugetierkunde* 39: 87–99.
- Schaller GB, Mirza ZB (1974) On the behavior of Punjab Urial (*Ovis orientalis punjabensis*). In: Geist V, Walther F (eds) *The Behaviour of Ungulates and Its Relation to Management*, 306–323. IUCN Publications, Unwin Brothers Limited, Morges, Switzerland.
- Shackleton DM (ed) (1997) *Wild Sheep and Goats and their Relatives. Status Survey and Conservation Action Plan for Caprinae*. IUCN, Gland, Switzerland and Cambridge, UK.
- Shuster SM (2009) Sexual selection and mating systems. *Proceedings of the National Academy of Sciences of the United States of America* 106: 10009–10016.
- Shuster SM, Wade MJ (2003) *Mating Systems and Strategies*. Princeton University Press, Princeton, New Jersey, USA.
- Shuster SM, Willen RM, Keane B, Solomon NG (2019) Alternative mating tactics in socially monogamous prairie voles, *Microtus ochrogaster*. *Frontiers in Ecology and Evolution* 7: 7.
- Singer FJ, Zeigenfuss LC (2002) Influence of trophy hunting and horn size on mating behavior and survivorship of mountain sheep. *Journal of Mammalogy* 83: 682–698.
- Smith TE (1976) *Reproductive Behavior and Related Social Organization of the Muskox on Nunivak Island*. MSc thesis, University of Alaska, Fairbanks, Alaska, USA.
- Smith TE (1989) The role of bulls in pioneering new habitats in an expanding muskox population on the Seward Peninsula, Alaska. *Canadian Journal of Zoology* 67: 1096–1101.
- Snook RR (2017) Sexual selection and its impact on mating systems. In: Losos JB (ed) *The Princeton Guide to Evolution*, 634–642. Princeton University Press, Princeton, New Jersey, USA.
- Sullivan BK, Ryan MJ, Verrell PA (1995) Female choice and mating system structure. In: Heatvole H (ed) *Amphibian Biology*, 469–517. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.
- Szemán K, Liker A, Székely T (2021) Social organization in ungulates: revisiting Jarman's hypothesis. *Journal of Evolutionary Biology* 34: 604–613.
- Taborsky M, Oliveira RF, Brockmann HJ (2008) The evolution of alternative reproductive tactics: concepts and questions. In: Oliveira RF, Taborsky M, Brockmann HJ (eds) *Alternative Reproductive Tactics: An Integrative Approach*, 1–21. Cambridge University Press, Cambridge, UK.
- Takada H, Minami M (2021) Open habitats promote female group formation in a solitary ungulate: the Japanese serow. *Behavioral Ecology and Sociobiology* 75: 60.
- Takada H, Washida A, Yano R, Tezuka N, Minami M (2023) Evolution from monogamy to polygyny: insights from the solitary Japanese serow. *Behavioral Ecology and Sociobiology* 77: 28.
- Telwala Y, Brook BW, Manish K, Pandit MK (2013) Climate-induced elevational range shifts and increase in plant species richness in a Himalayan biodiversity epicentre. *PLoS ONE* 8: e57103.
- Tidière M, Gaillard J-M, Garel M, Lemaître J-F, Toïgo C, Pélabon C (2020) Variation in the ontogenetic allometry of horn length in bovids along a body mass continuum. *Ecology and Evolution* 10: 4104–4114.
- Toïgo C, Gaillard J-M, Festa-Bianchet M, Largo E, Michallet J, Maillard D (2007) Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. *Journal of Animal Ecology* 76: 679–686.
- Wade MJ, Arnold SJ (1980) The intensity of sexual selection in relation to male sexual behavior, female choice and sperm precedence. *Animal Behaviour* 28: 446–461.
- Wasser SK, Waterhouse ML (1983) The establishment and maintenance of sex biases. In: Wasser SK (ed) *Social Behavior of Female Vertebrates*, 19–35. Academic Press, New York, New York, USA.
- Weinberg P, Lortkipanidze B (2022) Caucasian Tur *Capra caucasica* Güldenstaedt et Pallas, 1783. In: Corlatti L, Zachos F (eds) *Handbook of the Mammals of Europe – Terrestrial Cetartiodactyla*, 433–458. Springer Nature, Heidelberg, Germany.
- Wickler W, Seibt U (1983) Monogamy: an ambiguous concept. In: Bateson P (ed) *Mate Choice*, 33–50. Cambridge University Press, Cambridge, UK.
- Willisch CS, Neuhaus P (2010) Social dominance and conflict reduction in rutting male Alpine ibex, *Capra ibex*. *Behavioral Ecology* 21: 372–380.
- Willisch CS, Biebach I, Koller U, Bucher T, Marreros N, Ryser-Degiorgis M-P, Keller L, Neuhaus P (2012) Male reproductive pattern in a polygynous ungulate with a slow life-history: the role of age, social status and alternative mating tactics. *Evolutionary Ecology* 26: 187–206.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Data collection method.

Appendix S2. Full list of literature.