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Social behaviour as a predominant driver of sexual, age-dependent and reproductive segregation in Mediterranean mouflon

Gilles Bourgoin [a, b, *], Pascal Marchand [c], A. J. Mark Hewison [d], Kathreen E. Ruckstuhl [e], Mathieu Garel [c]

[a] Univ Lyon, VetAgro Sup, Marcy L'Etoile, France
[b] Univ Lyon, Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Evolutive (LBBE), Villeurbanne, France
[c] Office National de La Chasse et de La Faune Sauvage, Unité Faune de Montagne, Juvignac, France
[d] CEFS, Université de Toulouse, INRA, Castanet Tolosan, France
[e] Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada

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Segregation between the sexes or related to age and/or reproductive status is common in many animal taxa, particularly in dimorphic species. The causes of this segregation remain difficult to disentangle, despite numerous attempts. This is probably due to the difficulty of obtaining sufficient data on animal behaviour (e.g. habitat use, activity budgets) and group composition (age/sex and reproductive status) during the various phases of the species' reproductive cycle. Based on an intensive long-term monitoring of a Mediterranean mouflon, *Ovis gmelini musimon* × *Ovis* sp., population, we concurrently assessed five hypotheses for segregation linked to forage selection (FSH), reproductive strategy (RSH), social preference (SPH), activity budget (ABH), and weather sensitivity (WSH). We found marked segregation between most age/sex classes. Age-dependent segregation among males was increasingly marked as their age difference increased and segregation between the sexes also increased as males became older and larger. Over the year, segregation between sex, age and reproductive status classes was lowest during the rut. We also observed the highest synchrony of activity in groups composed of individuals of similar age/sex class or reproductive status. Females occurred closer to both secure and high-quality food habitats, especially during the lambing and rearing periods, whereas males used less secure and lower quality habitats as they aged. Differences in habitat use between age/sex classes provided partial or full support for the RSH and FSH. Large males were preferentially observed at higher altitude than females during hot summer days to buffer against heat stress, in agreement with the WSH. A preference for interacting and grouping with peers that express similar activity patterns (ABH and SPH) appears to be the main driver of segregation in this population. Our study confirms the strong multifactorial nature of segregation in ungulates.

Segregation between males and females, or between individuals of different ages and/or reproductive status, is common across the animal kingdom (Ruckstuhl & Neuhaus, 2005). This is particularly true in sexually dimorphic herbivores in which sexual segregation is particularly widespread and pronounced (e.g. red deer, *Cervus elaphus*: Alves, da Silva, Soares, & Fonseca, 2013; fallow deer, *Dama dama*: Ciuti & Apollonio, 2008; bighorn sheep, *Ovis canadensis*: Geist, 1971; Ruckstuhl, 1998; Svalbard reindeer, *Rangifer tarandus platyrhynchus*: Loe et al., 2006; Tibetan argali, *Ovis ammon hodgsoni*: Singh, Bonenfant, Yoccoz, & Côté, 2010). Segregation is hypothesized to be the result of differences in habitat use or social behaviour (Bon & Campan, 1996; Conradt, 1999, 2005; Ruckstuhl, 2007; Table 1). However, differences in body size are considered the main driver of segregation due to the potential links with resource requirements, reproductive strategies, activity patterns, social preferences and sensitivity when faced with adverse weather conditions (Ruckstuhl & Neuhaus, 2005).

First, differential use of habitats between animals of different age/sex classes (i.e. habitat segregation) may be explained by several nonexclusive mechanisms. The two most often proposed hypotheses rely on different resource requirements ('forage

* Correspondence: G. Bourgoin, VetAgro Sup, 1 Avenue Bourgelat, BP 83, F-69280 Marcy l'Etoile, France.
E-mail address: gilles.bourgoin@vetagro-sup.fr (G. Bourgoin).

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Table 1
Hypotheses tested in this study and the corresponding predictions according to sex, reproductive status and age for the Mediterranean mouflon

Hypotheses	General predictions		Detailed predictions					Source
	Main assumptions	Seasonal pattern (outside rut)	Females–adult males	Reproductive status of females		Age of males		
				Reproductive females–adult males	Reproductive –nonreproductive females	Females–males of different age classes	Adult males –younger males	
Reproductive strategy hypothesis (RSH)	Each sex chooses habitat favouring reproductive success	Mostly around lambing and early lactation periods	Males closer to food-rich habitats, even if less secure	**Females with lambs closer to refuge habitats during early lactation**		Use of food-rich habitats, even if less secure, increases as males become older		Bowyer, 1984; Jakimchuk et al., 1987; Main & Coblentz, 1990, 1996; Main et al., 1996
Forage selection hypothesis (FSH)	Different nutritional requirements and processing abilities. Smaller individuals in habitats with higher quality food compared to larger individuals selecting abundant and lower quality food	No pattern (except around lambing and lactation for reproductive females)	**Males in habitats with abundant but lower quality food**	**Different nutritional requirements during the end of gestation and early lactation for reproductive females → Higher segregation**	**→ Segregation**	**Increased use of habitats with abundant low-quality food as males become older**		Barboza & Bowyer, 2001; Beier, 1987; Bowyer, 1984
Weather sensitivity hypothesis (WSH)	Large individuals are more sensitive to harsh weather. They select habitats buffering harsh climatic conditions	During season with harsh weather conditions	**Large males in habitats buffering harsh climatic conditions**	*Not related to reproductive status*		Increased use of habitats buffering harsh climatic conditions as males become older		Conradt et al., 2000
Social-preference hypothesis (SPH)	Individuals prefer to interact and group with peers	No pattern	**Segregation, except during rut**	No specific patterns		**As males become older, segregation with females increases but decreases with adult males**		Bon, 1991; Bon & Campan, 1996
Activity budget hypothesis (ABH)	Differences in activity associated with body mass dimorphism and/or different nutritional requirements lead to segregation	No pattern (except around lambing and lactation for reproductive females)	**Lower synchrony in mixed-sex groups**	*Lower synchrony*	**Lower synchrony in heterogeneous reproductive status groups**	**Synchrony decreases with higher body size dimorphism**		Conradt, 1998a; Ruckstuhl, 1998, 1999

Supported, or partially supported, detailed predictions in this study are in bold. Predictions in italics were not tested here.