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Society formation and maintenance in yellow-bellied marmots

Daniel T. Blumstein [a, b, *]

[a] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, U.S.A.
[b] The Rocky Mountain Biological Laboratory, Crested Butte, CO, U.S.A.

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Yellow-bellied marmots, *Marmota flaviventer*, are facultatively social and may form multigenerational societies, which are characterized by individuals sharing and defending space, possessing the ability to distinguish group members from outsiders and potentially persisting for many generations. I review some 63 years of continuous study that has revealed a number of insights about the adaptive value of sociality and societies. Because of their facultative sociality and because we have studied social behaviour and societies a variety of different of ways over the years, this social variation makes it difficult to make simple summary statements about society structure and formation. None the less, this variation may make them a good system in which to study incipient society formation.

The yellow-bellied marmots, *Marmota flaviventer*, in and around the Rocky Mountain Biological Laboratory (Gothic, CO, U.S.A.) are one of the world's best-studied mammals since the late Kenneth B. Armitage of the University of Kansas began marking and following the fate of individuals in the summer of 1962 (Armitage, 2014; Blumstein, 2013). Armitage directed the study until 2001 when I took over leadership, which I currently co-direct with Julien G. A. Martin. Now, 63 years on, the marmots have become a model of how a hibernating rodent responds to environmental changes as well as providing foundational insights into communication, antipredator behaviour and social behaviour. My goal in this essay is to focus on whether marmots can be viewed as a society, which, following Moffett's (2024) definition, requires animals to share and defend space and have the ability to distinguish members from nonmembers in groups that may persist for generations. Armitage (2014) described yellow-bellied marmots from a female's perspective as matrilineal and from a male's perspective as harem polygynous in that they are associated with one or more matrilines and, overall, described the species as facultatively social.

Marmots live in physical areas that have burrows that provide protection from the elements and predators, as well as places to sleep and hibernate. The population at these sites, known as 'colonies', may contain one or more territorial groups, or 'societies' sensu this special issue, of marmots, and large sites may contain many more marmots than small sites. Within a society, the members may or may not hibernate together or sleep together, but nevertheless they share space and interact amicably with each other, and both sexes may defend their burrows and foraging area from others. At our study site, marmots hibernate for 7–8 months per year; emerging in mid-April to May and again in September or October.

Marmot colonies are in areas that have been populated by marmots before (a Zen-like statement that requires some explanation). Some colonies are in clearings; others are in more contiguous habitat. Larger cleanings and contiguous habitat can support more marmots. In a cross-sectional study that compared habitat characteristics associated with where marmots lived with a set of adjacent places where they did not live, we found that visibility from their main burrows and the presence of rocks around their burrows were more important than plentiful vegetation or other food characteristics (Blumstein et al., 2006). Specifically, the presence of large rocks provides places where marmots can look for predators, and we assumed that burrows dug in rocky ground provided protection from fossorial predators like badgers, *Taxidea taxus*, and black bears, *Ursus americanus*. Interestingly, when we compared locations where marmots persisted (at the time) for over 40 years versus those that had gone periodically extinct, the same 'safety' factors emerged as important determinants of where marmots are. Some societies may persist for generations simply because they have the luck to exist in a good physical location (see Smith et al., 2023).

Armitage emphasized that, within a colony, breeding females may form one or more matrilines, which each control a territory and represent the female-based societies of this species.

* Corresponding author.
E-mail address: marmots@ucla.edu.

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Matrilines form when tolerant females permit their yearling daughters to remain in their territory and are defined as a female and her female descendent kin. Since 2003, about 33 % of females lived alone and, if they bred, they lived with their young of the year and predispersal yearlings. These females lived in simple nuclear families. The remainder lived in multifemale matrilineal societies in that they included multiple generations of offspring, among them reproductively mature individuals that had stayed with the group. Once the original female dies, a matriline will persist as long as her descendants inhabit the same location (e.g. Armitage, 1984). Natal dispersal occurs annually before the newborns of the year emerge, and virtually all yearling males and about half of the yearling females disperse. Not all females tolerate the presence of their daughters. A notable female physically forced her litter out (which included her biting the tail off at least one of them!). While alive, she was the only breeding female at the Marmot Meadow Colony. Still, a society of her descendants emerged in her territory after she died, when several of her not-yet-dispersed female yearlings stayed on and reproduced. A matrilineal society contained at maximum 13 reproductively mature females.

Perhaps it is time to be more specific about marmot social structure, which as Kappeler (2019) noted, can be defined in several ways. Rather than focusing on matrilines specifically, in the past 2.5 decades we have focused on these societies defined not simply by space use but also by social interactions. Studied this way the composition of marmot societies largely parallel matrilines. However, by focusing on social interactions, we see there is substantial and consequential individual variation in social interactions. Indeed, while all members of the society share space and may defend the burrows and foraging areas they occupy, not all individuals interact with each other in similar ways.

Female defence is typically done by members who do not permit outside females into their matrilineal territories; intruders are chased away immediately and female migration into the area is only seen after all the residents die. The death of a female in a multifemale society will not result in a new female moving in; the remaining residents will defend their society from immigrants.

Females have a (roughly) size-based dominance hierarchy within their societies (Huang et al., 2011). Unlike in some mongooses or in meerkats (family Herpestidae), we do not typically see collective defence. Rather, in the relatively rare situations when a foreign female comes into a territory, individuals acting on their own ultimately chase her out (female yellow-bellied marmots have not been observed engaging in escalated fights as males occasionally do). Additional research is needed to better understand the rules that determine who engages in territorial defence.

Adult males may be associated with one or more matrilines in a colony. Males (for whom dominance rank is also size-based; Huang et al., 2011) directly chase out male intruders. In some cases, we see multiple males co-occupying in the same matriline. Yet, in these multimale groups, we have no evidence of any sort of coordinated male coalitionary defence against intruder males, and we rarely see females acting to keep them out (Olson & Blumstein, 2010). Here too, more research is needed to better understand the rules that determine who engages in territorial defence.

As Armitage noted, matrilines may persist over many generations and contain numerous related females across generations, but society structure varies annually based on dispersal, mortality and recruitment. At a single point in time, Armitage and Schwartz (2000) showed that there is an optimal matriline size of around three females, but societies as we define them here may contain many more individuals (average = 13, range 3–31; e.g. Philson et al., 2024). Still, life in a society is somewhat optional in this species. In cases where a female actively drives out her daughters and breeds alone, she may share space with a single adult male and their predispersal offspring until (and if) their young of the year emerge from their natal burrows. In other cases, the male may include a solitary female in his larger home range and harem.

How do marmots distinguish their fellow society members from outsiders? Marmots almost certainly know other individuals. We have studied acoustic and olfactory discrimination, and our studies of visual predator discrimination (Blumstein et al., 2009) suggest that marmots potentially use visual features to help identify individuals.

Marmots utter alarm calls that contain information about age, sex and individual identity (Blumstein & Munos, 2005). Unlike contact calls or 'names' that some species vocally communicate, conditions favouring individually specific alarm calls may stem from understanding caller reliability to aid in risk assessment. In principle, an unreliable caller's calls may be discounted. Experiments have shown that marmots are sensitive to caller reliability and this indeed may select for individually specific calls (Blumstein et al., 2004). However, comparative work on the evolution of individually specific calls in marmots, prairie dogs and ground squirrels has shown that group size is correlated with the degree to which calls are individually specific (Pollard & Blumstein, 2011). This suggests that alarm calls may have social recognition functions in addition to being associated with predator detection.

Marmots have anal and facial glands (Armitage, 1976) that produce olfactory secretions, which in principle, could be used to discriminate among individuals, as seen in other mammals. However, we have not yet been able to conclusively demonstrate this in the field. To study this, we conducted neighbour–stranger and resident–stranger tests. Neighbours were defined as individuals in adjacent territories with whom residents could have interacted with, while strangers were individuals from other parts of the valley where individuals had no ability to interact with. We found no evidence that resident female marmots responded differently to anogenital secretions from neighbours or strangers (Cross et al., 2013). Moreover, resident males seemingly do not discriminate between other resident males and nonresident males using olfactory cues (Olson & Blumstein, 2010).

Armitage (1987) questioned the importance of animals acting to maximize their indirect fitness and emphasized that marmots likely focused on maximizing their direct fitness. Ultimately, because females can permit their daughters to stay, societies are composed of female relatives. Thus, it is difficult to tease apart preferential behaviour based on kinship versus familiarity.

In recent years, my focus has been to understand the causes and consequences of the social structure within marmot societies, which we define by space use overlap and/or from observed (typically) affiliative social interactions (marmots may sit amicably with each other, allogroom each other, forage together or engage in social play). We then calculate social network statistics that emerge from observed social interactions within the matrilines (e.g. Blumstein et al., 2018; Fuong & Blumstein, 2019; Montero et al., 2020; Philson & Blumstein, 2023a, 2023b; Philson et al., 2022). Interestingly, like European badgers, *Meles meles* (Macdonald & Newman, 2022), yellow-bellied marmot society members are certainly social but they are not particularly cooperative (Blumstein, 2013) from the perspective that they do not coordinate defence or engage in obviously altruistic behaviours.

At times, a society may die out (Armitage, 2014) and a new one is formed within the same area by the settlement of a new yearling female who migrated from another location. That said, in years with high population densities, yearling (or sometimes 2-year-old) females may dig new burrows around the territory of their natal colony. In some cases, they continued to be recognized by their birth society, but in other cases, they were no longer treated as

members of that matriline and restricted their interactions with them. Some of these peripheral sites persisted for some years, but invariably were not as good as more persistent locations, and the new residents and their offspring eventually died out.

From a male's perspective, the species is harem polygynous (Armitage, 2014). Males obligately disperse as yearlings; in rare cases, a male will remain in or around his natal matriline or colony. Thus, most males immigrate to another society or several adjacent societies where they are likely unrelated to existing group members. The most successful males defend and reproduce with multiple females and they do so by defending one or more matrilines. In colonies occupied by several territories, males may defend more than a single female within one matriline or defend females across multiple societies.

Most males never reproduce and hence the species is characterized by substantial reproductive skew. In some situations, multiple males may share space and females (Olson & Blumstein, 2010). In this situation, molecular work has shown that sometimes a single male sires all offspring, while in other situations, females mate with multiple males, leading to mixed paternity litters (Olson et al., 2012). The most successful males are those that have long tenures. We have no evidence of active inbreeding avoidance (Olson et al., 2012); marmots emerge from hibernation and either decide to mate with whomever is there or forgo reproduction for that year. Since marmots become reproductively mature after two hibernations, those males with longer tenures often mate with their daughters. Inbreeding is costly. Inbred offspring are less likely to survive the summer and more likely to die over winter. But given the alternative of not mating, some degree of inbreeding is likely better than none.

Together, this social variability is a hallmark of a facultatively social species. Facultative sociality creates opportunities to study the adaptive basis of sociality, and we have learned a lot about the adaptive basis of sociality from six decades of marmot study. Yellow-bellied marmots conform to the conception of society put forward for this issue by distinguishing members from non-members and by defending a group territory. An individual may remain with the same society, and defend its territory, throughout its life, but because of natal dispersal, some marmots disperse and attempt to survive on, and defend, their own territory. Over time these animals can create a society of their own.

Data availability

No data were used for the research described in the article.

Declaration of competing interest

None.

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