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Correlates and Consequences of Dominance in a Social Rodent

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Abstract

In harem-polygynous societies, body condition is often correlated with dominance rank. However, the consequences of dominance are less clear. High-ranking males do not inevitably have the highest reproductive success, especially in systems where females mate with multiple males. In such societies, we expect male reproductive success to be more highly skewed than female reproductive success, but reproductive skew in females can still arise from rankings established within matrilineal societies. Dominance can also impact life-history decisions by influencing dispersal patterns in yearlings. To better understand the function of dominance in harem-polygynous societies, we studied the causes and consequences of dominance in yellow-bellied marmots (*Marmota flaviventris*), a social rodent with skewed male reproductive success and female reproductive suppression. Specifically, we examined body condition as a predictor and the probability of breeding, number of offspring, and dispersal as outcomes of dominance. Additionally, we looked at variation in dominance between males and females and adults and yearlings, because marmots can engage in distinct interactions depending on the type of individuals involved. We found that marmots in better body condition have higher dominance rank than those in poorer condition. In addition, adults are dominant over yearlings. Within yearlings, dominance does not influence dispersal, but those in better body condition are less likely to disperse. Within all adults, individuals in better condition produce more offspring per year. Within adult males, more dominant males have greater reproductive success. Despite previous evidence of reproductive suppression in females, we found no effects of dominance rank on female reproductive success in the current study. The function of dominance in female marmots remains enigmatic.

Introduction

Competition for resources, such as food and mates, often leads to the formation of dominance hierarchies (Wilson 1975; Wittig & Boesch 2003). Dominance is a measure that is derived from repeated agonistic interactions between individuals (Bernstein 1981; de Waal & Tyack 2003), and dominance relationships have been studied in many taxa (e.g., insects – Molet et al. 2005; McCauley 2010; reptiles – Tokarz 1985; birds – Liker & Barta 2001; freshwater fish – Earley 2006; terrestrial mammals – Wittemyer & Getz 2007; marine mammals – Cox 1981; and volant mammals – Ortega et al. 2003 as well as in many species of primates – Bernstein 1976). There is evidence that dominance relationships are not only influenced by agonistic interactions but also by affiliative interactions, such as grooming (Marolf et al. 2007), and social play (Panksepp et al. 1985; Bekoff & Byers 1998).

Dominance rank is often associated with reproductive success. In harem-polygynous species, a limited number of males defend and mate with multiple females, creating a system where male reproductive success is more skewed than female reproductive success (e.g., black-tailed prairie dogs *Cynomys ludovicianus* – Hoogland & Foltz 1982; Southern elephant seals, *Mirounga leonina* – Fabiana et al. 2004; greater sac-winged bats, *Saccopteryx bilineata* – Heckel & von Helversen 2002; Verreaux's sifakas, *Propithecus verreauxi* – Kappeler & Schäffler 2008). Thus, the consequences of dominance may be particularly pronounced in these species. In many cases, dominance drives the observed patterns of skew in both sexes (Rubenstein & Nuñez 2009).

Size is also often an important factor in dominance and consequently reproductive success. Larger individuals are typically higher ranked than smaller individuals (e.g., gray triggerfish, *Balistes capriscus* – Cleveland & Lavalli 2010; blue dashers, *Pachydiplax longipennis* – McCauley 2010; fallow deer, *Damadama* – McElligott et al. 2001; house sparrows, *Passer domesticus* – Liker & Barta 2001). In harem-polygynous systems, males are often larger than females (e.g., Jarman 1983; Weckerly 1998; Pérez-Barbería et al. 2002) and are consequently higher ranking (Gabathuler et al. 1996). Furthermore, adults are larger than subadults (Morbeck et al. 1997), and thus, adults are usually dominant to subadults (e.g., Diamond & Bond 1999; Gonyou 2001).

Female reproductive skew may emerge from dominance rankings established within matrilineal organizations. Within a matriline, dominance rank may influence access to resources and access may influence fertility (Pusey & Packer 1997; van Noordwijk & van Schaik 1999). For example, foraging success in squirrel monkeys (*Saimiri sciureus*) is contingent on female rank (Boinski et al. 2005). Likewise, spotted hyena (*Crocuta crocuta*) cubs eat more at group feeding events if their mothers have higher dominance rankings (Frank 1986). Indeed, matrilineal inheritance of rank occurs in spotted hyenas (Frank 1986; Jenks et al. 1995) and several species of primates (Horrocks & Hunte 1983; Holekamp & Smale 1991; Chapais 1996). Female rank can also affect breeding success in several mammals such as ungulates (Côté & Festa-Bianchet 2001), carnivores (Holekamp et al. 1996), and primates (Pusey et al. 1997; van Noordwijk & van Schaik 1999). Higher-ranking females can reproduce earlier (Holekamp et al. 1996), produce more young (Dunbar & Dunbar 1977; Côté & Festa-Bianchet 2001), and have more surviving offspring (Reiter et al. 1981; Pusey et al. 1997; van Noordwijk & van Schaik 1999) than subordinate females.

Dominance can additionally influence dispersal. According to the social subordination hypothesis, dominant individuals are less likely to disperse than subordinate individuals because dominant individuals can force subordinates to leave the natal territory through acts of aggression or control over resources (Christian 1970). For example, in a study of coyotes (*Canis latrans*), Gese et al. (1996) found that dispersers were low-ranking individuals who had little access to food compared with the philopatric high-ranking individuals. In addition, Cant et al. (2001) discovered that dominant banded mongooses (*Mungos mungo*) evict members from natal groups using intense aggression. In contrast to the social subordination hypothesis, the opposite situation can also occur in species where individuals gain greater benefits from dispersing, such as access to better territories (Ellsworth & Belthoff 1999).

Marmots (*Marmota* spp.) are a model system for the study of the evolutionary causes and consequences of sociality. These ground-dwelling, social rodents have a variety of mating systems (polygynous, harem-polygynous, bigamous, monogamous), which have evolved in association with varied ecological conditions (Armitage 1999). We studied dominance in yellow-bellied marmots (*Marmota flaviventris*), a species where adult males defend harems, and the most successful males have multiple mates (Armitage 1991; Olson & Blumstein 2010). About half the female yearlings (i.e., 1-yr-olds) are philopatric, and most yearling males disperse and attempt to form their own harems (Armitage 1991; Blumstein et al. 2009; Armitage et al. 2011). Despite this female philopatry, reproductive competition may suppress reproduction in 2-yr old and 3-yr old females and hence cause skew in females (Armitage 1998). In this complex system, it is likely that dominance plays a factor in community structures, resource availability, and reproductive success. There has been little formal study on either the causes or consequences of dominance in the 14 species of marmots. Two exceptions are the studies of different populations of Alpine marmots (*Marmota marmota* – King & Allainé 2002; Hackländer et al. 2003), which focused on reproductive consequences of rank and had few details about how dominance was measured or the role of agonistic and affiliative interactions on dominance relations. To our knowledge, there has been no formal study of the correlates and consequences of dominance in yellow-bellied marmots. This is a remarkable shortcoming because dominance often has both reproductive and survival consequences (Bernstein 1976; Ellis 1995; Creel & Sands 2003).

The aim of this study was to examine correlates and consequences of dominance rank in yellow-bellied marmots. To do so, we examined agonistic and affiliative interactions because dominance relationships may emerge from both types of interactions (e.g., Panksepp et al. 1985; Bekoff & Byers 1998; Fabiana et al. 2004). Because body size often is associated with rank, we hypothesized that individuals in better condition would outrank those in worse condition. Because rank may influence reproductive opportunities and likelihood of dispersal, we also examined the relationship between dominance and number of offspring produced as well as the relationship between dominance and probabilities of breeding and dispersal. In particular, we predicted that more dominant adults would have greater reproductive success, while subordinate yearlings would be more likely to disperse. And, because different dispersal dynamics exist in male and female marmots (e.g., Blumstein et al. 2009), we also conducted parallel analyses on males and females separately. Together, this comprehensive analysis of dominance in yellow-bellied marmots allows us to evaluate these predictions, as derived from patterns observed in other taxa, on this facultatively social rodent.

Methods

Yellow-bellied marmots are facultatively social, and group composition varies annually because of immigration, dispersal, recruitment, and death (Armitage 1991); thus, we analyzed each colony in each year separately. Among the individuals in our study, 44.7%, on average, remained in the same colony for the following year. Of those that dispersed, most dispersed outside our system rather than moving to a different colony site included in our study.

We determined dominance hierarchies using 6 years (2003–2008) of dyadic win–loss social interaction data, collected in the wild at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado. During these years, we followed a total of 953 individual marmots living in social groups at seven colony sites (Bench, Boulder, Horse Mound, Marmot Meadow, Picnic, River, and Town). Colony sites were defined by geographically distinct areas, between which there is rarely any exchange of individuals within a year. Within a colony site, one or more males defend females; we refer to these groups of individuals that share burrows and interact as social groups.

During mornings and afternoons, observers watched colonies from a distance ranging from 20 to 150 m (depending on habitat characteristics and habituation of colonies) and followed social interactions through binoculars and 15–45× spotting scopes. We used all-occurrence sampling of social interactions. For each interaction, we recorded the type and the initiator and recipient. We divided interaction types into affiliative and agonistic (for ethogram details, see Johns & Armitage 1979 and Nowicki & Armitage 1979). Affiliative interactions included greeting, allogrooming, sitting in close proximity, and play behavior. Agonistic interactions included overt aggression (biting, chasing, and fighting) and displacements. We excluded interactions that we could not classify clearly as affiliative or agonistic.

We calculated dominance hierarchies with interactions within seven different sets of individuals: all individuals, adults, adult males, adult females, yearlings, yearling males, and yearling females. We included all individuals in the hierarchies in which there were win–loss interaction data available, regardless of if it had died or dispersed at some point in that year (most interactions occur before the period of dispersal and relatively few individuals die each year). Similarly, if we did not have interaction data for a marmot that was present for the entire year, we did not include that individual in the hierarchies.

Within each set of individuals, we calculated dominance hierarchies with two different sets of interactions – one with only agonistic interactions (aggression and displacement) and another with both agonistic and affiliative interactions. Only interactions with a clear winner and loser were included (of all interaction data, approximately 29% had a clear winner–loser). In affiliative interactions, generally, only play interactions had winner–loser outcomes. Occasionally, other affiliative interactions would result in displacement-like outcomes (e.g., a marmot might move away after greeting or being greeted). Although these interactions ended in displacements, we still categorized them as ‘‘affiliative’’ because they originated from non-aggression interactions. We included outcomes of affiliative interactions because animals may work out social relationships through affiliative interactions as well as agonistic interactions (Panksepp et al. 1985; Bekoff & Byers 1998).

To measure dominance, we used the Clutton-Brock index – a method that evaluates dominance based on an individual's relative number of wins and losses and is particularly suited for systems where interactions are somewhat sporadic (Clutton-Brock et al. 1979; Bang et al. 2010). On average, across all years and all marmot colonies, the interaction rate was 3.1 interactions/hour observation (yearly rates: 2003 = 1.7, 2004 = 2.9, 2005 = 3.5, 2006 = 3.2, 2007 = 4.3, 2008 = 3.0), indicating low levels of interaction appropriate for the Clutton-Brock index. We assigned relative ranks by the proportion of individuals dominated in a given hierarchy (e.g., the highest ranking dominated all other individuals and was always rank 1, while the lowest ranking dominated no individuals and was rank 0). After assigning ranks, we found that marmots exhibit both linear and non-linear (e.g., included ties) dominance hierarchies. In instances of ties, we assigned each tied individual with the average of their rankings (e.g., two individuals tied for rank 2 would both be assigned rankings of 2.5) (Lehner 1996).

Are marmots in better condition higher ranking?

Marmot masses were measured to the nearest 25 g during regular trapping sessions throughout the marmots' active season (trapping details in Blumstein et al. 2008). Because marmots continue to gain mass regularly throughout their short summer active season, we could not use absolute mass measurements, which are date dependent. Thus, we first developed an index of body condition based on mass. Snowmelt and onset of the growing season occur significantly earlier at lower elevation colonies (Van Vuren & Armitage 1991), and higher elevation sites emerge on average 2 weeks after colonies at lower elevation (Blumstein et al. 2004). Thus, we separated high- and low-elevation individuals because there are likely to be differences in mass on a given day because of these ecological differences. Formally, for each year and for each part of our study site (lower and higher elevation sites), we used the residuals from a regression of mass against age, sex, and trapping date (Julian date). Therefore, individuals with large positive residuals are heavier than would be expected for a given date while those with negative residuals are lighter than would be expected on a given date. We used the residuals from these models as our index of body condition, and we averaged the yearly residuals per individual to get one measure of body condition for each individual in each year.

We fitted linear mixed models with R (R Development Core Team 2009) using the 'lmer' command in the lme4 package (Bates & Maechler 2009). We specified Gaussian error structures and included individual as a grouping factor with a random intercept for each individual. Relative rank of all individuals was the outcome variable, and we fitted separate models for rank calculated from agonistic interactions only, and for rank calculated from both agonistic and affiliative interactions. Average yearly body condition was a predictor, and we also included age class (adult or yearling) and sex (female or male) as fixed factors. In addition, we looked at interactions between sex and body condition and between age class and body condition. We omitted the interaction terms from the final analysis if they were not significant (i.e., $p > 0.05$).

Do higher-ranking marmots have higher reproductive success?

We quantified reproductive success for adults in two ways: first by whether or not an individual reproduced in a given year (a binary variable: 1/0), and second by the number of offspring each individual produced in a given year. We used a pedigree based on likelihood parentage assignment methods (Blumstein et al. 2010) to determine reproductive success for adults each year. Twelve microsatellite loci were amplified from DNA extracted from marmot hair samples (QIAamp Mini kit; Qiagen Inc., Valencia, CA, USA), analyzed with Genemapper software (version 3.0; Applied Biosystems, Carlsbad, CA, USA), and used to assign parentage in the program Cervus (version 3.0; Kalinowski et al. 2007). The full pedigree, which refers to all animals for which we had samples and thus includes animals not in the current dominance analysis, included 1098 individuals from over five generations from 2001 to 2009, and parentage was assigned to 1006 offspring at 95% confidence, 5 at 80% confidence, and 17 from behavioral observations alone. Based on the intensive trapping regime at RMBL, we assume a 99% sampling proportion for candidate mothers, a 95% sampling proportion for candidate males, and a 99% sampling proportion of pups. See Blumstein et al. (2010) and Olson & Blumstein (2010) for further details on genotyping and parentage assignment.

We again fitted linear mixed models, with individual as a grouping factor and a random intercept for each individual. We tested two different outcomes variables: number of offspring and likelihood of reproducing.

For number of offspring, we fit six different models with three different measures of rank (relative rank within all adults, relative rank within adult males, and relative rank within adult females) calculated for the two different sets of interactions (agonistic interactions only and agonistic and affiliative interactions combined). Here, we used generalized linear mixed models with a Poisson error structure and log link function.

For likelihood of reproducing, we fit four different models with two different measures of rank (relative rank within all adults and relative rank within adult females) calculated for the two different sets of interactions (agonistic interactions only and agonistic and affiliative interactions combined). We did not fit models examining the relationship between relative rank and likelihood of reproducing within adult males only because of small sample size and insufficient variation in the outcome variable. We used generalized linear mixed models with a binomial error structure and a logit link function.

All models included body condition as an additional fixed effect. For the models that included both sexes (i.e., where relative rank of all adults was a predictor), we also included main effect of sex as a fixed factor. In addition, we examined interactions between sex and rank and omitted the interaction terms from the final analysis if they were not significant.

Are higher-ranking yearling marmots less likely to disperse?

To determine whether rank influenced the tendency to disperse, we focused on yearlings (marmots in their second active season). In each year, we distinguished dispersal from mortality based on the time of year that animals disappeared. Most yearlings disperse in the weeks prior to the above-ground emergence of new litters in their group (Armitage 1991). Animals that disappeared soon after emergence from hibernation were assumed to have dispersed, and those that disappeared weeks after pups emerged in their colony site were assumed to be killed. However, it is possible that some disappearances assigned as dispersal could have been because of mortality. We ran binary logistic regression models with the outcome variable as ‘‘dispersed’’ (1/0). We fit six separate models with three measures of rank (relative rank within all yearlings, relative rank within yearling males, and relative rank within yearling females) calculated for the two different sets of interactions (agonistic interactions only and agonistic and affiliative interactions combined).

All models included body condition as an additional fixed effect. For the models including both sexes (i.e., models that used relative rank of all yearlings), we also included main effect of sex as a fixed factor. In addition, we examined interactions between sex and rank and omitted the interaction terms from the final analysis if they were not significant.

Results

From 4946 h of observation, we included 2870 affiliative and 1697 agonistic social interactions on 593 marmots from 155 different group years. See Table 1 for a summary of sample sizes. We calculated 293 total dominance hierarchies – one hierarchy per set of individuals per colony per year. Of all hierarchies, 32.1% were linear, and 67.9% contained ties and thus were non-linear. Of the 138 agonistic hierarchies, 32.2% were linear and 67.8% were non-linear. Of the 155 agonistic and affiliative hierarchies, 28.4% were linear and 71.6% were non-linear. There was an average of 1.26 ties per matrix.

Are marmots in better condition higher ranking?

Marmots in better body condition were more dominant, but this relationship was more pronounced in females than in males (condition, agonistic only: Est = 0.138, $p < 0.001$; agonistic and affiliative: Est = 0.149, $p < 0.001$) (Table 1, Fig. 1a). There was a significant sex*body condition interaction [(sex = male)*condition, agonistic only: Est = −0.0551, p = 0.031; agonistic and affiliative: Est = −0.070, p = 0.005]. Additionally, adults were higher ranking than yearlings (age = yearling, agonistic only: Est = −0.123, p = 0.021, agonistic and affiliative: Est = 0.080, p = 0.008) (Table 1, Fig. 1b). There were no significant age class*body condition interactions, and this interaction was omitted.

Do higher-ranking marmots have higher reproductive success?

When rank was calculated from only agonistic adult male interactions, higher-ranking adult males produced more offspring each year (rank, Est = 1.126, p = 0.024) (Fig. 2a). However, when rank was derived from agonistic and affiliative adult male interactions combined, there was no relationship between dominance and number of offspring produced in a year (rank, Est = 0.263, p = 0.560) (Table 1, Fig. 2b). For adult females, there was no relationship between dominance, calculated from only adult female interactions, and reproductive success, scored as either the likelihood of reproducing (rank, agonistic only: Est = 0.017, p = 0.981; agonistic and affiliative: Est = 0.617, p = 0.378) or number of offspring (rank, agonistic only: Est = 0.019, p = 0.956; agonistic and affiliative: Est = 0.159, p = 0.616) in a year (Table 1).

Table 1: Summary of results from all models

Outcome variable	Predictor		No of Individuals		No of Colony-Year Groups	Estimate	SE	*t*-value	*z*-value	p-value
			M	F						
Total rank agonistic	A	Body condition	178	280	34	0.138	0.034	4.020		**<0.001**
		Age class = Y				−0.123	0.057	−2.146		**0.021**
		Sex = M				0.071	0.034	2.076		0.053
		(Sex = M) * Body condition				−0.055	0.028	−1.987		**0.031**
Total rank agonistic + affiliative	A	Body condition	207	312	34	0.149	0.032	4.732		**<0.001**
		Age class = Y				−0.109	0.053	−2.063		**0.040**
		Sex = M				0.080	0.029	2.740		**0.008**
		(Sex = M) * Body condition				−0.069	0.024	−2.836		**0.005**
Probability of reproducing	A	All adult rank agonistic	43	177	30	0.272	0.575		0.473	0.636
		Body condition				0.386	0.380		1.014	0.311
		Sex = M				2.519	0.837		3.010	**0.003**
	B	All adult rank agonistic + affiliative	50	190	30	0.117	0.574		0.204	0.838
		Body condition				0.362	0.369		0.982	0.326
		Sex = M				2.642	0.823		3.209	**0.001**
	C	Adult female rank agonistic		177	14	0.017	0.696		0.024	0.981
		Body condition				0.241	0.546		0.441	0.659
	D	Adult female rank agonistic + affiliative		136	14	0.617	0.700		0.882	0.378
		Body condition				−0.144	0.516		−0.280	0.779
# Offspring	A	All adult rank agonistic	42	178	30	0.206	0.205		1.011	0.312
		Body condition				0.483	0.102		4.733	**<0.001**
		Sex = M				1.519	0.300		5.059	**<0.001**
		(Sex = M) * rank				−0.925	0.329		−2.810	**0.005**
	B	All adult rank agonistic + affiliative	48	191	30	−0.051	0.157		−0.324	0.746
		Body condition				0.466	0.097		4.793	**<0.001**
		Sex = M				0.968	0.227		4.264	**<0.001**
	C	Adult female rank agonistic		177	14	0.019	0.345		0.055	0.956
		Body condition				0.574	0.249		2.311	**0.021**
	D	Adult female rank agonistic + affiliative		136	14	0.159	0.317		0.502	0.616
		Body condition				0.400	0.240		1.666	0.096
	E	Adult male rank agonistic	21		4	1.126	0.498		2.260	**0.024**
		Body condition				0.393	0.263		1.493	0.135
	F	Adult male rank agonistic + affiliative	22		6	0.263	0.452		0.583	0.560
		Body condition				0.861	0.239		3.606	**<0.001**
Probability of dispersing	A	All yearling rank agonistic	63	62	26	−1.765	0.947		−1.864	0.062
		Body condition				−2.226	1.0067		−2.211	**0.027**
		Sex = M				3.024	0.719		4.206	**<0.001**
	B	All yearling rank agonistic + affiliative	115	98	29	−0.256	0.640		−0.401	0.689
		Body condition				−1.606	0.636		−2.525	**0.012**
		Sex = M				1.913	0.420		4.552	**<0.001**
	C	Yearling female rank agonistic		37	15	−2.870	1.829		−1.569	0.117
		Body condition				−6.867	5.674		−1.210	0.226
	D	Yearling female rank agonistic + affiliative		66	20	0.514	1.329		0.387	0.699
		Body condition				−3.392	2.622		−1.294	0.196
	E	Yearling male rank agonistic	46		15	−2.793	1.748		−1.598	0.110
		Body condition				−9.667	4.072		−2.374	**0.018**
	F	Yearling male rank agonistic + affiliative	102		22	−1.131	0.896		−1.262	0.207
		Body condition				−3.176	1.098		−2.893	**0.004**

When dominance was based on only agonistic interactions within all adults, there was a significant sex*rank interaction [(sex = male)*rank, Est = −0.925, p = 0.005], with more dominant males producing more offspring, but there was no effect of rank in females (Table 1, Fig. 3a). However, dominance calculated from all adult interactions did not predict the likelihood of reproducing (rank, Est = 0.117, p = 0.838) or number of offspring (rank, Est = −0.051, p = 0.746) (Fig. 3b). There was no significant sex*rank interaction.

When looking at all adults and their interactions, individuals in better body condition produced more offspring (condition, agonistic only: Est = 0.483, p < 0.001; agonistic and affiliative: Est = 0.466, p < 0.001) (Fig. 3c). There were no significant sex*body condition interactions. In addition, males were more likely to reproduce (sex = male, agonistic only:

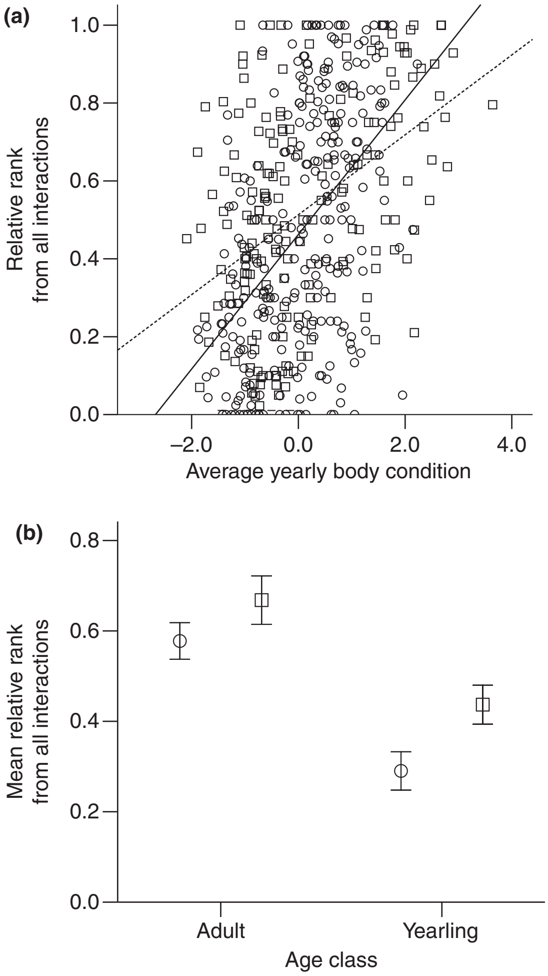

Fig. 1: (a) Graphical representation of the relationship (circles and solid lines are females: $R^2 = 0.234$; squares and dotted lines are males: $R^2 = 0.202$) between average yearly body condition and relative rank calculated from agonistic and affiliative interactions combined (N = 519). (b) Graphical representation of the effect of age (adult N = 279, yearling N = 420) and sex (circles are females N = 312, squares are males N = 207) on mean (±95% CI) relative rank for all individuals calculated from agonistic and affiliative interactions combined.

Est = 2.519, p = 0.003; agonistic and affiliative: Est = 2.642, p = 0.001) and, on average, produced more offspring (sex = male, agonistic only: Est = 1.519, p < 0.001; agonistic and affiliative: Est = 0.968, p < 0.001) than adult females.

Are higher-ranking yearling marmots less likely to disperse?

Dominance did not predict the likelihood of dispersing for any yearling group (Table 1). Instead, body condition appeared to influence dispersal; yearlings in better body condition were less likely to disperse (condition, agonistic only: Est = −2.226, p = 0.027; agonistic and affiliative: Est = −1.606, p = 0.012) (Fig. 4). Additionally, when only looking at yearling males and their interactions, body condition also predicted dispersal, with yearling males in better condition being less likely to disperse (condition, agonistic only: Est = −9.667, p = 0.018; agonistic and affiliative: Est = −3.176, p = 0.004). On the other hand, when only looking at yearling females and their interactions, body condition did not explain dispersal for this subset of individuals (condition, agonistic only: −6.867, p = 0.226; agonistic and affiliative: −3.392, p = 0.196). As expected, males were more likely than females to disperse (sex = male, agonistic only: Est = 3.024, p < 0.001; agonistic and

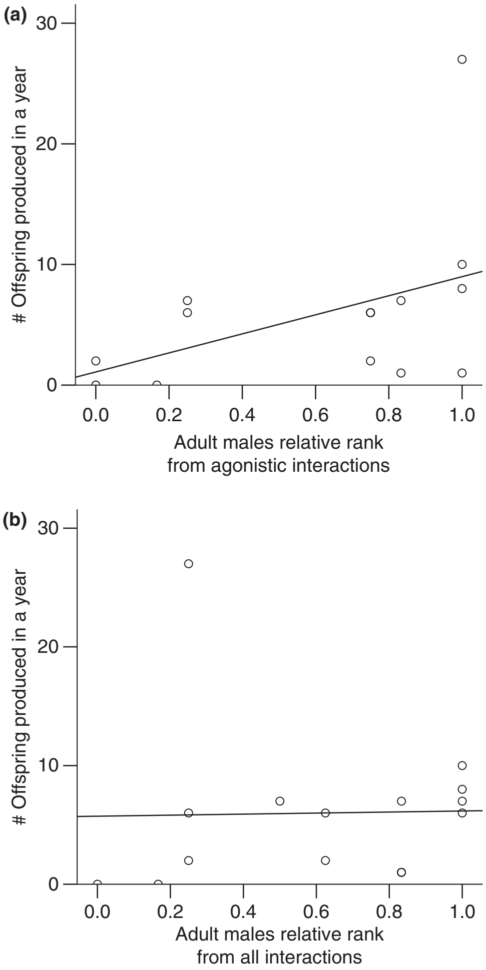

Fig. 2: Graphical representation of the relationship between relative ranks and annual number of offspring produced when rank is calculated from (a) adult male agonistic interactions only (N = 21) and (b) agonistic and affiliative interactions combined (N = 22).

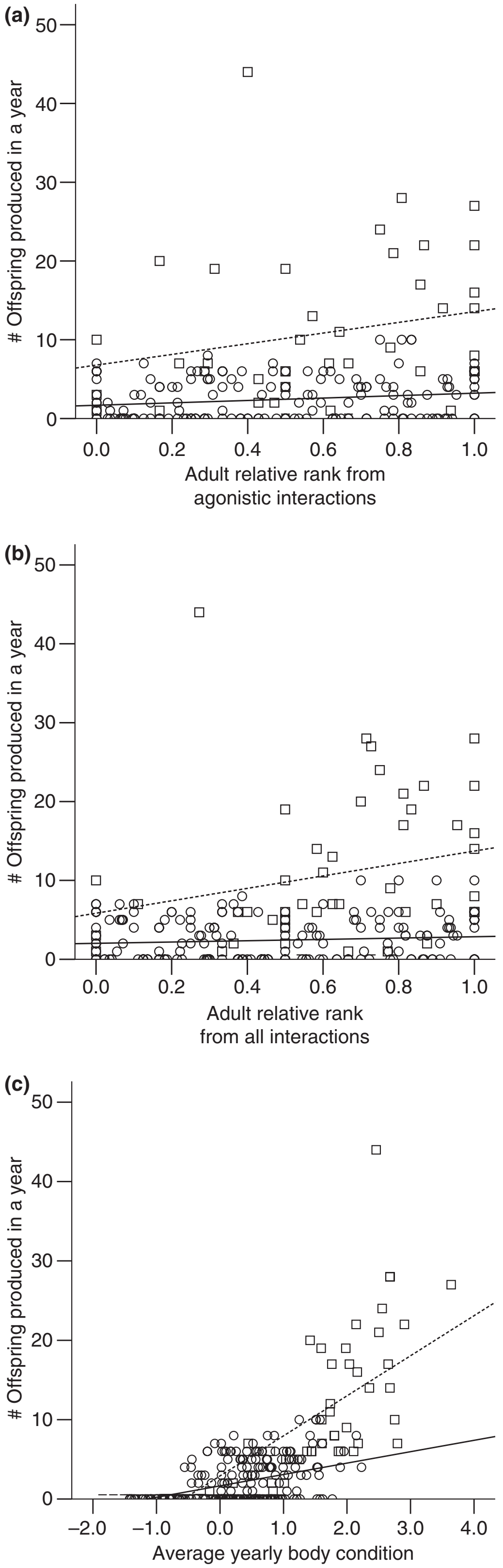

Fig. 3: Graphical representation of the relationship between relative ranks and annual number of offspring produced when rank is calculated from (a) all adult agonistic interactions only and (b) agonistic and affiliative interactions combined, split by sex. (c) Graphical representation of the effect of body condition on annual number of offspring produced. Circles and solid lines are females (agonistic only: N = 178, agonistic and affiliative: N = 191); squares and dotted lines are males (agonistic only: N = 42, agonistic and affiliative: N = 48).

affiliative: Est = 1.913, $p < 0.001$, Table 1). There were no significant sex*ranking interactions, and interaction terms were therefore excluded.

Discussion

Overall, we found similar causes and consequences of dominance in yellow-bellied marmots as seen in various other species. Our findings supported our prediction that body condition (i.e., size) would be positively correlated with dominance. A similar pattern is seen in rodents (*Clethrionomys glareolus* – Lopuch & Matula 2008), ungulates (*Cervus elaphus* – Clutton-Brock et al. 1984), and birds (*Parus major* – Carrascal et al. 1998). Our finding that adults are higher ranking than yearlings is consistent with this idea, because adults are usually larger than yearlings (Morbeck et al. 1997). Additionally, the relationship between body condition and dominance rank was more pronounced in females, signifying that body condition is especially important in female rank hierarchies.

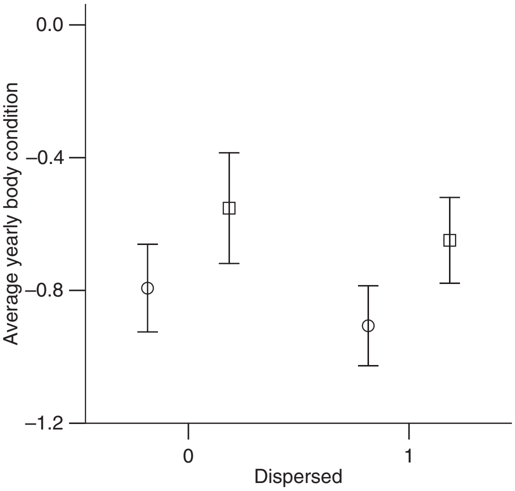

Fig. 4: Average (±95% CI) yearly body condition for yearlings who did not disperse (0) vs. those who dispersed (1). Circles are females (agonistic only: N = 62, agonistic and affiliative: N = 98), squares are males (agonistic only: N = 63, agonistic and affiliative: N = 115).

Higher-ranking male marmots produced more offspring, indicating that social dominance may be adaptive in this system. Because males defend groups of females, male fitness is directly proportional to the number of females (Armitage 1998) and inversely proportional to the number of males (Olson & Blumstein 2010) in the harem, a finding also seen in other species, such as elephant seals (*Mirounga leonine* – Modig 1996) and feral horses (*Equusca ballus* – Stevens 1990). Thus, dominant males should be more successful than subordinate males at defending harems from competitors. Furthermore, our results indicate that outcomes of male–male agonistic interactions specifically, rather than affiliative or male–female interactions, influence the number of offspring a male marmot has in a year.

By contrast, there was no relationship between dominance and likelihood of a female reproducing or the number of offspring produced. Other factors such as the length of the growing season (Armitage 1991), snow cover (Van Vuren & Armitage 1991), precipitation (Schwartz & Armitage 2002), food resources (Andersen et al. 1976), matriline size (Armitage & Schwartz 2000), fertility rate, and age of first reproduction (Oli & Armitage 2004) have been reported to influence the number of offspring produced in yellow-bellied marmots. While there is evidence that agonistic interactions influence fitness (Armitage & Schwartz 2000), social dominance rankings derived from these interactions in our study do not seem to have the same effect. Likewise, our results show that dominance, *per se*, is unlikely to drive the reproductive suppression seen in this population (Armitage 2003). Dominance could be less important for females because they do not compete for mates and thus do not experience intense sexual selection (Armitage 1991). Rather, female reproductive success appears to be limited more by ecological and other social factors. Because females need not compete for mates, dominance may not be a significant determinant of reproductive success for females. Instead, dominance within females could perhaps influence access to food resources, as seen in other species such as hyenas (Frank 1986) and primates (Boinski et al. 2005).

While dominance influenced the number of offspring produced within adult males, body condition determined the number of young when observing interactions among all adults. Although rank and body condition both influence reproductive success, the relative importance of these factors may depend on the types of individuals and interactions being observed. Our results suggest that dominance is more influential within sexes, namely males, than between sexes. Rather, body condition seems to provide a better explanation for reproductive success variation among all adults.

We found that dominance among yearlings did not influence dispersal. Although our study did not specifically examine outcomes of adult-yearling interactions only, it is possible that dominance relationships between yearlings and adults influence dispersal. Yearlings are subordinate to adults, and aggression from adults may precede yearlings dispersal (e.g., Armitage 1973, 1991), thus supporting the expectations of the social subordination theory (Christian 1970). However, Blumstein et al. (2009) found dispersal patterns in yellow-bellied marmots to be more consistent with the social cohesion hypothesis. In that study, a measure of social embeddedness (being in a cohesive subgroup where individuals interact extensively with each other) based on affiliative interactions predicted dispersal in yearling females, while agonistic interactions did not, and no measures of social embeddedness predicted yearling male dispersal. Similarly, Armitage et al. (2011) found that kin cooperation, as defined by amicable behaviors and space sharing with the mother, also determined yearling female dispersal patterns.

Our results showed that body condition was a better predictor than dominance for dispersal patterns, suggesting that yearlings in better body condition were stronger competitors. Our study offers a different perspective on body condition than in Downhower & Armitage's (1981) study, which found that yearling males delay dispersing until attaining a sufficient mass. On the other hand, our findings correspond with evidence that body size is not an important indicator of dispersal for yearling females (Armitage et al. 2011).

Dominance can have different outcomes depending on how it is defined and depends on the type of interactions being considered. Dominance only had significant effects when hierarchies were calculated from agonistic interactions alone. Dominance derived from agonistic and affiliative interactions combined appears to mask any effects. This is not surprising, given the way in which dominance is generally determined (i.e., calculated from outcomes of agonistic interactions), and our results confirm that it is most relevant to consider agonistic interactions only when studying yellow-bellied marmot dominance hierarchies.

The 14 species of marmots (*Marmota* spp.) are a model system for studies of sociality (Barash 1989; Armitage 1999), and some species are flagships for the consequences of climate change (Inouye et al. 2000; Blumstein 2009; Ozgul et al. 2010). Despite decades of study, no previous study has focused in any detail on the causes or consequences of dominance. Our study confirms that a well-documented pattern in animal systems (larger individuals, who are typically in better condition, tend to be more dominant than smaller individuals) explains some variation in yellow-bellied marmot life-history decisions and influences marmot fitness. Further, the difference of rank effects between adult males and females shows that dominance is more influential for the sex with greater reproductive skew (e.g., Clutton-Brock et al. 2006). These insights should inform future studies of reproductive and life-history patterns in marmots and other social animals.

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