

Applying the coalitionary-traits metric: sociality without cooperation in male yellow-bellied marmots

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Mammalian sociality varies both within and between species. We developed a trait-based method to quantify sociality in a continuous way to study the adaptive utility and evolution of male social behavior. The metric is based on 3 key traits—mutual tolerance, collaboration, and partner preference; males with no traits are not social, whereas those with all 3 traits are described as forming coalitions. We applied this framework to systematically describe sociality in the yellow-bellied marmot (*Marmota flaviventris*). Male marmot sociality varies: social groups contain one to several adult males, who may or may not monopolize reproduction. Through a series of experiments and demographic analyses, we found that male marmots do not appear to discriminate among individuals and thus do not show evidence of partner preference, males do not adjust alarm-calling behavior in a way consistent with male–male collaboration (but may alarm call to preferentially warn kin), and males do not increase their reproductive success by forming multiple-male groups. We conclude that yellow-bellied marmots show rudimentary sociality, with multiple-male groups maintained mainly by an environmental constraint and possible kin selection. The coalitionary-traits metric allowed us to systematically and objectively evaluate the degree of sociality in a socially plastic species. *Key words*: coalitions, *Marmota flaviventris*, mutual tolerance, reproduction, sociality, yellow-bellied marmot. [*Behav Ecol* 21:957–965 (2010)]

Coalitions occur when 2 or more individuals cooperate to access a resource that neither could obtain alone (Harcourt 1992). Coalitions formed by males usually increase the members' chances of securing a mate or maintaining position in a hierarchy (Watts 1998; Silk 1999). Coalitions have been studied extensively in social species such as lions (*Panthera leo*) (Packer et al. 1991) and dolphins (*Tursiops truncatus*) (Connor et al. 1992), but little attention has been paid to less-social species. Increasingly, however, research on species believed to be nonsocial has yielded surprising results. For instance, raccoons (*Procyon lotor*) are considered a solitary species, yet recent work has shown that males share territories and denning sites with other males (Gehrt et al. 2008). Striped hyenas (*Hyaena hyaena*) maintain territories in which several males tolerate each other's presence, yet individuals are otherwise behaviorally solitary (Wagner et al. 2008). Although these species show elements of coalitionary behavior, they do not appear to possess all the behavioral traits needed to be formally termed "coalitionary."

The currently limited description of coalitions prevents the evolution of this behavior from being clearly understood because coalition formation is seen as a binary trait, either present or absent, with no transitory form. Furthermore, by limiting the description of coalitions to social species, the behavior is not expected in less-social species and is therefore not looked for, despite the presence of some preconditions in some species.

We previously developed what we refer to as the coalitionary-traits metric (Olson and Blumstein 2009). This metric defines various degrees of coalitionary behavior as a continuous function of a species' possessing 1–3 of the following traits: mutual

tolerance, collaboration, and partner preference. Mutual tolerance occurs when any social group, here defined as individuals coexisting both spatially and temporally within a distinct geographic area, contains 2 or more males with neither male forced to leave the group because of conflict. Without mutual tolerance, species cannot possess even the basics of coalition formation. Collaboration occurs when animals act in concert to perform a task beneficial to at least one participant, including cooperation, kin selection, or mutual benefits (West et al. 2007). Instances of collaboration can include working together to take over existing social groups and oust the dominant males, as seen in the banded mongoose (*Mungos mungo*) (Waser et al. 1994) or to coerce a female into mating, as seen in dolphins (Connor et al. 1992). Nonsimultaneous collaboration can also occur, such as joint independent scent marking of a territory, exhibited by oribi (*Ourebia ourebi*) (Arcese 1999) and kinkajous (*Potos flavus*) (Kays and Gittleman 2001). Partner preference is considered the most complex trait and occurs when males prefer to associate with certain individuals over others within a group. Partner preference is seen in bonnet macaques (*Macaca radiata*) when individuals preferentially solicit coalition support from group members who outrank both themselves and their opponents (Silk 1999).

With these 3 traits, every species in which males mutually tolerate each other can be categorized according to degree of social complexity, here considered as coalition complexity. The traits represent a continuum of sociality and so each builds on the trait before it. For instance, species that only possess mutual tolerance and do not perform either of the other 2 traits would represent rudimentary coalitions. Species that possess mutual tolerance and collaboration would be considered moderately complex. Species that possess all 3 traits would be considered highly complex and correspond to what is typically considered a coalition in the literature. Species possessing only one or 2 traits would not technically be considered

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a coalition, but there may be utility in ranking traits in a coalitionary continuum. With this expanded approach, we are able to directly compare species that were not previously considered socially complex with those that are. By doing so, we generate novel insights (such as social and environmental correlates) into the evolution of complex coalitionary behavior (Olson and Blumstein 2009).

Although the coalitionary-traits metric has generated novel comparative insights, it has not been applied to better understand factors maintaining apparent coalitionary behavior in a single species. We focused on the facultatively social yellow-bellied marmot (Blumstein and Armitage 1999; Allaine 2000) and used the coalitionary-traits framework to determine the degree to which male marmots engage in some form of coalitionary behavior. Although previously described as harem polygynous (Allaine 2000), pilot data found that many social groups possessed multiple males during the spring breeding season. This social variety created the opportunity for male coalitionary behavior. Indeed, more than one male was often observed in a single social group, thus indicating the potential for mutual tolerance. It was unknown whether marmots collaborated in any complex way or preferentially tolerated certain individuals over others. The fitness consequences for adult males living with varying numbers of other males had also not been described.

The need for an inclusive metric to study the continuous nature of sociality has been expressed in several studies of social behavior (Sherman et al. 1995; Kays and Gittleman 2001). The coalitionary-traits metric responds to this problem and offers what we hope is a versatile framework to allow the study and comparison of male sociality in a diverse array of species. By testing this framework on yellow-bellied marmots, we intend to not only explore the efficacy of the metric but also elucidate the costs and benefits of marmot sociality and determine the causes of their facultative sociality.

We examined marmot sociality through a series of field experiments and quantitative behavioral observations. We studied each trait separately so that we could document its presence or absence. Partner preference was evaluated by looking for individual discrimination; collaboration by looking for cooperative alarm calling. Mutual tolerance was assessed by group census and observation. We looked for the adaptive benefits of mutual tolerance by examining reproductive benefits gained through grouping. The graded nature of the metric allowed us to combine the answers from these questions into a cohesive whole to explain the adaptive utility of male sociality and to place marmots along the coalitionary-traits metric.

MATERIALS AND METHODS

General methods

Yellow-bellied marmots (hereafter marmots) are large (2.5–3.5 kg) ground-dwelling sciurid rodents. They live in geographically stable groups usually consisting of adult females, adult males, yearlings from the previous breeding season, and young of the year (Frase and Hoffmann 1980). Whereas about 50% of females are philopatric, more than 95% of males disperse as yearlings or 2 year olds (Armitage and Downhower 1974; Armitage and Schwartz 2000). Marmots are obligate hibernators and are active at our study area from mid-April to early September. Males generally emerge first from hibernation and mate with females belowground, usually within 2–3 weeks of emergence. Females produce one litter of 3–8 young per year (Frase and Hoffmann 1980). Marmots are facultatively social: females are found in groups of 1–5 (Armitage and Schwartz 2000) and approximately 45% of behavioral social groups from 2001 to 2008 contained multiple males.

Our study site was located in and around the Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado, USA (lat 38°57'29"N; long 106°59'06"W). Marmots at this site have been continuously studied since 1962 (Armitage 1991; Blumstein et al. 2006). Marmots were live-trapped in Tomahawk traps baited with Omolene 100 horse feed (Ralston Purina, St. Louis, MO). Once caught, subjects were permanently marked with uniquely numbered ear tags and a unique fur mark was dyed (using Nyanzol fur dye) into their dorsal pelage. Details of trapping and marking are published elsewhere (Blumstein et al. 2008). Marmots were studied under a research protocol, Animal Research Committee 2001-191-01, approved by the University of California, Los Angeles (UCLA) Animal Care Committee on 13 May 2002 and renewed annually, and trapped under permits issued annually by the Colorado Division of Wildlife.

Throughout this study, we quantified a social group as a distinct geographic group containing at least an adult male and female. Social groups averaged 0.015 km² (standard deviation [SD] ± 0.029 km², range: 26.8 m² to 0.1 km²) in area and were an average of 372.9 m (SD ± 171.5 m, range: 205.4–723.1 m) away from their nearest neighbor. We defined multiple-male social groups in 2 ways. For experiments that dealt with behavioral response of a multiple-male group, males were considered group members if they were consistently seen or trapped in the area for the duration of the active season (mid-April to September), whereas those that were observed few times were deemed transients and not included. There were 74 behavioral groups with 69 unique males studied from 2001 to 2008; no males occurred in more than one behavioral group per year. For analyses that dealt with reproductive success, all males that had been seen or trapped in an area even once during spring (April–June), as well as those that had never been observed but were determined to parent offspring in the area, were deemed reproductive group members. There were 22 instances (18 unique males) in which a male was identified as a genetic father but not observed or trapped in the area. We studied 83 distinct reproductive groups with 112 males from 2001 to 2008. Because males could occur in more than one year and in more than one reproductive group per year, we used the “male-year” as the unit of analysis, which was simply one male in a given group and year. There were 255 male-years in the reproductive analyses and 140 male-years in the behavioral analyses; 20 males from 2001 to 2008 were assigned to more than one reproductive group in a single year. We distinguished between behavioral and reproductive groups because when considering behavior such as cooperation or social interaction, the relevant males would be those perceived by others as continuing residents of a group, whereas in reproductive analyses any males that were present during the breeding season, even for a very short duration, could potentially father offspring.

The population consisted of 17 behavioral social groups; not all groups were present in a given year. We studied an average of 12 social groups annually (range: 10–14). Behavioral social groups varied in size, with an average of 1.6 adult males (SD ± 1.4, *N* = 74), 5.2 adult females (SD ± 5.2, *N* = 74), 6.4 yearlings (SD ± 7.3, *N* = 74), and 11.0 juveniles (SD ± 10.9, *N* = 74). Each social group was observed and trapped regularly from mid-April to mid-September. Observations took place daily during the periods of greatest marmot activity, from 0700 to 1100 h and 1500 to 1800 h. Observations were carried out through a spotting scope and at a distance that appeared not to interfere with general marmot activity. Regular scans allowed us to collect information on the individual identity and spatial location of all visible marmots, the types and instances of social interactions between marmots in a social group, the frequency, duration, and identity of alarm callers,

and any predator sightings. We attempted to livetrapped all marmots in the study population every 2 weeks for individual identification and sampling purposes. Sex and reproductive status was determined visually, and blood and hair were collected for DNA analysis.

We used spatial and temporal overlap to define mutual tolerance. Males were considered to be mutually tolerant when more than one male was present in a behavioral social group for the duration of the active season or in a reproductive social group during spring (April–June). The degree of social tolerance between males varied. In general, males interacted infrequently: in approximately 6000 h of observation at all colonies from 2001 to 2008, we witnessed 80 male–male interactions, 31% (25 of 80) of which were affiliative, the rest agonistic. Because the coalitionary-traits metric defines mutual tolerance as “(toleration) to the point that neither (male) is forced to leave the group” (Olson and Blumstein 2009), we considered all males that occurred in geographic social groups with at least 1 other male to be mutually tolerant.

Can males discriminate among each other based on familiarity?

To determine whether marmots may be capable of partner preference, we conducted an olfactory discrimination test. We chose to focus on an olfactory modality because scent has been shown to be an important form of communication in many rodents, including ground-dwelling squirrels (Eisenberg and Kleiman 1972; Johnston 2003; Mateo 2006). We acknowledge that individual discriminatory ability does not necessarily infer partner preference; nevertheless, we consider individual discrimination a necessary precursor to the more complex partner preference behavior. Therefore, we hypothesized that if male marmots preferred to tolerate certain males over others, they would show a differential response to males that they routinely tolerated versus those that they had no experience with. We predicted that male marmots would respond more strongly to the scents of unfamiliar males, as they would be seen as “intruders” in the social group. In an earlier study by Brady and Armitage (1999), marmots were shown to respond more to stimuli marked with glandular secretions than blank controls and to investigate familiar secretions more than unfamiliar. That study was conducted mainly on females and juveniles, however (only 1 adult male was sampled).

We collected samples of perioral glandular secretions when adult male marmots ≥ 2 years were livetrapped. Samples were collected on 4 clean cotton balls (2 were swabbed on each gland) using methods outlined in Brady and Armitage (1999). Cotton balls were stored at -20°C , and samples were used for experiments within 2 weeks of collection.

In May and June 2006 and 2007, we focused on 23 males from 10 social groups with multiple males (using the behavioral definition) and baited focal males to an experimental array with a handful of Omolene horse food. Subjects were presented with a simultaneous choice test of 4 olfactory stimuli on cotton balls fastened 40 cm aboveground to clean PVC pipes (Brady and Armitage 1999): a familiar male (from the subject’s social group), an unfamiliar male (from a social group >2.5 km away), an unscented cotton ball, and a cotton ball that had been rubbed on a domestic sheep (to control for interest in purely novel smells). The pipes were arranged in a square, with 50 cm between each pipe and its nearest neighbors. Olfactory stimuli were randomly assigned to each pipe to control for order effects. Once a subject was within 50 cm of the experimental array, we initiated a 15-min focal observation. We recorded the number of times the target individual sniffed, reared up, and investigated or scent overmarked on

or around the stimulus, and the total time spent investigating each stimulus.

We analyzed total olfactory response, which included sniffs, rearing sniffs, and scent overmarks, using a random-effects negative binomial regression with the individual marmot included as a random effect to control for nonindependence among the responses of an individual (Cameron and Trivedi 1998). The number of total olfactory responses was the dependent variable and stimulus type compared with a blank control was the independent variable. We used the amount of time each marmot was in sight during the experiment as an exposure variable so that an individual’s responses effectively became a rate of response per time in sight. This allowed us to control for differences in how long each marmot remained in the experimental setup. Statistical analysis was performed using STATA 10.1 (StataCorp 2007).

Do males cooperatively alarm call?

Male marmots produce alarm calls (Blumstein 2007) and therefore can potentially call cooperatively. We chose to focus on alarm calls because marmots have limited options for other types of collaboration. They are herbivores with abundant forage, so cooperative food collection is unlikely (Kilgore and Armitage 1978; Blumstein et al. 2006). They have limited (or no obvious) male parental care (Fraser and Hoffmann 1980; Blumstein and Armitage 1999). They could cooperate during the winter by social thermoregulation in the hibernacula (Arnold 1988; Blumstein and Arnold 1998), but this is unlikely because marmots are extremely efficient solitary hibernators (Armitage et al. 2003; Armitage and Woods 2003) and males do not necessarily hibernate with their offspring (Blumstein et al. 2004). We hypothesized that if males did exhibit collaborative alarm calling, the number of calls given per male would decrease in multiple-male groups. Alarm calling can be costly to the caller by attracting the attention of potential predators (Sherman 1977; Alatalo and Helle 1990). If males in multiple-male groups collaboratively alarm call, the burden of alarm calling could be spread over many individuals, thus allowing each individual to benefit by calling less while still being afforded a consistent level of vigilance.

To test whether males collaboratively alarm called, we analyzed data on natural alarm calling collected from 2002 to 2008. During 3707 h of regular field observations, all instances of alarm calls were recorded, and the identity of the caller, duration of the calling bout, and numbers of calls were noted. We observed calling bouts from 30 unique males in 10 social groups. We used a zero-truncated negative binomial regression (Cameron and Trivedi 1998) with the number of calling bouts as the dependent variable. We performed 2 analyses, one on the full data set ($N = 49$ male-years) and one on a restricted data set including only males in behavioral multiple-male groups ($N = 39$ male-years). We divided the analysis so that we could include average group relatedness as an independent variable, which cannot be calculated for groups with one male. For the full analysis, we included the number of times a predator was observed in the area (also recorded during observations), total group size, and the residuals from a linear regression of the number of males in a group on the number of females in a group. We used the residuals because the number of males and females in a group was highly correlated ($r = 0.76$, $N = 74$), so the regression residuals allowed us to determine the effect of excess males in a group while controlling for the number of females. In the restricted analysis, we included the same independent variables as well as the average relatedness of the males in the group. We included the individual marmot as a random effect and controlled for the amount of time each group was observed.

Is being a male in a multiple-male group beneficial?

Males in multiple-male groups may be expected to increase their reproductive success if, by forming multiple-male groups, they gain access to more females or are better able to compete for females with the help of male group-mates (Emlen and Oring 1977; Clutton-Brock 1989). We tested whether annual reproductive success of males was influenced by the number of males in a social group. We also quantified the relatedness of males within a reproductive group to determine whether males were more likely to tolerate kin than nonkin.

To determine annual reproductive success, DNA was extracted from hair using Qiagen QIAamp DNA Mini Kits following the protocol included in the kit (Qiagen Inc., Valencia, CA). Fifteen previously developed polymorphic microsatellite primers were used (see Table 1 for details and references), and primers were multiplexed to include 2 primers per reaction. Multiplexed primers and DNA were amplified using polymerase chain reaction on a Peltier thermal cycler (MJ Research PTC-200) and genotyped on an ABI 3730 DNA capillary sequencer (Applied Biosystems). Alleles were analyzed using GeneMapper Version 3.0 software (Applied Biosystems).

Microsatellite loci were tested for Hardy-Weinberg equilibrium and linkage disequilibrium using GENEPOP 4.0 (Raymond and Rousset 1995). After performing a Bonferroni correction, no loci had significant ($P < 0.05$) heterozygous deficits. We found evidence of significant linkage disequilibrium in an average of 7% of all geographic groups in a given year (range: 2–13%). Linked loci were not consistent across groups, suggesting that linkage disequilibrium was most likely due to population structure rather than physical linkage. The program CERVUS 3.0 (Kalinowski et al. 2007) was used to test for null alleles; loci SS-Bibl25 and MS45 had null alleles at frequencies greater than 0.05, so neither locus was used in the analysis. Locus MA002 was also excluded because it failed to amplify in the majority of samples. Thus, we used 12 loci for all subsequent analyses.

Parentage was assigned using the programs CERVUS and COLONY 2.0 (Wang 2004). We used CERVUS to determine the most likely mother and father of an offspring using maximum likelihood for each offspring/mother/father trio. To determine parentage assignment critical values, we ran a sim-

ulation accounting for population allele frequencies, the number of candidate parents of each sex, the proportion of parents sampled, the proportion of loci typed, the proportion of highly ($r \geq 0.4$) related mothers, and the proportion of loci mistyped (Jones and Arden 2003). We used a strict confidence level of 95% and a relaxed confidence level of 80%. We assumed a sampling proportion of 99% for candidate mothers and 96% for candidate fathers due to the trapping regime at RMBL. The proportion of loci typed was 0.948, and the proportion mistyped was set at 0.01. Candidate mothers were selected for each offspring based on colony location and nipple size measurements (an index which reflects pregnancy and nursing; routinely recorded at trap events). Candidate fathers were grouped into 2 distinct geographical areas, separated by approximately 2.5 km, which represent a natural break in the marmot population. All offspring from each geographic area were given the same list of potential fathers. Observational data were used to confirm that parents lived in the same geographic area as the offspring assigned to them by genetic methods; males that did not belong to the same social group as the offspring but that lived in groups < 0.5 km away were also accepted as fathers.

The program COLONY was used to supplement assignments made by CERVUS. We set the mating system parameter in COLONY to "Polygamy" for both males and females and did not select any previously known sibships or parentage assignments. COLONY uses likelihood methods that are robust to typing error (Wang 2004); therefore, we used this method to confirm the assignments made with CERVUS. We assigned both mothers and fathers for 805 of 920 sampled offspring at the 95% confidence level and 4 more at the 80% confidence level. Six offspring had no genetic data but parentage was inferred from behavioral observations.

We determined average relatedness for male dyads with genetic samples in multiple-male reproductive groups from 2002 to 2008 using the program STORM 1.0 (Frasier 2008), which calculates relatedness based on methods used in Li et al. (1993). We excluded 2001 from this analysis because too few males were genetically sampled to calculate group relatedness in that year. Significance values for group relatedness were generated using STORM to randomly shuffle adult males present in a given year among groups, keeping group size constant. Average relatedness was then calculated for each group, and this was repeated for 1000 iterations. The actual group relatedness value was then compared with the generated distribution, with $P < 0.05$ considered significant. The type of relationships among males in multiple-male groups was also evaluated using the program KINGROUP 2.0 (Konovalov et al. 2004), which uses maximum likelihood methods to compare the observed relatedness between a pair of individuals with relatedness values generated by the program for both a primary hypothesis (males are parent/offspring, full-siblings, or half-siblings) and an alternate hypothesis (males are unrelated).

To determine the effect of the number of males in a group on each individual's annual reproductive success, we counted the number of males observed, trapped, or placed by genetic assignment into each geographic location (reproductive group definition). We quantified the number of offspring each male sired, from 2001 to 2008. We also quantified the number of females observed or trapped at each geographic location. We used a random-effects negative binomial regression model (Cameron and Trivedi 1998) to determine the effect of the number of males (using the residuals from a regression of males on females, explained above) on the annual number of offspring produced by each male. We also included year in the model to test whether changes in number of offspring were caused by an especially productive or harsh year.

Table 1
Locus information

Locus	N_a	H_{obs}	H_{exp}	Ref
MS45	16	0.705	0.882	1
MS47	22	0.882	0.910	1
ST10	11	0.720	0.816	1
GS22	9	0.799	0.782	2
GS14	12	0.818	0.840	2
MA018	13	0.772	0.836	3
GS25	21	0.860	0.916	2
MA002	14	0.495	0.509	3
MA091	11	0.760	0.781	3
2g2	16	0.772	0.841	4
IGS-6	12	0.713	0.769	5
SS-Bibl18	10	0.791	0.808	6
SS-Bibl25	9	0.456	0.825	6
SS-Bibl31	13	0.735	0.807	6
SS-Bibl4	11	0.799	0.820	6

Locus names, the number of alleles found at each locus (N_a), and the observed (H_{obs}) and expected (H_{exp}) heterozygosity for each primer. Primers are described by the following references: 1, Hanslik and Kruckenhauser (2000); 2, Stevens et al. (1997); 3, da Silva et al. (2003); 4, Kyle et al. (2004); 5, May et al. (1997); 6, Goossens et al. (1998).

Does an environmental constraint account for male group size?

Burrows, here defined as distinct openings for a group of interconnected belowground tunnels, are time intensive to construct, and thus burrow availability may be a limiting environmental resource. We calculated the number of burrows at a colony to see whether multiple-male groups were more likely to form with increased burrow availability. We calculated burrows per colony by counting the number of burrows where marmots were either observed or trapped for 14 unique colonies from 2001 to 2008, for a total of 88 group-years. We used a random-effects negative binomial regression to determine the effect of burrow number at a colony on the number of males in a group (behavioral definition) (Cameron and Trivedi 1998), with colony used as a random effect. The number of burrows at which each adult male marmot was observed or trapped was also calculated. For this analysis, we had burrow information for 69 males with a total of 138 male-years (we had no burrow information for 2 behavioral male-years). We used a random-effects negative binomial regression with number of burrows used by an individual as the dependent variable to determine whether number of burrows used (out of total burrows available) was related to the number of males in a group. We included total burrows available as an exposure variable to control for the different number of burrows at each colony, and individual was included as a random effect.

RESULTS

Can males discriminate among each other based on familiarity?

We found no significant effect of stimulus on the number of total olfactory responses elicited (Table 2). Marmots responded to the familiar male stimulus with 19 sniffs, 8 rearing sniffs, and 3 scent overmarks, the unfamiliar male elicited 21 sniffs, 8 rearing sniffs, and 4 scent overmarks, the novel sheep smell received 20 sniffs, 3 rearing sniffs, and 0 scent overmarks, and the blank control received 11 sniffs, 5 rearing sniffs, and 0 scent overmarks. Although none of the results were significant, the sheep stimulus elicited the least difference from the blank control ($P = 0.297$), whereas the unfamiliar male stimulus elicited the greatest ($P = 0.095$) (Table 2).

Do males cooperatively alarm call?

Males in single-male groups each gave an average of 2.5 (SD \pm 2.8, $N = 10$ male-years) calling bouts in a season, whereas

males in multiple-male groups each gave 2.8 (SD \pm 1.9, $N = 39$ male-years) calling bouts. There were fewer calling bouts in areas with higher numbers of predators and larger social group sizes, and there were more calling bouts with greater numbers of males per female (Table 3). In groups with greater than 1 male, the effect of predator sightings and group size became nonsignificant, whereas there were significantly more calling bouts in groups with more males per female as well as in groups with higher average relatedness (Table 3). We also examined the distribution of alarm-calling bouts among male group members and found that some males produced most of the calls, whereas others rarely or did not call at all. The proportion of males in multiple-male groups that called averaged 0.62 (SD \pm 0.29, $N = 21$ group-years).

Is being a male in a multiple-male group beneficial?

Male annual reproductive success decreased with more males per female in a group (Table 4). Although there was an overall annual effect, we found that in only 3 of the 8 years was there a significant positive effect of year on per capita offspring production (2004, 2007, and 2008). The number of offspring produced each year by males in single- and multiple-male groups is shown in Figure 1.

Average relatedness among pairs of males in a group was significantly higher ($P < 0.05$) than expected by chance for 12 of 47 reproductive multi-male groups (Table 5). To determine whether overall group relatedness was greater than random, we carried out a Fisher's combined probability test (Fisher 1948). We found that males in reproductive multiple-male groups were significantly more related than expected by chance ($\chi^2_{94} = 201.43$, $P < 0.05$). Out of 458 pairs of males in reproductive groups, 128 were found to be related at the parent/offspring or full-sibling level, with another 12 pairs related as half-siblings.

Does an environmental constraint account for male group size?

A summary of the mean number of burrows for behavioral groups with varying numbers of males is shown in Table 6. Groups with more active burrows (those which marmots were

Table 2
Effects of olfactory stimulus type

	Coefficient	Standard error	<i>z</i>	<i>P</i>	95% Confidence interval
Sheep	0.476	0.456	1.04	0.297	-0.418 to 1.370
Unfamiliar	0.734	0.439	1.67	0.095	-0.127 to 1.595
Familiar	0.677	0.441	1.53	0.125	-0.188 to 1.542
Intercept	-4.999	0.547	-9.14	0.000	-6.072 to -3.923

The total olfactory responses (numbers of sniffs, rearing sniffs, and scent overmarks) performed by marmots in multiple-male groups were not significantly different between the control and any stimulus type (negative binomial regression: $N_{\text{males}} = 23$, Wald $\chi^2_3 = 3.19$, $P = 0.36$). The coefficient for each stimulus type represents the difference in the log of expected number of total olfactory responses given the presentation of each stimulus type versus the blank control. The *z* value is the test statistic used to calculate whether the coefficient for each term in the model is significantly different from 0 (*P*).

Table 3
Factors affecting alarm-calling bouts

	Coefficient	Standard error	<i>z</i>	<i>P</i>	95% Confidence interval
All groups					
Predators	-0.043	0.017	-2.50	0.012	-0.077 to -0.009
Group size	-0.093	0.031	-2.97	0.003	-0.154 to -0.032
Excess males	0.792	0.317	2.50	0.012	0.171 to 1.412
Intercept	-17.254	4.809	-3.59	0.001	-26.678 to -7.829
Multiple-male groups					
Predators	-0.020	0.015	-1.36	0.174	-0.050 to 0.009
Group size	-0.059	0.0325	-1.81	0.071	-0.122 to 0.005
Excess males	1.83	0.521	2.27	0.023	0.162 to 2.203
Average <i>R</i>	4.249	1.945	2.18	0.029	0.436 to 8.062
Intercept	-4.242	1.067	-3.97	0.001	-6.334 to -2.150

The effects of the number of times a predator was seen, group size, and number of excess male marmots per female on the number of calling bouts given by individual males per year ($N = 49$ male-years), as well as for only males in multiple-male groups ($N = 39$ male-years). Multiple-male groups include the effect of average group relatedness on the number of calling bouts.

Table 4
Effects of multiple males on offspring number

	Coefficient	Standard error	<i>z</i>	<i>P</i>	95% Confidence interval
Excess Males	-0.247	0.056	-4.41	<0.001	-0.356 to -0.137
Year	0.096	0.047	2.05	0.041	0.004 to 0.188
Intercept	-193.256	93.923	-2.06	0.040	-377.341 to -9.170

The number of offspring produced by a male marmot decreases with more excess male marmots in the group (calculated as the residuals from a regression of the number of males on the number of females). The effects of a given year on the number of offspring each male produced in one year are also shown (negative binomial regression: $N_{\text{male-years}} = 255$, $N_{\text{males}} = 112$, Wald $\chi^2 = 21.99$, $P = 0.001$).

observed to use) generally had a greater number of males sharing that location (Table 7). The proportion of available burrows that an individual male used was smaller for males in groups with greater numbers of males (Table 7). Males used from 1 to 22 burrows each (mean = 4.24, SD \pm 4.18). Males in single-male groups each used an average of 0.63 of the burrows available (SD \pm 0.41, $N = 38$ male-years). Males in multiple-male groups used 0.35 of the available burrows each (SD \pm 0.25, $N = 100$ male-years).

DISCUSSION

Using the coalitionary-traits metric, we systematically tested for the presence of key traits in a facultatively social species to objectively assess male social complexity. Yellow-bellied marmots in multiple-male groups engage in rudimentary coalitionary behavior: We found no strong evidence for partner preference or collaboration, but we did find social groups in which more than one male occurred, indicating mutual tolerance. We have shown that mutual tolerance is not maintained by an increase in male reproductive success in multiple-male groups. Rather, males in multiple-male groups produce fewer offspring per year than those in single-male groups. Mutual tolerance seems

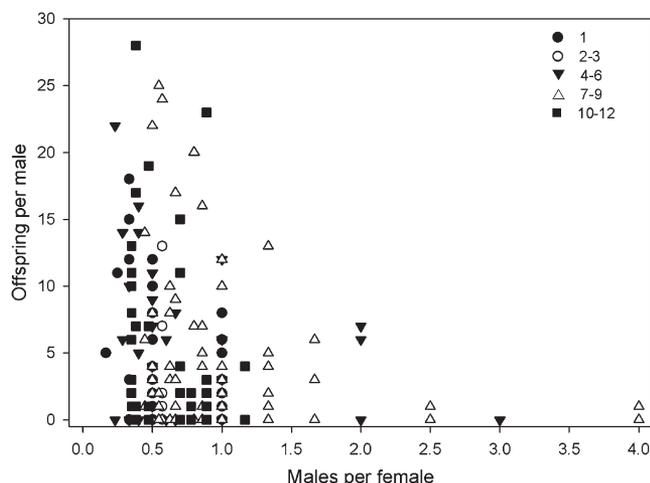


Figure 1
A scatter plot of the number of offspring produced annually by males in reproductive groups with varying male:female ratios. The total number of males in the group is indicated by symbol type. Each point represents one male-year; all male-years for all reproductive group members from 2001 to 2008 are shown ($N = 255$).

Table 5
Average relatedness of multiple-male groups

Year	Geographic group	No. of males	Group <i>r</i>	<i>P</i>
2002	Marmot Meadow	2	0.15	0.066
	Picnic	7	-0.04	0.580
	River	2	-0.04	0.422
2003	Stonefield	3	-0.16	0.845
	Bench	2	-0.04	0.336
	Boulder	2	0.09	0.146
	Gothic Townsite	2	-0.01	0.306
2004	Picnic	6	-0.05	0.463
	River	4	0.27	0.006*
	Stonefield	4	-0.14	0.887
	Bench	2	0.20	0.201
	Gothic Townsite	4	0.01	0.415
2005	Marmot Meadow	5	0.35	0.006*
	Picnic	7	0.00	0.589
	River	8	0.22	0.014*
	River Mound	4	0.06	0.245
	Gothic Townsite	4	0.05	0.175
	Marmot Meadow	7	0.23	0.001*
	Picnic	9	-0.05	0.744
	River	3	0.30	0.015*
	Stonefield	3	0.18	0.058
2006	Bench	2	0.06	0.292
	Boulder	2	-0.43	1.000
	Gothic Townsite	6	0.02	0.298
	Marmot Meadow	4	0.03	0.310
	North Picnic	2	-0.14	0.709
	Picnic	8	0.01	0.331
	River	6	0.32	0.003*
	River Mound	2	0.06	0.301
Stonefield	2	0.25	0.088	
2007	Bench	4	0.21	0.054
	Boulder	2	0.46	0.077
	Gothic Townsite	6	0.02	0.303
	Marmot Meadow	2	-0.10	0.584
	North Picnic	4	-0.10	0.827
	Picnic	8	0.01	0.344
	River	5	0.36	0.006*
	River Mound	3	0.14	0.134
2008	Bench	5	0.28	0.007*
	Boulder	2	0.17	0.179
	Gothic Townsite	4	-0.05	0.711
	Marmot Meadow	4	0.21	0.041*
	North Picnic	7	0.05	0.258
	Picnic	11	-0.02	0.684
	River	6	0.28	0.004*
	River Mound	4	0.32	0.016*
Stonefield	5	0.30	0.009*	

The year and name of each geographic group, as well as the number of adult male marmots per group, average male group relatedness (Group *r*), and the likelihood of a randomly formed male group having greater relatedness (*P*). Groups with significantly greater than random relatedness ($P < 0.05$) are marked with an asterisk.

to be maintained by an environmental constraint as well as a possible preference for kin.

At a theoretical level, this approach allowed us to frame classic questions about the maintenance of social variation and complexity in a novel way. Our trait-based approach breaks a complex suite of social behaviors into a series of simpler traits, thus allowing researchers to study one aspect of the behavior at a time and build on previous knowledge. By looking at coalitionary behavior as a graded trait, we are also able to compare the social complexity of diverse species with a single metric, an ability that will lead to increased understanding of social evolution (Olson and Blumstein 2009). Although it is undeniable that socially complex species are more likely to possess

Table 6
Summary of group burrow availability

<i>N</i> males	Mean <i>N</i> of burrows	SD	<i>N</i> groups
1	5.65	6.10	40
2	13.71	8.50	14
3	17.6	10.60	10
4	37.2	4.02	5
5	29.67	17.37	3
7	71	—	1

The mean number of burrows in use by marmot social groups containing from 1 to 7 males; SD and number of groups of each type are also shown. Only one group contained 7 males, thus we only report total number of burrows used in this group.

coalitionary behavior, it is troubling that this type of behavior is only expected, and therefore only looked for, in social species. Species with seemingly low levels of sociality tend to be less well represented in the literature, and yet often when the sociality of these species is thoroughly studied, they show unexpectedly complex social behavior (Rowell 1988). Our coalitionary-traits metric provides a framework to study preconditions of more complex behavior in species that we would not normally think to examine and therefore to potentially discover unknown facets of sociality in less-social species. Through the application of this metric to marmots, we were able to gain insight into this species' social behavior.

Male marmots reacted similarly to all olfactory stimuli, indicating awareness of scents but either no perception of difference between them or a similar reaction to both familiar and unfamiliar individuals. It seems unlikely that males were unable to tell the stimuli apart because studies with other marmot species and female yellow-bellied marmots have found evidence for olfactory individual discrimination (golden marmots [*Marmota caudata aurea*] [Blumstein and Henderson 1996], woodchucks [*Marmota monax*] [Meier 1991], Alpine marmots [*Marmota marmota*] [Bel et al. 1999], yellow-bellied marmots [Brady and Armitage 1999]). Therefore, it appears that although males may be able to differentiate known and unknown individuals, they do not react differently to either. This may reflect the level of group cohesion possessed by male marmots; that is, male marmots tolerate each other's presence but interact infrequently and do not direct specific behaviors to specific individuals. There is also the possibility that the experimental setup was not conducive to eliciting a behavioral response from males. Our experimental setup, however, was based on that used in a previous study by Brady and Armitage (1999), which successfully elicited differential olfactory responses from females and one male. Thus, although we did

not find a strong differential response from male marmots to familiar and unfamiliar males, we believe our methods and results are valid.

When in groups with greater numbers of males per female, we found that male marmots were more likely to produce alarm calls. We predicted that males might give fewer alarm calls per capita if calling cooperatively; thus, these results do not support the hypothesis that males reduce their alarm calls based on the calls of others around them. It is possible that males collaborate with other males by increasing their calling bouts, thereby warning group-mates of the presence of danger. However, our finding that the number of calling bouts decreased as the number of predator sightings in a group increased contradicts this interpretation. Theory predicts that individuals should call more when there is increased danger (Macedonia and Evans 1993; Furrer and Manser 2009). The males in our study called less when predation pressure was high, however, supporting the idea that marmots that feel truly threatened seek refuge without taking the time to warn group-mates, thus making collaboration unlikely. This is in accordance with the threat-sensitivity hypothesis, which states that individuals should adjust their antipredator behavior based on the severity of their perceived risk (Helfman 1989). We also found that males in larger groups engaged in fewer alarm calling bouts, which is unexpected if one assumes that the likelihood of alarm calling may vary depending on the number of additional pairs of eyes scanning for predators. Finally, we found that males produced more bouts of alarm calls when the other male group members were kin. Kin selection theory predicts that individuals should call more when group relatedness is high to preferentially warn relatives (Hamilton 1964; Sherman 1977). Blumstein et al. (1997) found no evidence that individuals increased calling with greater total group kinship; our results, however, indicate that kin selection may influence alarm calling in adult males.

Reproductive benefits are unlikely to be the cause of mutual tolerance among the marmots in our study. Our genetic assessment of parentage revealed that the number of offspring produced by each male declined as the number of males in a group increased. Rather than marmots choosing to be in a multiple-male group because of benefits received, they may instead be forced to live in such a group and incur an annual cost in direct fitness. The finding that males in many of the multiple-male groups are more related than expected by chance, however, suggests that mutual tolerance may be facilitated by kin grouping produced by delayed dispersal. Individuals may derive indirect fitness benefits from the reproductive success of kin that could potentially lead to a net fitness benefit in terms of inclusive fitness over an individual's lifetime.

Environmental constraints might also influence multiple-male group formation. We found that males appear to

Table 7
Burrow availability

	Coefficient	Standard error	<i>z</i>	<i>P</i>	95% Confidence interval
Burrow availability					
Available burrows	0.033	0.003	10.44	0.001	0.027 to 0.039
Intercept	-0.025	0.113	-0.22	0.825	-0.247 to 0.197
Proportion of burrows used					
No. of males in group	-0.165	0.036	-4.58	0.001	-0.235 to -0.094
Intercept	-0.694	0.149	-4.67	0.001	-0.985 to -0.403

The top portion shows that groups with more available burrows were more likely to have greater numbers of males (negative binomial regression: $N_{\text{group-years}} = 88$, $N_{\text{colonies}} = 14$, Wald $\chi^2_1 = 109.06$, $P < 0.001$). The bottom portion shows that males use a smaller proportion of the burrows available to them when the number of males in a social group increases (negative binomial regression: $N_{\text{male-years}} = 138$, $N_{\text{males}} = 69$, Wald $\chi^2_1 = 21.01$, $P = 0.001$).

distribute themselves according to the number of burrows available at each geographic area. Burrow availability is important for predator protection because most marmot predators catch marmots when aboveground; protection from predators has been shown to be an important factor in the persistence of marmot populations (Blumstein et al. 2006). Extensive burrows are also difficult and time consuming to construct, which makes them an even more important and scarce resource. When individual burrow use was examined, males in single-male groups used a greater proportion of the burrows available to them, indicating that single males may benefit from a lack of competition from other males for burrow use.

Sociality without obvious benefits has previously been explained by the resource dispersion hypothesis, which states that multiple individuals can share a patchily distributed resource without incurring fitness costs (Carr and Macdonald 1986; Johnson et al. 2002). This hypothesis has found support in a variety of species, including badgers (*Meles meles*) (Johnson et al. 2001), foxes (*Vulpes cana*) (Geffen et al. 1992), and Emballonurid bats (Bradbury and Vehrencamp 1976). For marmots, patchily distributed burrows may be a resource able to be used by many individuals without incurring a cost from sharing. Thus, although marmots may gain little or no direct reproductive or collaborative benefits, indirect benefits gained from grouping with kin combined with a low cost of sharing a geographic area may be enough to maintain mutual male tolerance.

In conclusion, the coalitionary-traits metric is useful for this type of analysis at both an experimental and theoretical level. Using the metric, we determined the complexity of multiple-male interactions within marmot social groups and defined marmots as rudimentary coalition formers. We found that multiple-male groups in marmots do not appear to be maintained by a preference for certain individuals or a reduction in alarm calling due to collaboration but may be influenced by inclusive fitness benefits gained from tolerating kin and an environmental constraint due to burrow availability.

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REFERENCES

Alatalo R, Helle P. 1990. Alarm calling by individual willow tits, *Parus montanus*. *Anim Behav*. 40:437–442.

Allaine D. 2000. Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. *Behav Processes*. 51:21–34.

Arcese P. 1999. Effect of auxiliary males on territory ownership in the oribi and the attributes of multimale groups. *Anim Behav*. 57:61–71.

Armitage KB. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Ann Rev Ecol Syst*. 22:379–407.

Armitage KB, Blumstein DT, Woods BC. 2003. Energetics of hibernating yellow-bellied marmots (*Marmota flaviventris*). *Comp Biochem Physiol A Mol Integr Physiol*. 134:101–114.

Armitage KB, Downhower JF. 1974. Demography of yellow-bellied marmot populations. *Ecology*. 55:1233–1245.

Armitage KB, Schwartz OA. 2000. Social enhancement of fitness in yellow-bellied marmots. *Proc Nat Acad Sci U S A*. 97:12149–12152.

Armitage KB, Woods BC. 2003. Group hibernation does not reduce energetic costs of young yellow-bellied marmots. *Physiol Biochem Zool*. 76:888–898.

Arnold W. 1988. Social thermoregulation during hibernation in Alpine marmots (*Marmota marmota*). *J Comp Physiol B Biochem Syst Environ Physiol*. 158:151–156.

Bel MC, Coulon J, Sreng L, Allaine D, Bagnères AG, Clement JL. 1999. Social signals involved in scent-marking behavior by cheek-rubbing in Alpine marmots (*Marmota marmota*). *J Chem Ecol*. 25:2267–2283.

Blumstein DT. 2007. The evolution, function, and meaning of marmot alarm communication. *Adv Study Behav*. 37:371–402.

Blumstein DT, Armitage KB. 1999. Cooperative breeding in marmots. *Oikos*. 84:369–382.

Blumstein DT, Arnold W. 1998. Ecology and social behavior of golden marmots (*Marmota caudata aurea*). *J Mammal*. 79:873–886.

Blumstein DT, Henderson SJ. 1996. Cheek-rubbing in golden marmots (*Marmota caudata aurea*). *J Zool*. 238:113–123.

Blumstein DT, Ozgul A, Yovovich V, Van Vuren DH, Armitage KB. 2006. Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. *J Zool*. 270:132–138.

Blumstein DT, Richardson DT, Cooley L, Winternitz J, Daniel JC. 2008. The structure, meaning and function of yellow-bellied marmot pup screams. *Anim Behav*. 76:1055–1064.

Blumstein DT, Steinmetz J, Armitage KB, Daniel JC. 1997. Alarm calling in yellow-bellied marmots: II. The importance of direct fitness. *Anim Behav*. 53:173–184.

Blumstein DT, Verneyre L, Daniel JC. 2004. Reliability and the adaptive utility of discrimination among alarm callers. *Proc R Soc Lond Ser B Bio Sci*. 271:1851–1857.

Bradbury J, Vehrencamp S. 1976. Social organization and foraging in emballonurid bats. II. A model for the determination of group size. *Behav Ecol Sociobiol*. 2:383–404.

Brady KM, Armitage KB. 1999. Scent-marking in the yellow-bellied marmot (*Marmota flaviventris*). *Ethol Ecol Evol*. 11:35–47.

Cameron A, Trivedi P. 1998. Regression analysis of count data. Cambridge: Cambridge University Press.

Carr G, Macdonald D. 1986. The sociality of solitary foragers: a model based on resource dispersion. *Anim Behav*. 34:1540–1549.

Clutton-Brock TH. 1989. Mammalian mating systems. *Proc R Soc Lond Ser B Biol Sci*. 236:339–372.

Connor RC, Smolker RA, Richards AF. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp). *Proc Nat Acad Sci U S A*. 89:987–990.

Eisenberg JF, Kleiman DG. 1972. Olfactory communication in mammals. *Ann Rev Ecol Syst*. 3:1–32.

Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*. 197:215–223.

Fisher RA. 1948. Combining independent tests of significance. *Am Stat*. 2:30.

Frase BA, Hoffmann RS. 1980. *Marmota flaviventris*. *Mamm Species*. 135:1–8.

Frasier TR. 2008. Storm: software for testing hypotheses of relatedness and mating patterns. *Mol Ecol Res*. 8:1263–1266.

Furrer RD, Manser MB. 2009. The evolution of urgency-based and functionally referential alarm calls in ground-dwelling species. *Am Nat*. 173:400–410.

Geffen E, Hefner R, Macdonald D, Ucko M. 1992. Habitat selection and home range in the Blanford's fox, *Vulpes cana*: compatibility with the resource dispersion hypothesis. *Oecologia*. 91:75–81.

Gehrt SD, Gergits WF, Fritzell EK. 2008. Behavioral and genetic aspects of male social groups in raccoons. *J Mammal*. 89:1473–1480.

Goossens B, Graziani L, Waits LP, Farand E, Magnolon S, Coulon J, Bel M-C, Taberlet P, Allaine D. 1998. Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. *Behav Ecol Sociobiol*. 43:281–288.

Hamilton WD. 1964. Genetical evolution of social behaviour. I. *J Theor Biol*. 7:1–16.

- Hanslik S, Kruckenhauser L. 2000. Microsatellite loci for two European sciurid species (*Marmota marmota*, *Spermophilus citellus*). *Mol Ecol*. 9:2163–2165.
- Harcourt AH. 1992. Coalitions and alliances: are primates more complex than non-primates? In: Harcourt AH, De Waal FBM, editors. *Coalitions and alliances in humans and other animals*. Oxford: Oxford University Press. p. 445–471.
- Helfman GS. 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behav Ecol Sociobiol*. 24:47–58.
- Johnson D, Kays R, Blackwell P, Macdonald D. 2002. Does the resource dispersion hypothesis explain group living? *TREE*. 17:563–570.
- Johnson D, Macdonald D, Newman C, Morecroft M. 2001. Group size versus territory size in group-living badgers: a large-sample field test of the Resource Dispersion Hypothesis. *Oikos*. 95:265–274.
- Johnston RE. 2003. Chemical communication in rodents: from pheromones to individual recognition. *J Mammal*. 84:1141–1162.
- Jones AG, Arden WR. 2003. Methods of parentage analysis in natural populations. *Mol Ecol*. 12:2511–2523.
- Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program Cervus accommodates genotyping error increases success in paternity assignment. *Mol Ecol*. 16:1099–1106.
- Kays RW, Gittleman JL. 2001. The social organization of the kinkajou *Potos flavus* (Procyonidae). *J Zool*. 253:491–504.
- Kilgore D Jr., Armitage K. 1978. Energetics of yellow-bellied marmot populations. *Ecology*. 59:78–88.
- Kononov DA, Manning C, Henshaw MT. 2004. Kingroup: a program for pedigree relationship reconstruction and kin group assignments using genetic markers. *Mol Ecol Notes*. 4:779–782.
- Kyle CJ, Karels TJ, Clark B, Strobeck C, Hik DS, Davis CS. 2004. Isolation and characterization of microsatellite markers in hoary marmots (*Marmota caligata*). *Mol Ecol Notes*. 4:749–751.
- Li CC, Weeks DE, Chakravarti A. 1993. Similarity of DNA fingerprints due to chance and relatedness. *Hum Hered*. 43:45–52.
- Macedonia JM, Evans CS. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*. 93:177–197.
- Mateo JM. 2006. The nature and representation of individual recognition odours in Belding's ground squirrels. *Anim Behav*. 71:141–154.
- May B, Gavin TA, Sherman PW, Korves TM. 1997. Characterization of microsatellite loci in the northern Idaho ground squirrel *Spermophilus brunneus brunneus*. *Mol Ecol*. 6:399–400.
- Meier PT. 1991. Response of adult woodchucks (*Marmota monax*) to oral-gland scents. *J Mammal*. 72:622–624.
- Olson LE, Blumstein DT. 2009. A trait-based approach to understand the evolution of complex coalitions in male mammals. *Behav Ecol*. 20:624–632.
- Packer C, Gilbert DA, Pusey AE, O'Brien SJ. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature*. 351:562–565.
- Raymond M, Rousset F. 1995. Genepop: population genetics software for exact tests and ecumenicism. *J Hered*. 86:248–249.
- Rowell T. 1988. Beyond the one-male group. *Behaviour*. 104:189–201.
- Sherman PW. 1977. Nepotism and the evolution of alarm calls. *Science*. 197:1246–1253.
- Sherman PW, Lacey EA, Reeve HK, Keller L. 1995. The eusociality continuum. *Behav Ecol*. 6:102–108.
- Silk JB. 1999. Male bonnet macaques use information about third-party rank relationships to recruit allies. *Anim Behav*. 58:45–51.
- da Silva A, Luikart G, Allaine D, Gautier P, Taberlet P, Pompanon F. 2003. Isolation and characterization of microsatellites in European alpine marmots (*Marmota marmota*). *Molec Ecol Notes*. 3:189–190.
- StataCorp. 2007. Stata statistical software: release 10. College Station (TX): StataCorp LP.
- Stevens S, Coffin J, Strobeck C. 1997. Microsatellite loci in Columbian ground squirrels *Spermophilus columbianus*. *Mol Ecol*. 6:493–495.
- Wagner A, Frank L, Creel S. 2008. Spatial grouping in behaviourally solitary striped hyaenas, *Hyaena hyaena*. *Anim Behav*. 75:1131–1142.
- Wang J. 2004. Sibship reconstruction from genetic data with typing errors. *Genetics*. 166:1963–1979.
- Waser PM, Keane B, Creel SR, Elliott LF, Minchella DJ. 1994. Possible male coalitions in a solitary mongoose. *Anim Behav*. 47:289–294.
- Watts DP. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behav Ecol Sociobiol*. 44:43–55.
- West S, Griffin A, Gardner A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J Evol Biol*. 20:415–432.