
Social skew as a measure of the costs and benefits of group living in marmots

THEA B. WANG, PETER NONACS, AND DANIEL T. BLUMSTEIN

Summary

In group-living animals reproduction is often skewed such that some group members reproduce more than others. In addition to reproductive skew, group members may also exhibit social skew, where some individuals show particular behaviors more often than others. Significant social skew in behaviors such as anti-predator defense or social interactions may influence survival and reproduction. Therefore, social skew has the potential to translate into reproductive skew and affect group productivity. We measured social skew across groups in a population of yellow-bellied marmots (*Marmota flaviventris*). Several behaviors such as agonistic interactions, affiliative interactions, and first emergence were significantly skewed in most groups. Alarm calling, however, was infrequently skewed more than would be expected by random chance. Thus, marmot groups do not appear to have behavioral roles in terms of individuals acting like sentinels. Although significant social skew was present, it did not obviously affect fitness as measured by female reproductive success for each group. However, skew in individual-directed behavior (e.g. agonistic and affiliative interactions) did significantly correlate with the level of reproductive skew. Finally, the results were independent of the scale at which groups were defined. Behavioral variability appears to occur similarly across the entire marmot population. The results of this study illustrate that the quantification of social skew has potential to be a powerful tool for understanding the evolution of sociality.

Reproductive Skew in Vertebrates: Proximate and Ultimate Causes, ed. Reinmar Hager and Clara B. Jones. Published by Cambridge University Press. © Cambridge University Press 2009.

Introduction

Animal groups are characterized by variation in the degree to which individuals exhibit specific behaviors and variance across group members in the distribution of such variables has come to be called “skew” (Reeve & Ratnieks 1993, Keller & Reeve 1994, Ruzzante *et al.* 1995, Kokko & Lindström 1997, Kokko *et al.* 1999, Nonacs 2000). Within cooperative groups, research has largely focused on reproductive skew (Johnstone 2000, Magrath & Heinsohn 2000, Nonacs 2001, Reeve & Keller 2001). Indeed, the degree of reproductive skew has been proposed as a valuable evolutionary metric for comparing species (Sherman *et al.* 1995, Lacey & Sherman 2005). Such a eusociality index would differentiate between species by how strictly breeder and non-breeder roles are defined within groups. Similar levels of reproductive skew could therefore imply similar evolutionary pressures across taxonomically very different groups (e.g. ants similar to naked mole-rats and paper wasps similar to cooperatively breeding birds).

This eusociality index for comparing species has been criticized by Costa & Fitzgerald (1996, 2005) on the basis that many species show complex cooperative behavior, but do not skew reproduction. However, these authors offer no mathematical solution to this problem, and it may be impossible as a practical matter to have a single skew index that measures variance simultaneously across various social behaviors and reproduction. Instead, Nonacs (2000, 2001) suggested that skew indices could be applied separately across reproductive and non-reproductive behaviors. The degree of skew in non-reproductive behaviors could correlate with outcomes for the group in survival, foraging, or reproduction. Thus, the degree to which individual group members have defined roles may have positive or negative consequences for group success in terms of survival and productivity. Here, we will extend the use of skew to study roles in yellow-bellied marmots (*Marmota flaviventris*; Figure 5.1), a moderately social ground-dwelling rodent (Frase & Hoffmann 1980).

A “role” within a group is defined in this chapter by the presence of significant skew. For example, if the frequency of alarm calling in a group of marmots shows significant skew, this could imply that the more alert individuals are acting as sentinels. Conversely, a lack of skew would imply that there is no sentinel role within groups and all individuals are equally likely to watch for predators. Roles could exist for any activity with variance in events or productivity between individuals. The combination of all the roles will define the structure and patterns of relationships within the group.



Figure 5.1 Yellow-bellied marmot pup, sex unknown. Courtesy of Daniel T. Blumstein.

Skew indices

Skew can be described in over 20 different mathematical ways (Kokko *et al.* 1999, Nonacs 2000), and, for purposes of comparing social groups, not all methods are equally valid (Nonacs 2003). Suppose we want to measure whether alarm-calling behavior in marmots is skewed. We record K alarm calls over some time period, and if there are N marmots in our defined group, the mean would be K/N alarm calls per marmot. The first problem in quantifying skew is that our null hypothesis of no skew is not an expectation that each marmot gives exactly K/N alarms. This would imply that marmots are somehow dividing up sentinel duty exactly equally, and this would require a behavioral explanation as much as would a finding of significant skew. Instead, our null expectation would be a random distribution around the mean, with some animals calling more and others calling less due to random chance. Therefore, a skew index must have a set value for a random distribution.

A second problem arises if all marmots are not present for equal periods of time. If for instance, a marmot does not emerge from its burrow, it would not be expected to give an alarm call. Therefore, apparent skew in alarm calling could be an artifact of different times spent above ground. Any skew index that

cannot adjust for differing times spent in the group is not reliably measuring behavioral differences and roles (Crespi & Yanega 1995).

Nonacs (2000, 2003) compared a variety of skew indices and recommended the *B* index as the most useful and reliable under a wide range of assumptions. The *B* index was found to be sensitive to robust differences in skew and can compare groups with different productivities, sizes, and differential residence times. This allows us to account for random processes and differential survival or duration within a group. Therefore, the *B* index is resistant to bias due to group numerical characteristics. It was also determined to be more powerful and to have better-defined statistical properties than other skew indices (Nonacs 2000). The *B* index as we use it here is not a direct replacement for the eusociality index, but rather a way of measuring skew in the performance of any social behavior.

The *B* index calculates variance across *i* individuals in a group, $\Sigma(p_i - n_i/N)^2$, where p_i is the proportion of total events performed or benefits received by the *i*-th individual and n_i is the time the *i*-th individual spent in the group. Differential time spent in the group is handled by changing *N* from the number of individuals to the total time spent in the group across all individuals. Thus, variance is the observed proportion of all acts across all individuals, minus their proportional contribution to the total group time. A random distribution has a positive variance, the magnitude of which varies with *K* and *N*. Fortunately, we can estimate a random distribution of *K* events across *N* individuals as following a binomial distribution (Sokal & Rohlf 1995). The *B* index, therefore, is the observed variance minus the expected binomial variance, and would equal zero if the behavioral activity was distributed randomly.

Social skew

To study behavioral roles in social groups, the group itself must first be defined. Groups can be determined according to geographic boundaries, but these boundaries and therefore group composition may depend on the scale at which interactions occur (e.g. alarm calls can potentially connect individuals that never physically interact). Thus, one individual can be part of many different spatially nested groups. For example, marmots that live in a meadow can be considered as a group. However, within the meadow, members may share different burrow systems and at a finer scale some individuals may be associated with specific burrows. Which geographic level to use for study may depend on the question being asked and its scale of biological relevance. Returning to our example of alarm calling, we could use a definition of a group that contains the active space of a call (i.e. all individuals within earshot), or we could focus on the set of subjects that could both hear and see a potential

caller. This distinction is important for the specific benefits that subjects can obtain. Potentially more information might be transmitted by a multimodal signal (i.e. seeing and hearing the caller: Partan & Marler 2005). Biologically meaningful group boundaries, however, may become apparent only after experimental observation when statistical patterns emerge. These patterns could identify group membership from similar individual responses to detected signals or resulting fitness consequences.

For any given defined group, it is possible to calculate skew in behavior. There are no a-priori predictions that marmot groups with well-defined behavioral roles would be more or less efficient, in terms of productivity and survival, than groups without defined behavioral roles. Certainly there will be trade-offs in time allocation. If individuals spend less time in social interactions they could allocate more time to foraging, grooming, or other forms of self-maintenance (e.g. K.A. Pollard & D.T. Blumstein, unpublished data). Energy gain and injury avoidance could come from reduced territory defense, when only a few individuals fight off transient individuals. In addition, animals that engage in the majority of the activity could draw predators away from the rest of the group. The rest of the group may be able to forage and rest unnoticed by predators.

On the other hand, the existence of behavioral roles could cause group productivity to decline. One individual performing more aggressive interactions could disrupt the other members. An individual dominating all behavioral activity could suppress other group members and prevent them from engaging in personally beneficial activities. In this way, behavioral roles in non-reproductive behaviors could have a strong influence on mating and reproductive skew. A few aggressive individuals could prevent others from gaining enough nutrition to be able to reproduce, or even prevent contact with members of the opposite sex.

Do behavioral roles have fitness consequences, and are they evolutionarily important? This might depend on whom they affect and the level of the skew. For example, if juveniles, but not adult females, have structured behavioral roles, these roles might have less of an impact on offspring production. On the other hand, if group success is limited by juvenile survival, then behavioral roles may have more fitness consequences. Roles could also vary in the degree of the consequences of skew. Behavioral roles within groups where dominants completely suppress subordinates from grooming and foraging activities would have a large fitness effect. Groups could also compensate for the effects of behavioral roles. If dominant individuals are able to prevent subordinates from reproducing but they end up having more offspring themselves, total group productivity would stay the same.

In this chapter we will examine yellow-bellied marmot reproductive and non-reproductive behavior for evidence of skewed social roles. We will use the *B* index as a metric for suggesting roles within groups and to identify potential fitness consequences of behavioral skew.

Methods

Study animals and study site

Yellow-bellied marmots, a semi-fossorial ground-dwelling sciurid rodent, were studied in the upper East River valley near the Rocky Mountain Biological Laboratory, Colorado, USA (Figure 5.2). This population has been observed continuously since 1962 (Armitage 1991, Ozgul *et al.* 2006) and social groups subdivide most colony sites (Blumstein *et al.* 2006). Each year of the study, all subjects were live-trapped and marked (with fur dye to facilitate observations from afar, and with ear tags for permanent identification). Subjects were observed from a distance known not to influence their behavior (this varied by site and ranges from 50 to 200 m), through 8×40 binoculars and 15–45× spotting scopes, during morning (06:30–10:00) and afternoon (16:00–19:00) activity bouts. All-event recording (Martin & Bateson 1993) quantified social interactions (occurring about once every 20 minutes), and alarm calling

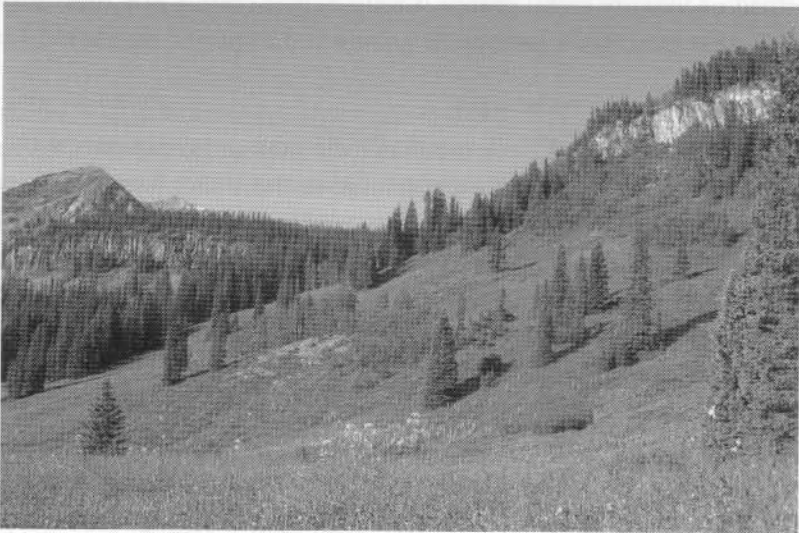


Figure 5.2 Example of yellow-bellied marmot habitat at the Rocky Mountain Biological Laboratory, Colorado. The shown site is called “Picnic” where groups P18, P20, and P21 can be found. Courtesy of Lucretia Olson.

(which is much less frequent). For the following analysis of social skew, we focus on data collected in the 2004 active season (April through August).

Group composition

Social groups were defined by calculating a simple ratio association index (Cairns & Schwager 1987). The ratio calculates the proportion of observations in which individuals are seen together (at the same burrow entrance) as a fraction of all times they were seen both together and alone. We used the entire set of observations and trap locations from 2004 to calculate ratios. We measured skew across a range of association levels (0.1, 0.3, 0.5, and 0.7). The low 0.1 association level compared groups that included individuals observed in the same general geographic colony (which consists of several burrows) and the higher levels are increasingly smaller subdivisions within the colony. Different association levels allow us to examine behavioral roles at different scales in the population. We used a 0.5 association level to compare skew across different age-sex classes. This level is appropriate for individuals known to share burrows, and has been used in previous studies (Baird & Whitehead 2000, Nanayakkara & Blumstein 2003). The age-sex classes that we considered included: all marmots, all marmots excluding juveniles, adult females and yearling females, adult males and yearling males, only adult females, and only adult males. We used SOCPROG 2.2 (Whitehead 2004), a program for analyzing social structure, to calculate association indices and plot dendrograms that helped us identify social groups. Group names consist of a one- or two-letter prefix that indicates a geographic colony and a specific number.

Non-reproductive behaviors

We analyzed skew in individual-directed and group-directed behaviors. Individual-directed behaviors are defined as those that have a clear recipient, such as allogrooming or biting. We grouped individual-directed behaviors into two categories: (1) affiliative or positive, or (2) agonistic or negative (Table 5.1). In contrast, group-directed behaviors may have no targeted individual and potentially a large number of recipients. Examined group-directed behaviors were alarm calling and first emergence. Alarm calls have a demonstrable conspecific warning function (Blumstein *et al.* 1997). Each time a marmot initiated a bout of alarm calling, we recorded the number of individual calls within a bout, the duration of the bout, and the likely cause for the alarm. For analysis, we used bouts of alarm calls as a measure rather than the number of separate calls within a bout, because these are likely to be directed at the same stimulus. Bouts were considered separate if at least 1 minute elapsed between calls.

Table 5.1 *Individual-directed behaviors*

Affiliative (positive)	Agonistic (negative)
Follow another marmot	Posture aggressively
Forage with another marmot	Vocalize aggressively
Lie down with another marmot	Snarl
Greet	Snap
Sniff	Hiss
Play	Displace
Groom	Fight
Nurse	
Mate	

The first marmot to emerge from the burrow each day can be thought of as a "scout." This marmot incurs an extra degree of predation risk because it may be the first to be detected by a lurking predator. All subsequent marmots potentially gain information from what happens to the first marmot through group eavesdropping. Because the visibility and total activity levels during the end of the summer are reduced (thus making it difficult in our subalpine system for eavesdroppers to benefit), we only looked at emergences before July 1, 2004. First emergence was recorded during observations begun before 07:30 hours, and only when the observer could clearly identify which marmot emerged first.

Skew calculation

Skew was calculated using the B index as described in Nonacs (2000). It determines whether K events are spread randomly over i number of individuals in a group. For affiliative and agonistic social behaviors and alarm calls, we transformed for each marmot its observed number of social behaviors (k_i) into its proportional contribution to the total number of social interactions ($k_i/K = p_i$). Because individuals were observed for different lengths of time, group size was defined relative to the total number of minutes that all individuals were observed (N_t), such that weighted mean group size equals N_t/n_{\max} , where n_{\max} is the maximum time any individual could be present (often equal to the length of time the group was observed). Therefore, the expected proportion of K events performed by the i -th individual is the number of minutes it was observed, divided by the total time ($= n_i/N_t$). Observed variance is the sum across all marmots of $(p_i - n_i/N_t)^2$.

To calculate the B index value for a group we subtracted the expected variance from the observed variance. The expected variance follows the binomial distribution such that it equals $(1 - 1/N)/K$. For first emergence, N_t was total number of animals known to be present in a group (independent of whether they did or did not emerge on a particular day), and all n_t equalled one. The significance of skew for each group was determined by simulation. We assigned a probability level that the observed B value was due to random chance for each group. All B index values and their significance levels were calculated using Skew Calculator (available at: www.ceb.ucla.edu/Faculty/Nonacs). Statistically significant skew as measured by the B index values implies that marmots within a group have different behavioral propensities that might be considered behavioral roles.

Fitness consequences

The next question is whether strongly defined roles within groups have fitness consequences. Therefore, we correlated observed social skew with reproductive skew (measured again with the B index) and overall reproductive success of groups. Individual reproductive success was measured by the number of pups born to each female. For mixed litters, we calculated the average number of pups per associated adult female (Armitage 2004). Group reproductive success was measured by the total number of pups divided by the total number of adult females in the group.

The range of the B index increases with larger group size (N) and both N and K affect the absolute values that represent complete skew and completely equal sharing (see Nonacs 2000 for details on calculating the potential minimum and maximum B index values). Therefore, we cannot use them for across-group comparisons. Instead, we converted the B index values to standardized values by dividing positive and negative B values by the absolute values of the maximum and minimum possible B value (Nonacs 2000). This creates a parameter range of -1 to 1 . The adjusted B index should be used with caution because it tends to overweight distributions with less than random variance (Nonacs 2003). For our purposes, however, this does not represent a problem as we do not use the adjusted B index to determine deviations from random expectations.

Results

When groups were defined using association indices ranging from 0.1 to 0.7, we found no substantial differences in the proportion of groups that indicated significant skew. This was found for both group-directed and individual-directed behaviors (Figure 5.3). Higher association levels subdivided the

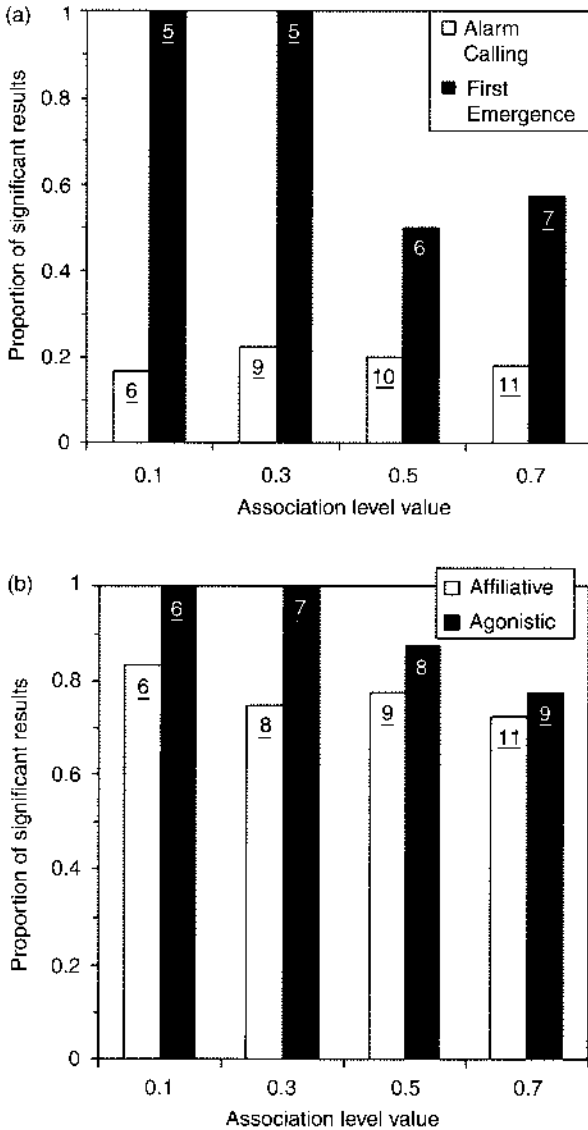


Figure 5.3 Proportion of significantly skewed groups at each of the four levels of association. The total number of groups for each behavior at that association level is indicated at the top of each bar. (a) Group-directed behavior; (b) Individual-directed behavior.

population into more groups but similar proportions of them were significantly skewed. Not all groups for the four behaviors were used because we could not calculate skew for groups with only 1 member or only ≤ 1 event. We

found consistently significant skew in first emergence, affiliative, and agonistic social behaviors. At least 60% of the groups at each association level were significantly skewed in these three behaviors. Alarm calling was much less often significantly skewed.

A detailed analysis at the 0.5 level of association shows that skew for all behaviors was consistent across different demographic and age-sex classes (Table 5.2). In general, groups that were significantly skewed across all marmots were also skewed when juveniles were excluded from the analysis, and when only one sex was included. In addition, neither age nor sex was a significant predictor for which marmots were the most likely to emerge first in the morning (Table 5.3).

Skew in individual or group-directed behaviors did not significantly correlate with a group's reproductive success. Reproduction itself, however, was significantly skewed across females in four of the seven groups, and marginally skewed in another (Table 5.4). Two groups, however, shared reproduction more equally than would have been predicted by chance, and across all seven groups reproduction was more skewed than expected by chance. There was no significant relationship between a group's reproductive skew and the mean number of offspring produced per adult female in the group (Figure 5.4), nor did reproductive skew predict the success of individual females.

Skew in both individual-directed social interactions was significantly associated with reproductive skew (Figure 5.5). Group P20, however, is an outlier in these comparisons, and if excluded, neither relationship remains significant. Although both individual-directed behaviors exhibited significant levels of skew, there was no significant correlation between the skew of affiliative and the skew of agonistic social behaviors (Figure 5.6). Skew in neither of the group-directed behaviors significantly correlated with reproductive skew.

Discussion

Within a social group or neighborhood, functional roles can result from individuals that are recognizably different in their personalities and propensities towards certain actions (Bouchard & Loehlin 2001, Sih *et al.* 2004). While the majority of the observed yellow-bellied marmot groups exhibited significant skew across several behaviors, the functional implications of this skew were not dramatic.

Sentinels and scouts

We found that in almost all groups no sentinel role could be detected through a differential likelihood to issue alarm calls. This result parallels the

Table 5.2 Skew in behaviors at the 0.5 level of association. For some groups, there were not enough observed behaviors to calculate B values

Group	All marmosets	N	Alarm calling		Scouting		Social affiliative		Social agonistic	
			B	P-level	B	P-level	B	P-level	B	P-level
BR10		11	-0.0077	0.735	0.0396	0.034	0.0106	<0.001	0.0752	<0.001
BR12		4	0.2536	0.283						
BR14		48	0.0005	0.486	0.0717	<0.001	0.0274	<0.001	0.0903	<0.001
M5		30	0.0296	0.076	0.0844	0.001	0.0218	<0.001	0.0582	<0.001
P18		22	0.0155	0.333	0.1236	0.057	0.0964	<0.001	0.0723	0.012
P20		15	0.2484	0.030			-0.0257	0.841	0.3849	<0.001
P21		22	-0.0352	0.769	0.0277	0.094	0.0772	<0.001	0.0169	0.107
T2		5	0.0517	0.483			0.5178	0.033	0.4724	0.005
T8		10	0.4080	0.003			0.0897	0.104		
T9		13	-0.0107	0.699	0.0373	0.054	0.0303	<0.001	0.0228	0.014
All adults and yearlings										
BR10		11	-0.0077	0.714	0.0396	0.028	0.0106	<0.001	0.0752	<0.001
BR12		3	0.1903	0.385			0.0342	<0.001	0.0844	<0.001
BR14		20	-0.0041	0.545	0.0436	0.004				
M5		20	0.0318	0.113	0.0689	0.003	0.0265	<0.001	0.0516	<0.001
P18		13	0.0234	0.202	0.0985	0.109	0.1089	<0.001	0.0679	0.008
P20		6	0.2518	0.033			-0.0289	0.851	0.3837	0.003
P21		12	0.0309	0.658	0.0043	0.298	0.0792	<0.001	0.0161	0.117
T2		2	0.0160	0.607					0.9479	0.024
T8		2	0.0409	0.382						
T9		13	-0.0107	0.697	0.0373	0.061	0.0303	<0.001	0.0228	0.006

Table 5.2 (cont.)

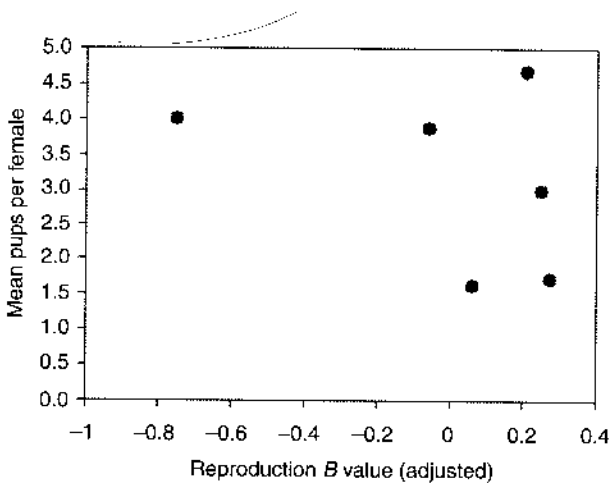
	N	Alarm calling		Scouting		Social affiliative		Social agonistic	
		R	P-level	B	P-level	B	P-level	B	P-level
All adult females and yearling females									
BR10	7			0.1353	0.015	0.0162	0.010	0.0385	0.036
BR14	15	0.0054	0.419	0.0771	0.003	0.0570	<0.001	0.0525	<0.001
M5	7	0.0082	0.421	0.0714	0.101	0.0227	0.004	0.2159	<0.001
P18	9			0.0711	0.25	0.0570	0.006	0.0566	0.046
P20	3					0.0025	0.559		
P21	8	-0.0501	0.772	0.0186	0.203	0.0302	0.007	0.0129	0.227
T9	5	-0.0328	0.801	0.0556	0.269	0.0617	0.003	0.0288	0.237
All adult males and yearling males									
BR10	4	-0.0200	0.662	-0.0247	0.583	-0.0034	0.793	0.0640	0.001
BR14	5	-0.1530	0.760	0.0327	0.291	0.0175	0.004	0.3705	<0.001
M5	13	-0.0294	0.565	0.1785	0.048	0.0321	<0.001	0.0291	0.011
P18	4					0.0738	<0.001		
P20	3	0.3259	0.130			-0.0414	0.713	0.5179	0.006
P21	4			-0.1667	1.000	0.1364	<0.001	0.1637	0.073
T9	8	0.0134	0.362	0.0875	0.045	0.0318	<0.001	0.0077	0.224

Table 5.3 The distribution of the number of observed first-emergence events across marmots within groups, by age-sex class (no. first / no. in class)

Group	Adult females	Adult males	Yearling females	Yearling males
BR10	1/3	2/1	11/4	7/2
BR14	14/8	2/3	7/6	5/2
M5	4/3	3/3	6/4	2/10
P18	5/8	0/1	0/1	0/3
P21	10/7	2/2	1/1	1/2
T9	2/3	0/2	4/2	10/6
Total	36/32	9/12	29/18	25/25

Table 5.4 Reproductive skew among adult females

Group	Females	Pups	B value	P
BR10	3	12	0.1111	0.064
BR14	8	31	-0.0018	0.447
M5	3	9	0.1481	0.040
P18	8	13	0.0514	0.015
P20	3	12	-0.0417	0.927
P21	7	12	0.2163	<0.001
T9	3	14	0.1293	0.022
Means	5.0	14.7	0.0875	<0.001

Figure 5.4 Mean number of pups per female for each group relative to the adjusted B index values ($P = 0.526$).

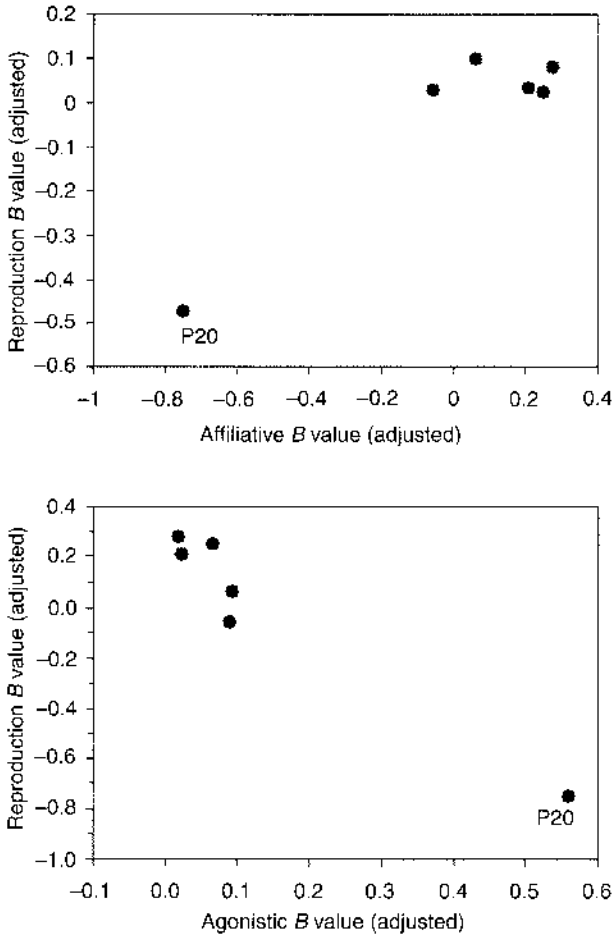


Figure 5.5 Skew in behavior versus skew in reproduction: (a) $P = 0.0023$ and (b) $P = 0.0003$ with all the data points. If the outlier point (group P20 in both panels) is removed, there is no significant relationship.

finding of Blumstein *et al.* (1997) that most age-sex classes call at similarly low rates. In contrast, however, the majority of groups had individuals that were significantly likely to act as scouts (defined as the first marmot to emerge from its burrow in the morning). Emerging first is a risky behavior as this individual would be the first to encounter a waiting predator (predators were observed outside marmot burrows early in the morning), and other marmots would gain information from the experience of the first one out. Overall, which marmots had a propensity to emerge first was not significantly predicted by age or sex. Thus, a tendency to act as a scout may reflect consistent behavioral differences in the personalities of marmots relative to their risk

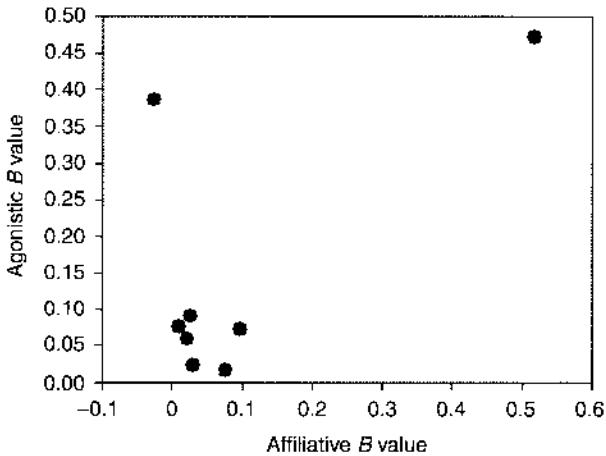


Figure 5.6 The relationship between index values for agonistic and affiliative behaviors.

taking (Blumstein *et al.* 2004). In contrast, Armitage *et al.* (1996) found that adult males spent more time above ground than other age-sex classes. This would suggest that adult males act more often as scouts and have increased opportunities to use other marmots as scouts. Whether scouting truly has a social role requires further study.

Individual-directed versus group-directed behaviors

Behavioral skew was more pronounced across groups in individual-directed behaviors than in group-directed behaviors (Figure 5.3). This also suggests stable personality differences across individuals in willingness to positively or negatively interact. These differences are not created by different patterns of interaction across the sexes, as both females and males show the same skew patterns (Table 5.2). We cannot rule out, however, that relatedness differences rather than personality differences play a role in creating skew in individual-directed behavior. We currently do not have precise coefficients of relatedness calculated for the observed animals. Therefore, particularly affiliative pairs may be close relatives, and agonistic pairs may be genetically distant or unrelated. A mixture of such pairs within a group could create an overall skewed pattern of behavior. A pattern of interaction that is based primarily on relatedness would, however, also predict similar and correlated levels of skew across groups in affiliative and agonistic acts. Such a correlation does not exist between these two measures (Figure 5.6), which suggests that aggressive and cooperative behavior may vary separately across individual

yellow-bellied marmots. Therefore, at least one of the traits must be independent of genetic relatedness.

The results described in this study are not highly sensitive to the size of the defined group as categorized by association index. This implies that the underlying factors affecting social skew are scale-independent. In other words, similar skew at low and high association levels implies that behavioral variability in personality appears to be the same within groups as it is across groups. This was unexpected, because some behaviors are limited to individuals that physically interact (e.g. affiliative behaviors), while others (e.g. alarm calling) can affect individuals with whom the caller has no physical relationship. Lower association indices imply a reduced opportunity for physical interaction. Given variation in the nature of who could be influenced by a behavior, we expected that social skew would be influenced by our definition of group. We also found that within colonies there was no evidence of individuals associating with others into groups that have similar behavioral patterns. It is possible that behavioral roles are constrained in some way, and that groups cannot be that different from each other. Further studies are required to elucidate why social behaviors appear to be scale-independent.

Functional implications

We found no relationship between either behavioral or reproductive skew and per capita fitness of females in terms of reproductive success. The degree to which a group had defined behavioral roles did not predict either more or less reproduction. Therefore, within the population we studied there is no evidence for strong selection operating to favor more advanced levels of sociality with pronounced social and reproductive skew. Yellow-bellied marmots appear stably ensconced at an intermediate level of social complexity (Nonacs 2001, Helms Cahan *et al.* 2002), a finding that parallels other classifications of this species (Armitage 1981, Michener 1983, Blumstein & Armitage 1998). We are unaware of other studies with vertebrates or social insects that have correlated social skew to group success, but the results from other species and populations would be interesting for comparisons.

We found two interesting relationships between behavioral skew and reproductive skew. Reproductive skew was positively correlated with affiliative skew and negatively with agonistic skew (Figure 5.5). This suggests that when reproductive skew occurs, it is not created through agonistic actions of a very dominant individual. It seems possible that because the existence of skew in different behaviors is not due to one particular individual, patterns of social skew in groups would be more resistant to changes in group composition. However, it should be noted that the results for reproductive, affiliative, and

agonistic skew are strongly influenced by the presence of one group (P20). Our dataset is currently not large enough to determine whether this group is a true outlier, or indicative of a more robust relationship. However, the analysis has identified this one group as behaving in a very different manner from others. Therefore, it will be interesting to pursue why this group appears to have different dynamics within its interactions. Following the entire RMBL population for several more years will allow us to answer this question.

Overall, we did not find a large effect of behavioral roles on group productivity. It is possible that our productivity measurement was insensitive to effects of behavioral roles. This could be taken into account by measuring weight gain or some other group factor. In this population of yellow-bellied marmots, productivity could be influenced more by past behavioral interactions or environmental factors, such as snowfall the year before, than by current behavioral interactions. We were also limited by a small number of groups and low event numbers for some behaviors. Increased size in both of these factors could possibly elucidate the effects of behavioral roles.

Conclusion

In summary, the study of social skew and the identification of behavioral roles can lead to insight and clarification regarding social evolution and social complexity. Using social skew for comparisons avoids taxa-based terminology, which is an important step in identifying patterns of sociality in social insects and vertebrates (Brockmann 1997). We can look at groups with similar social skew and behavioral roles to identify common constraints between social species as well as look at the effect of common constraints.

In this chapter, we have outlined the first steps of an approach to studying group behavior that can potentially be applied across numerous other taxa, and that may become a framework for comparison across groups that do not have clear reproductive skew (see Costa & Fitzgerald 2005). In regard to yellow-bellied marmots, there are several future areas of research. For example, additional group- and individual-directed behaviors can be examined to see if the latter have consistently higher levels of skew. Also, the *B* index identifies the presence of behavioral roles within a group, but not the specific individuals responsible. More detailed analysis may identify predictive characters for particular behavioral types. Finally, it is of interest to be able to follow the same groups across years and investigate whether social skew changes over time and whether there are any fitness consequences. The application of skew metrics to behavioral phenomena may have a very informative future.

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