HOW MUCH DOES SOCIAL GROUP SIZE INFLUENCE GOLDEN MARMOT VIGILANCE?

by

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Summary

A commonly cited benefit of group living is the ability for individuals to reduce the time devoted to scanning for predators with increasing group size — the 'group size effect'. Interestingly, most studies reporting a group size effect have focused on documenting a significant group size effect and did not discuss the relative 'importance' of group size. One way to study the relative importance of group size is to calculate the amount of

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variation in vigilance explained by group size. I studied effects of social group size on golden marmot (*Marmota caudata aurea*) vigilance in two ways. First, I estimated the overall amount of time marmots were vigilant during their morning active periods. Second, I estimated the amount of time marmots were vigilant specifically while foraging. Analyses statistically controlled for several factors that have been suggested to confound the study of group size effects. While marmots were active, only 14% of the variation in vigilance was explained by social group size. For foraging marmots, even less variation (about 6%) was explained by social group size. The amount of variation explained by social group size in golden marmots is considerably less that reported in several studies of other species where explained variation was reported or could be estimated from data. Some of the discrepancy between variation explained in this and other studies may stem from my focus on social group size which appears to explain less variation than the more commonly studied foraging aggregation size. However, species differ in the amount of time they devote to foraging and therefore vary in the magnitude of net benefit from group size effects. Future comparative work will be required to rigorously study the relationship between amount of time foraging and the magnitude of group size effects.

Introduction

Animals subject to predation should devote some time to antipredatory vigilance. A commonly cited benefit of aggregation is the ability for individuals to reduce their vigilance (*i.e.* time spent scanning for predators) with increasing group size — the 'group size effect' (reviewed in Elgar, 1989; Lima, 1990; Lima & Dill, 1990; Quenette, 1990; but see Catterall *et al.*, 1992). While group size effects are widely reported, we know less about the relative 'importance' of aggregation.

Specifically, comparatively few studies have reported the amount of variation in vigilance that group size explained. This appears to be an artifact of the analytical techniques used to study group size effects. For instance, many investigators clumped observations of different group sizes into two or more categories and then determined whether the mean values of vigilance variables were significantly different (*e.g.* small *versus* large 'coteries' — Hoogland, 1979; groups of $N = 1$, $N = 2$, $N = 3$ or 4 — Bertram, 1980; groups of $N = 1\text{-}2$, $N = 3\text{-}6$, $N = 7\text{-}12$, $N = 13\text{-}24$, $N = 25\text{-}49$, $N = 50+$ — Colagross & Cockburn, 1993). While estimating the strength of association between variables (one way to study the 'importance' of a significant effect) from an ANOVA is relatively simple (*e.g.* Tabachnick & Fidell, 1996), the strength of association is generally not reported. Many studies of vigilance have been conducted on unidentified animals. The inevitable data pooling that generally follows increases the likelihood of artificially increasing the sample size and detecting a significant group size effect (*e.g.* Machlis *et al.*, 1985; Leger & Didrichsons, 1994). Because significance alone is an inadequate measure of the 'importance' of an effect, 'means comparison' studies that do not estimate the strength of association leave open the question of the relative importance, or influence, of group size on vigilance.

In contrast, some investigators have treated group size as a continuous variable and calculated regressions or correlations to study the effect of group size on measures of vigilance. For these analyses, the square of the Pearson product-moment correlation coefficient, r, is a very interpretable measure of the strength of association between two variables (Tabachnick & Fidell, 1996). The square of the correlation coefficient, r^2, equals the amount of variation in one variable that is explained by the other variable (R and R^2 are the analogous terms in a regression: Cohen & Cohen, 1983). Lipetz & Bekoff (1982) found that about 16.2% of the variation in the proportion of pronghorn antelope (*Antilocapra americana*) vigilance was explained by group size. Lima (1995) found that 71-88% of the variation in foraging junco (*Junco hyemalis*) vigilance was explained by group size. Bekoff (1995) found that group size explained 62% of the variation in the average proportion of time spent scanning by individual western evening grosbeaks (*Coccothraustes vespertinus*) that foraged in circles, and much less variation when they foraged in lines. Some investigators reported Pearson or Spearman rank correlation coefficients from which r^2 values can be exactly or roughly estimated (r_s^2 may overestimate explained variation). For instance, Quenette & Gerard (1992) reported that individual vigilance and group size were negatively correlated ($r_s = -0.49$) in foraging wild boars (*Sus scrofa*). Thus, about 24% of the variation in individual vigilance is explained by group size. Yaber & Herrera (1994) reported that individual alert rates and group size were negatively correlated ($r_s = -0.649$) in foraging capybara (*Hydrochaeris hydrochaeris*). Thus, about 42% of the variation in alert rate is explained by group size. Burger & Gochfeld (1992) reported that coati (*Nasua narica*) drinking in larger groups, drank more (and therefore spent less time vigilant, $r = 0.66$). Thus, about 44% of the variation in drinking (and indirectly vigilance was explained by group size. And, Isbell & Young (1993) found that vervet monkeys (*Cerco-*

pithecus aethiops) scanned less in larger social groups ($r = -0.35$). Thus, about 12% of the variation in scanning was explained by social group size. Finally, some investigators reported data from which R^2 values could be estimated. For instance, re-analysis of Pulliam *et al.*'s (1982: Table 2) data suggests 49% of the variation in scanning rate is explained by group size (if group sizes of 1 are excluded from the regression, group size explains 77% of the variation in scanning rate). Explaining variation, rather than simply documenting an effect, should be a main goal of studies of group size effects (see also Bekoff, 1995).

The relationship between group size and vigilance has been measured in a variety of ways. Some studies have quantified vigilance during periods of general activity (*e.g.* Hoogland, 1979, 1995; Colagross & Cockburn, 1993; Loughry, 1993; Rose & Fedigan, 1995), while others focused specifically on vigilance while foraging (*e.g.* Monaghan & Metcalfe, 1985; Pöysä, 1994; Lima, 1995). Animals may be vigilant for reasons other than predator detection (Lima, 1990; Bekoff, 1995); they may look around to monitor the behavior of conspecifics (*e.g.* Roberts, 1988), or the behavior of non-predatory species (Thompson & Lendrem, 1985). Thus, correlational evidence of group size effects is necessary, but not sufficient, evidence of a vigilance-reduction benefit from aggregation. For instance, an observed group size effect could simply result from increased feeding competition (Elgar, 1989). Elgar discussed a number of other factors that could confound correlational studies of vigilance and suggested that experimentally controlled studies of vigilance were required (*e.g.* Kildaw, 1995). Nevertheless, statistical control of potentially confounding factors can help identify the magnitude of a group size effect.

The majority of group size effects have been documented in aggregations of foraging animals where group size and membership may change dynamically. However, some species live in longer-term aggregations called social groups. Wilson (1975, p. 585) defined a social group "as any set of organisms, belonging to the same species, that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics." Hoogland (1979) concluded that group-size effects were one benefit that may have led to social group formation and coloniality in prairie dogs (*Cynomys* spp.).

Other group-living social sciurid rodents (*Cynomys* spp., *Marmota* spp., *Spermophilus* spp.) are reported to decrease vigilance with group size. Carey & Moore (1986) focused on vigilance in foraging yellow-bellied marmots (*Marmota flaviventris*) and defined foraging groups to include all marmots within 15 m. They found that 11% of the variation in vigilance was explained by foraging group size. Results from several primarily univariate studies suggest that a number of other factors influence vigilance in some of the six species of New World marmots. Yellow-bellied marmot vigilance is influenced by location in 'colony' (Armitage, 1962), whether a marmot lives in a group (Svendsen, 1974), age (Armitage & Corona, 1994), and time of year (Armitage & Corona, 1994). Yellow-bellied marmot vigilance is apparently not influenced by vegetation type (Travis & Armitage, 1972). Olympic marmot (*M. olympus*) vigilance is influenced by proximity to other marmots, but not proximity to burrows (Barash, 1973). Hoary marmot (*M. caligata*) vigilance is influenced by time of year (Barash, 1989), age (Holmes, 1984), distance to refuge (Holmes, 1984), and proximity to other marmots (Holmes, 1984; Barash, 1989). Aside from brief mention of human disturbances in Gibault *et al.* (1994), and a study of the vigilance of three subjects in Massemin *et al.* (1993), I am aware of no published studies of vigilance in any of the eight species of Old World marmots. Information about Old World marmot vigilance is thus of some comparative interest and one might expect more pronounced group-size effects since Old World species tend to be more social (*i.e.* social groups contain more individuals in different age-sex categories: Blumstein & Armitage, unpubl. data) than some of their New World congeners (Arnold, 1990).

I studied vigilance in the golden marmot (*Marmota caudata aurea*), a 3-5 kg Old World sciurid rodent, living in a relatively intact predator community where marmots were preyed on by foxes (*Vulpes vulpes montana*), wolves (*Canis lupus*), snow leopards (*Panthera uncia*), golden eagles (*Aquila chrysaetos*), and possibly bearded vultures (*Gypaetus barbatus*) (Roberts, 1977; Blumstein, 1994; Blumstein & Robertson, 1995). Golden marmots are highly social and are found in social groups of 2-7 adults with younger offspring; occasionally, animals lived alone (D.T. Blumstein & W. Arnold, unpubl. data). All group members shared sleeping burrows, generally behaved amicably towards each other, had overlapping home ranges, and emitted reasonably complex alarm calls apparently designed to warn conspecifics about the relative risk of predation (Blumstein, 1994, 1995 a; D.T. Blumstein & W. Arnold, unpubl. data). Golden marmots were most active in the mornings, during which time they foraged 30-41% of the time (Blumstein, 1994; see below).

Methods

Golden marmot vigilance was studied during the summer active seasons of 1990-1993 as part of a longer-term study of how marmots assess and manage predation hazard (Blumstein, 1994). I studied golden marmots at Dhee Sar (36°81′N, 74°95′E) in Khunjerab National Park, Pakistan (Blumstein, 1995b). Dhee Sar is a relatively flat high alpine meadow (elevation 4100-4300 m) surrounded by steep lateral glacial moraines and punctuated with hilly terminal moraines. Marmots typically lived on or beside the moraines in obvious social groups. Social groups consisted of marmots whose home ranges overlapped other group members to a greater degree than non-group members. Group membership was unambiguously described: group members shared sleeping burrows and interacted amicably with other group members. Non-group members rarely, if ever, were observed near sleeping burrows of other social groups. Social group home ranges were large in contrast to other sciurids, averaging 3.1 ha (D.T. Blumstein & W. Arnold, unpubl. data). Vegetation was sparse and low, generally less than 20 cm, and the end-of-season standing crop in social groups averaged between 23 and 50 g/m^2 (D.T. Blumstein & J.M. Foggin, unpubl. data). Despite low vegetation, boulders and hillocks often created pockets of limited peripheral visibility. Observations were made from hides with binoculars and 15-45× spotting scopes between 0530 and 1000 h — the period of peak marmot activity. To identify marmots, all residents in the core area of the 250 ha study site were livetrapped, ear tagged (for permanent identification), and fur dyed (for distant identification — details in Blumstein, 1994). All observations (see below) were conducted on individually identified marmots.

To document social group size, marmot groups were censused weekly; for this paper I exclude juveniles from group size counts. Because golden marmots lived in social groups but did not forage in obvious aggregations I used the number of group residents as a metric of group size. This definition of 'group size' differs from that typically used in those studies that focused on foraging aggregations. By using social group size, I address the specific question of whether there is a current vigilance reduction benefit from living in social groups.

Foraging included head-down foraging, where the focal marmot quadrupedally stood and harvested vegetation with its mouth and occasionally a forepaw, and also rearing-up foraging, where the focal marmot reared-up on its hind legs and harvested vegetation with its mouth and forepaws. Vigilance behavior included standing bipedally or quadrupedally with the head raised from the substrate. I assumed that when a subject raised its head from the substrate it potentially scanned the environment and therefore was vigilant. Virtually all studies of vigilance similarly infer vigilance from postural changes (*e.g.* 'looking up'). For the focal observations (see below), vigilance also included locomotor activity where the focal marmot's head was elevated and the subject could have scanned the environment.

Marmots had a variety of other non-social and social behaviors in their repertoire (Blumstein, 1994). I measured vigilance behavior in two ways.

Overall vigilance

The identity and activity of individual non-juvenile marmots in 2-3 different social groups was noted every 30 min during morning observation periods. For each individual observed, I calculated an annual proportion of scans during which each subject foraged, looked, and was engaged in all other behaviors. This analysis overestimates both foraging and vigilance in the overall activity budget because it excludes animals that were out of sight or in their burrows. Focal results suggested that marmots were out of sight behind rocks and in gullies about 9% of the time during periods of peak activity (Blumstein, 1994). Nevertheless, scan samples do provide a metric by which to compare activity as a function of group size.

I treated each year's scan results as 'independent' samples for analysis (*e.g.* Hoogland, 1995). This data pooling resulted in some individuals contributing more than one point to the overall data set. Data pooling is justified because group sizes generally changed between years via recruitment of young, immigration, emigration, and mortality. I tested for sex differences in overall non-juvenile activity budgets, and upon finding none, combined sexes for this analysis. Annual modal group size (the independent variable) was regressed against the arc sine of each dependent variable (the annual proportion of time devoted to vigilance, foraging, and other behaviors). All bivariate and descriptive statistics were calculated using StatView 4.01 (Abacus Concepts Inc., 1993), variables were transformed to meet statistical assumptions, and I report the more conservative adjusted R^2 values. Because bivariate regressions focused on average annual activity patterns, the analysis was unable to statistically control for other confounding variables (Elgar, 1989). To study the effect of other potentially confounding variables, and to see if there were group size effects while subjects were engaged in a common and possibly risky behavior, I observed foraging marmots.

Vigilance while foraging

In 1992 and 1993, individually identified, non-juvenile, foraging marmots from throughout the study area were observed during two-minute focal animal samples. Two minutes was chosen because longer samples often included behaviors other than foraging or vigilance. A Tandy 102 portable microcomputer with non-commercial event-recording software was used to record the onset of both vigilance and foraging. The initiation of a behavior other than vigilance or foraging ended the focal animal sample and these focal samples were omitted from analysis. As each focal observation was conducted, six independent variables hypothesized to influence vigilance were noted: identity, age (yearling, two-year old, adult), current group size (because of within year intergroup transfers, current group size refers to the modal group size the week of the focal observation), distance to the nearest main burrow (main burrows are sleeping burrows and are preferred refugia: Blumstein, 1994), and distance to the nearest marmot (1993 data set only). Foraging marmots generally moved less than 10 m in 2 min. I excluded observations where marmots moved more than 15 m. Distances were either estimated from the location of marmots on a marked grid (observer accuracy ± 1 m) or estimated with respect to known distances between natural landmarks (observer accuracy approximately ± 5 m for distances 50 m, ± 10 m for distances 50-150 m, and ± 10-20 m for distances > 150 m).

More individuals were observed in 1993 ($N = 73$) than in 1992 ($N = 68$). Many of the subjects were observed in both years; 13 of the subjects observed in 1993 were observed $\geqslant 4$ times. I used the 1993 data set for a detailed analysis of vigilance while foraging and used the 1992 data to test for validity and robustness of 1993 results. Because most subjects were represented in both data sets, repeating the analysis with another year's data does not provide an independent test of external validity or robustness.

Each focal observation generated three dependent variables and had an associated set of six independent variables. Some of these independent variables changed between focal samples conducted on the same individual (*e.g.* current group size, distance to the nearest main burrow, distance to the nearest marmot), while others remained the same (id, sex, age). The multivariate nature of this analysis prevented the averaging of different observations to generate a single description of an individual's vigilance behavior that could be used in subsequent analyses (*e.g.* as was done to study overall vigilance). For instance, it would be meaningless to use an individual's average distance to the main burrow to explain variation in a dependent variable since there were other factors that were uniquely associated with each observation (*i.e.* group size, distance to the nearest marmot) and the goal of the multivariate analysis was to statistically identify the unique effect of each independent variable (*e.g.* Cohen & Cohen, 1983). Instead of averaging observations, a single observation from each subject was randomly selected from the 1993 data set and used in the detailed analysis of variation in vigilance while foraging. In doing so, I did not estimate the individual component of total variation and may have thus inflated the overall amount of variation in vigilance. The 'nested' analysis (see below) overcomes this limitation, albeit at the cost of describing the vigilance behavior of fewer subjects.

Five independent variables (sex, age, group size, distance to nearest marmot, distance to nearest main burrow) were entered into linear models to explain variation in the number of looks, the average time looking, and the total time looking during each two-minute focal sample. I used backward-stepwise ANCOVA to delete variables with Type III sums of square p-values > 0.1. Linear models were fitted with SuperAnova; I again report adjusted R^2 values (Abacus Concepts Inc., 1991).

Studies of a variety of animals, including yellow-bellied marmots, have documented individual behavioral phenotypes (Svendsen & Armitage, 1973; Wilson *et al.*, 1994). To study the effect of individuality on variation in vigilance, 13 marmots with four or five different focal observations were selected for further analysis. The covariate 'marmot identity' was entered as a dummy variable along with group size (the single variable remaining after the deletion process — see results). The significance of marmot identity in the model with group size was computed, and I examined the additional variation explained by a model containing identity. I also 'nested' group size within marmot identity and tested for the significance of nested models on explaining variation in the vigilance variables.

In 1992, I did not record the distance to the nearest marmot. Thus, I linearly modeled each of the dependent variables as a function of four independent variables (sex, age, group size, distance to the nearest main burrow), and applied the same backward stepwise deletion algorithm.

Distance to the nearest marmot was examined in more detail by checking if variation in vigilance or the amount of time devoted to foraging was explained by whether a marmot was within 5 m of the focal marmot. I selected 5 m because it seemed that marmots within 5 m of each other were in visible contact; habitat and topographic heterogeneity often made it difficult for a marmot foraging with its head near the ground to see more distant marmots.

Results

Overall vigilance

Although there were some significant effects of group size on vigilance, little variation in the time devoted to vigilance was explained by group size. There was a small but significant negative effect of group size on the frequency of vigilance (Fig. 1a: $R = 0.41$, Adjusted $R^2 = 0.144$, $p = 0.012$, $N = 37$), a weak positive effect of group size on foraging frequency (Fig. 1b: $R = 0.29$, Adjusted $R^2 = 0.06$. $p = 0.079$, $N = 37$), and no effect of group size on the frequency of other behaviors (Fig. 1c: $R = 0.24$, Adjusted $R^2 = 0.032$, $p = 0.149$, $N = 37$). Overall, 41% (0.7 SE, $N = 37$) of the scan samples were of foraging marmots, 44% (1.1 SE, $N = 37$) were of looking marmots, and 15% (1.3 SE, $N = 37$) were of marmots engaged in other behaviors.

Vigilance while foraging

There were no significant age-related differences in the number of looks, the total time looking, or the average bout length of looking between yearling (8.6 looks, 25.5 s looking, 2.9 s/look, $N = 15$), 2-year old (7.4 looks, 17.6 s looking, 2.4 s/look, $N = 5$), and adult marmots (9.9 looks, 22.6 s looking, 2.9 s/look, $N = 53$). I therefore report the combined averages for the 73 different subjects. Marmots looked an average of 8.72 times (SE = 0.50) per 2 min focal sample, and looking took up an average of 19% of a 2 min focal sample ($\bar{x} = 22.9$ s, SE = 1.78). The average bout length was 2.9 s (SE = 0.34). Marmots spent more time foraging than looking ($\bar{x} = 97.2$ s foraging/2 min focal sample, SE = 15.17, $p < 0.0001$) and bouts of foraging were longer than bouts of looking ($\bar{x} = 13.7$ s/forage bout, SE = 9.90, $p < 0.0001$).

Group size always remained after each stepwise deletion algorithm: sex, age, distance to the nearest marmot, and distance to the nearest main burrow explained no significant variation in any of the three dependent variables. Group size only explained significant variation in the total time looking

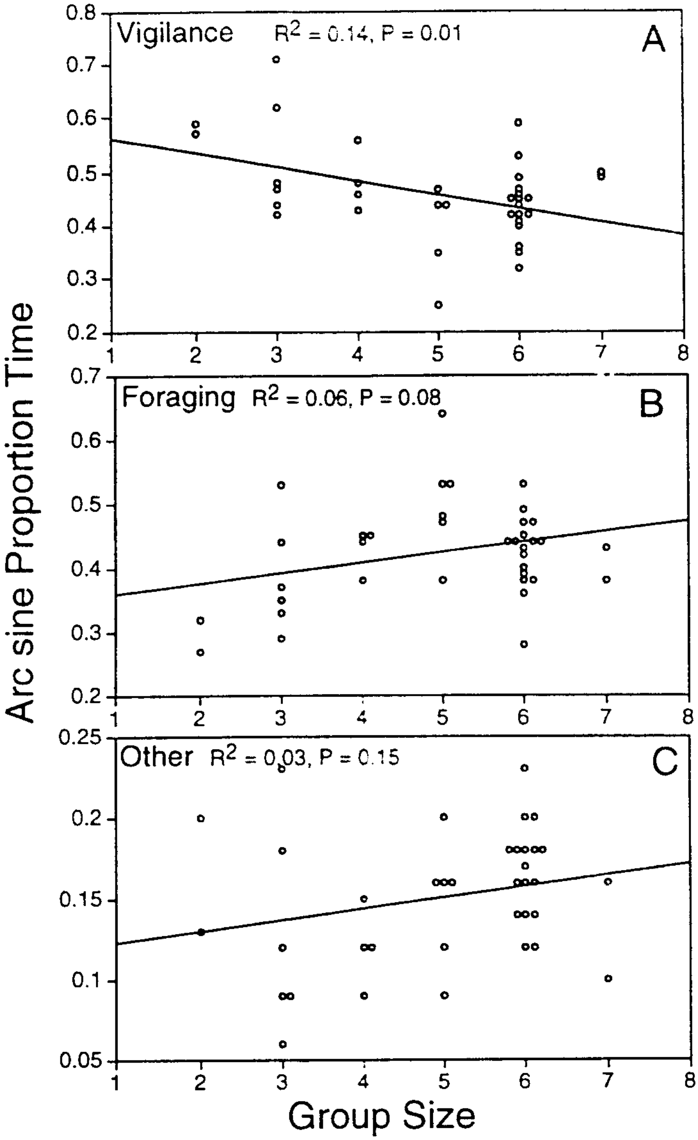

Fig. 1. The effect of group size (number of non-juveniles in a social group) on the proportion of time spent in each behavior (arc sine transformed): A, vigilance; B, foraging; and, C, a category containing all other behaviors. Variation in the time devoted to vigilance, but not other behavioral categories, was significantly explained by group size. $N = 37$ annual mean values. Values overlapping on the vertical axis are offset horizontally.

(Fig. 2a: Adjusted $R^2 = 0.055$, $p = 0.026$); since the group size coefficient was negative, marmots in larger groups looked less. A model with group size and age also explained significant variation in the total time looking (Adjusted $R^2 = 0.081$, model $p = 0.032$, group size $p = 0.006$, age $p = 0.140$). While not highly significant ($p = 0.059$), yearlings spent more time

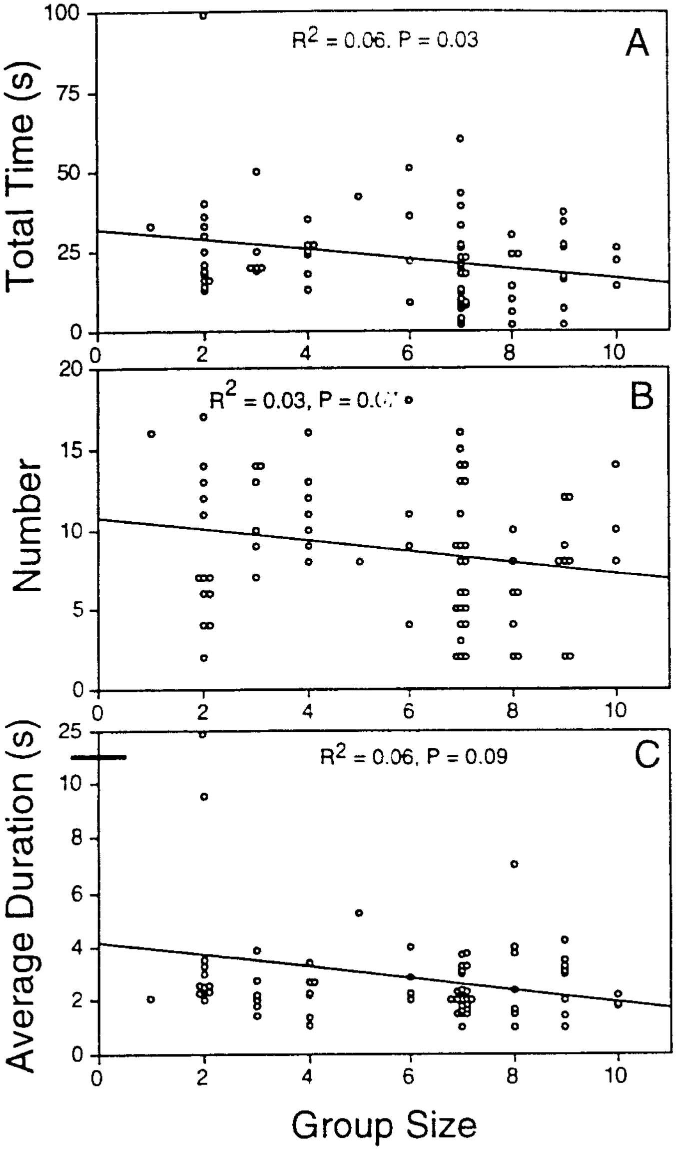

Fig. 2. The effect of group size (number of non-juveniles in a social group) on: A, the total time vigilant while foraging; B, the number of looks in a 2 min focal bout; and, C, the average duration of each look in the 2 min focal bout (note the split range of the vertical axis). Plotted results are from 1993 focal animal samples ($N = 73$ non-juvenile subjects). Values overlapping on the vertical axis are offset horizontally.

looking while foraging than adults, after controlling for variation accounted for by group size. Group size alone explained no significant variation in the number of looks (Fig. 2b: Adjusted $R^2 = 0.032$, $p = 0.072$), or the average duration of a looking bout (Fig. 2c: Adjusted $R^2 = 0.027$, $p = 0.087$).

Results varied between years. In 1992, group size significantly explained some variation in the number of looks (Adjusted $R^2 = 0.050$, $p = 0.038$), but none in the total time looking ($p = 0.368$). Group size was deleted in the second of three steps used to explain variation in average duration of a looking bout.

Inter-individual differences failed to significantly explain variation in vigilance behavior. Marmot identity did not significantly explain variation in any of the three dependent variables after accounting for variation explained by group size (all p's > 0.45, $N = 57$ observations on 13 subjects). When total group size was nested within marmot identity, models did not significantly explain variation in the vigilance variables (all p's > 0.26, $N = 57$ observations on 13 subjects).

There was a tendency for marmots to look more and spend more time looking when they foraged > 5 m from the nearest marmot (number of looks Adjusted $R^2 = 0.033$, $p = 0.070$: total time looking Adjusted $R^2 = 0.030$, $p = 0.079$). However, the average length of a looking bout was not influenced by the presence of a nearby conspecific ($p = 0.708$). Individuals had longer foraging bouts when within 5 m of another individual (Adjusted $R^2 = 0.049$, $p = 0.033$), but the presence of a close conspecific had little effect on the total time foraging (Adjusted $R^2 = 0.028$, $p = 0.084$).

Discussion

Only 14% of the variation in golden marmot's overall vigilance was explained by social group size. There was a suggestion that marmots in larger groups foraged more, but very little variation in the frequency of foraging or other combined behaviors was explained by group size. Evidence that group size reduced overall vigilance is, alone, insufficient evidence of a benefit from aggregation. Marmots in larger groups could have looked less because they were engaged in more social behaviors. In fact, unquantified observations suggest that larger groups had higher rates of both affiliative and agonistic social interactions than smaller groups.

If vigilance reduction was an important benefit from group living, marmots in larger groups should spend less time looking specifically while foraging, as has been reported in other studies of social sciurids. Other results suggest that foraging, a common behavior, exposes marmots to elevated predation risk as it is performed relatively far from refugia (Blumstein, 1994). Did marmots in larger groups spend less time looking (and therefore more time foraging) with increasing group size?

Results varied between years: group size explained about 6% of the variation in vigilance while foraging in the 1993 data set but no significant variation in the 1992 foraging data set. Moreover, unlike some New World marmots (Holmes, 1984; Barash, 1989), golden marmots did not spend more total time foraging when close to a conspecific. Bout length increased when marmots foraged very close to each other, yet this increased bout length could be a function of increased feeding competition, rather than a vigilance reduction benefit from aggregation.

There was limited evidence that vigilance behavior was influenced by other measured variables, and/or that the relationship between group size and vigilance would be 'revealed' after controlling for other variables. Marmot identity, sex, the distance to the nearest marmot, and the distance to the nearest main burrow (*contra* Holmes, 1984; Barash, 1989) explained no significant variation in vigilance behavior. After controlling for variation explained by group size, there was a tendency for younger animals to look more. Armitage & Corona (1994) found the opposite: yearlings spent the least amount of time vigilant.

Why is relatively little variation in golden marmot vigilance explained by social group size? Part of the answer may lie in how I defined group size and consequently where I looked for vigilance reduction benefits from aggregation. I focused on social group size while most, but not all (*e.g.* Hoogland, 1979; Rasa, 1989; Colagross & Cockburn, 1993; Isbell & Young, 1993; Kildaw, 1995; Rose & Fedigan, 1995), previous studies focused on foraging group size. Considerable variation in vigilance was explained by foraging group size in several species (*e.g.* Pulliam *et al.*, 1982; Burger & Gochfeld, 1992; Quenette & Gerard, 1992; Yaber & Herrera, 1994; Bekoff, 1995; Lima, 1995). However, there are exceptions to this generalization: Carey & Moore (1986), found that foraging group size explained only 11% of the variation in vigilance in yellow-bellied marmots, and Lipetz & Bekoff (1982) found that foraging group size only explained 16.2% of the variation in vigilance in foraging pronghorn.

Can social group formation provide a vigilance-reduction benefit, and if so, as large a vigilance-reduction benefit as that typically seen in foraging aggregations? The magnitude of the vigilance reduction benefit may depend on how spatially dispersed individuals are. Thus, the relative size of a social group's home range and the relative openness of the habitat may be important determinants of the magnitude of vigilance reduction benefits from forming social groups. For instance, black-tailed prairie dog (*Cynomys ludovicianus*) home ranges average 0.3 ha, animals spend much of the day above ground, and group members are often within eyesight of each other (Hoogland, 1995). In contrast, golden marmot's home ranges were approximately 10 times larger (*ca* 3 ha), marmots tended to forage > 15 m from each other, and most marmots at Dhee Sar lived in very heterogeneous terrain characterized by a plethora of boulders, gullies, cliffs, and rolling glacial moraines. Consequently, marmots were routinely out of eye contact. Prairie dogs, unlike golden marmots, lived in aggregations where individual's could presumably share vigilance responsibilities. Ultimately this suggests that the term 'group' may more aptly describe those individuals in visual contact with each other and/or arranged in certain geometric arrays (Elgar *et al.*, 1984; Lima, 1990; Bekoff, 1995). While Isbell & Young (1993) found a significant increase in vigilance as social group size decreased, their regression coefficient suggests that relatively little variation was explained by social group size. Vervet monkeys move as a social group throughout their home range, and sleep and rest in different locations (Estes, 1991). Because they live and move along the forest edge, individuals may not always be in eye contact. In general, substantial vigilance reduction benefits from grouping may only occur when animals are in visual contact with each other. Perhaps we should not expect group size to explain considerable variation in vigilance when groups ae dispersed and individuals cannot see each other.

However, my results do not simply suggest that group-size has no effect, they also suggest that other variables routinely reported to influence vigilance had a limited or non-existent effect. What unmeasured variables may influence marmot vigilance? The time since the last alarm call may have a profound influence on overall vigilance behavior in sciurid rodents (*e.g.* Carey & Moore, 1986; Loughry & McDonough, 1988; MacHutchon & Harestad, 1990; pers. obs.). Alarm calls clearly influence marmot behavior and presumably influence whether a given subject forages or not. If a nearby marmot alarm called, a focal foraging marmot almost invariably sprinted to a nearby burrow and looked around. I excluded these observations from the 'foraging' data set because subjects were not strictly foraging anymore and one of my goals was to study vigilance-reduction benefits specifically while foraging.

There is a fundamental and generally implicit assumption that vigilance is primarily visual. Yet many species assess predation risk using other modalities, such as hearing. For these species, individuals may be vigilant while foraging (but see Pöysä, 1987). In fact, foraging golden marmots responded to played-back alarm calls as quickly as did standing-and-looking marmots, suggesting that foraging and antipredatory vigilance are not mutually exclusive (Blumstein, 1994). If vigilance uses multiple sensory modalities, then defining vigilance by the time spent with the head elevated might bias conclusions. For instance visual vigilance may function to update information on conspecific distribution, while auditory vigilance might provide information about predation risk. Alarm calls of both golden and yellow-bellied marmots acoustically encoded degree of predation risk (Waring, 1966; Blumstein, 1995a, c; Blumstein & Armitage, in press). Moreover, golden marmots at Dhee Sar could hear the alarm calls of many other individuals, including those marmots in neighboring social groups. By acquiring potential information from relatively distant conspecifics, golden marmots may have been less sensitive than yellow-bellied marmots (*e.g.* Carey & Moore, 1986) to the effects of close conspecifics.

Species differ in the amount of time they devote to foraging. While selection should act to minimize predation risk whenever possible, species that spend more time foraging should gain more from group size effects than species who spend less time foraging. The former should gain both by reducing predation risk while foraging and by increasing foraging time. The latter might simply decrease predation risk while foraging. Black-tailed prairie dogs spent 62-74% of their above-ground time foraging (Loughry, 1993) and would thus be predicted to benefit more from vigilance-reduction. In contrast, yellow-bellied marmots spent 12-23% of their above ground time foraging (Armitage *et al.*, 1996), and golden marmots spent 41% of their time foraging. Future comparative work based on reports of the amount of explained variation will be required to more rigorously test the prediction that the magnitude of vigilance reduction benefits are associated with the proportion of time spent foraging.

In conclusion, only a small amount of variation in golden marmot vigilance was explained by social group size. That relatively little variation was explained by additional factors routinely reported to be important determinants of vigilance behavior in other species, suggests that unmeasured factors might be important determinants of golden marmot vigilance. Weak group size effects may have been expected because golden marmots used other modalities to detect predators and because marmots appeared not to be limited by their daily amount of time spent foraging. If future studies of vigilance behavior report variation explained by different factors including group size, we will be in a better position to understand the relative importance of group size effects in the formation of both short-term foraging aggregations and longer-term social groups.

References

Abacus Concepts (1991). SuperAnova. — Abacus Concepts, Inc., Berkeley.

— — (1993). StatView 4.01. — Abacus Concepts, Inc., Berkeley.

Armitage, K.B. (1962). Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). — Anim. Behav. 10, p. 319-331.

— — & Corona, M.C. (1994). Time and wariness in yellow-bellied marmots. — Ibex Jour. Mt. Environ. 2, p. 1-8.

— —, Salsbury, C.M., Barthelmess, E.L., Gray, R.C. & Kovach, A. (1996). Population time budget for the yellow-bellied marmot. — Ethol. Ecol. Evol. 8, p. 67-95.

Arnold, W. (1990). The evolution of marmot sociality: I. Why disperse late? — Behav. Ecol. Sociobiol. 27, p. 229-237.

Barash, D.P. (1973). The social biology of the Olympic marmot. — Anim. Behav. Mongr. 6, p. 173-245.

— — (1989). Marmots: social behavior and ecology. — Stanford University Press, Stanford.

Bekoff, M. (1995). Vigilance, flock size, and flock geometry: information gathering by western evening grosbeaks (Aves, Fringillidae). — Ethology 99, p. 150-161.

Bertram, B.C.R. (1980). Vigilance and group size in ostriches. — Anim. Behav. 28, p. 278-286.

Blumstein, D.T. (1994). Predation hazard assessment and management in golden marmots (*Marmota caudata aurea*). — PhD dissertation, University of California, Davis.

— — (1995a). Golden-marmot alarm calls. I. The production of situationally specific vocalizations. — Ethology 100, p. 113-125.

— — (1995b). An ecotourist's guide to Khunjerab National Park. — World Wide Fund for Nature-Pakistan, Lahore.

— — (1995c). Golden-marmot alarm calls. II. Asymmetrical production and perception of situationally specific vocalizations? — Ethology 101, p. 25-32.

— — & Armitage, K.B. (in press). Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. — Anim. Behav.

— — & Robertson, M. (1995). Summer diets of Tibetan red foxes in Khunjerab National Park, Pakistan. — Z. Saug. 60, p. 243-245.

Burger, J. & Gochfeld, M. (1992). Effect of group size on vigilance while drinking in the coati, *Nasua narica* in Costa Rica. — Anim. Behav. 44, p. 1053-1057.

Carey, H.V. & Moore, P. (1986). Foraging and predation risk in yellow-bellied marmots. — Amer. Midl. Nat. 116, p. 267-275.

Catterall, C.P., Elgar, M.A. & Kikkawa, J. (1992). Vigilance does not covary with group size in an island population of silvereyes (*Zosterops lateralis*). — Behav. Ecol. 3, p. 207-210.

Cohen, J. & Cohen, P. (1993). Applied multiple regression/correlation analysis for the behavioral sciences, 2nd edn. — Lawrence Erlbaum Associates, Inc., Hillsdale, New Jersey.

Colagross, A.M.L. & Cockburn, A. (1993). Vigilance and grouping in the eastern grey kangaroo, *Macropus giganteus*. — Aust. J. Zool. 41, p. 325-334.

Elgar, M.A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. — Biol. Rev. 64, p. 13-33.

— —, Burren, P.J. & Posen, M. (1984). Vigilance and perception of flock size in foraging house sparrows (*Passer domesticus* L.). — Behaviour 90, p. 215-223.

Estes, R.D. (1991). The behavior guide to African mammals: including hoofed mammals, carnivores, primates. — University of California Press, Berkeley.

Gibault, C., Ramousse, R. & Le Berre, M. (1994). Hiking impact on feeding behavior in alpine marmot. — In: Abstracts, second international conference on marmots, Aussois (France) (M. Le Berre, ed.). — Université Claude Bernard, Lyon, p. 76-77.

Holmes, W.G. (1984). Predation risk and foraging behavior of the hoary marmot in Alaska. — Behav. Ecol. Sociobiol. 15, p. 293-301.

Hoogland, J.L. (1979). The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). — Anim. Behav. 27, p. 394-407.

— — (1995). The black-tailed prairie dog: social life of a burrowing mammal. — University of Chicago Press, Chicago.

Isbell, L.A. & Young, T.P. (1993). Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. — Behav. Ecol. Sociobiol. 32, 377-385.

Kildaw, S.D. (1995). The effect of group size manipulations on the foraging behavior of black-tailed prairie dogs. — Behav. Ecol. 6, p. 353-358.

Leger, D.W. & Didrichsons, I.A. (1994). An assessment of data pooling and some alternatives. — Anim. Behav. 48, p. 823-832.

Lima, S.L. (1990). The influence of models on the interpretation of vigilance. — In: Interpretation and explanation in the study of animal behavior. Vol. II. Explanation, evolution, and adaptation (M. Bekoff & D. Jamieson, eds). — Westview Press, Boulder, p. 246-267.

— — (1995). Back to the basics of anti-predatory vigilance: the group-size effect. — Anim. Behav. 49, p. 11-20.

— — & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. — Can. J. Zool. 68, p. 619-640.

Lipetz, V.E. & Bekoff, M. (1982). Group size and vigilance in pronghorns. — Z. Tierpsychol. 58, p. 203-216.

Loughry, W.J. (1993). Determinants of time allocation by adult and yearling black-tailed prairie dogs. — Behaviour 124, p. 23-43.

— — & McDonough, C.M. (1988). Calling and vigilance in California ground squirrels: a test of the tonic communication hypothesis. — Anim. Behav. 36, p. 1533-1540.

Machlis, L., Dodd, P.W., Fentress, J.C. (1985). The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. — Z. Tierpsychol. 68, p. 201-214.

MacHutchon, A.G. & Harestad, A.S. (1990). Vigilance behaviour and use of rocks by Columbian ground squirrels. — Can. J. Zool. 68, p. 1428-1432.

Massemin, S., Ramousse, R. & Le Berre, M. (1993). Comportement de vigilance chez la marmotte alpine (*Marmota marmota*). — Bull. Soc. Zool. France 118, p. 195-201.

Monaghan, P. & Metcalfe, N.B. (1985). Group foraging in wild brown hares: effects of resource distribution and social status. — Anim. Behav. 33, p. 993-999.

Pöysä, H. (1987). Feeding-vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. — Behaviour 103, p. 108-122.

— — (1994). Group foraging, distance to cover and vigilance in the teal, *Anas crecca*. — Anim. Behav. 48, p. 921-928.

Pulliam, H.R., Pyke, G.H. & Caraco, T. (1982). The scanning behavior of juncos: a game-theoretical approach. — J. theor. Biol. 95, p. 89-103.

Quenette, P.-Y. (1990). Functions of vigilance behaviour in mammals: a review. — Acta Oecol. 11, p. 801-818.

— — & Gerard, J.-F. (1992). From individual to collective vigilance in wild boar (*Sus scrofa*). — Can. J. Zool. 70, p. 1632-1635.

Rasa, O.A.E. (1989). The costs and effectiveness of vigilance behaviour in the dwarf mongoose: implications for fitness and optimal group size. — Ethol. Ecol. Evol. 1, p. 265-282.

Roberts, S.C. (1988). Social influences on vigilance in rabbits. — Anim. Behav. 36, p. 905-913.

Roberts, T.J. (1977). The mammals of Pakistan. — Ernest Benn Ltd., London.

Rose, L.M. & Fedigan, L.M. (1995). Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. — Anim. Behav. 49, p. 63-70.

Svendsen, G.E. (1974). Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. — Ecology 55, p. 760-771.

— — & Armitage, K.B. (1973). Mirror-image stimulation applied to field behavioral studies. — Ecology 54, p. 623-627.

Tabachnick, B.G. & Fidell, L.S. (1996). Using multivariate statistics, 3rd edn. — Harper-Collins College Publishers, New York.

Travis, S.E. & Armitage, K.B. (1972). Some quantitative aspects of the behavior of marmots. — Trans. Kansas Acad. Sci. 75, p. 308-321.

Thompson, D.B. & Lendrem, D.W. (1985). Gulls and plovers: host vigilance, kleptoparasite success and a model of kleptoparasite detection. — Anim. Behav. 33, p. 1318-1324.

Waring, G.H. (1966). Sounds and communications of the yellow-bellied marmot (*Marmota flaviventris*). — Anim. Behav. 14, p. 177-183.

Wilson, D.S., Clark, A.B., Coleman, C. & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. — Trends Ecol. Evol. 9, p. 442-446.

Wilson, E.O. (1975). Sociobiology: the new synthesis. — Harvard University Press, Cambridge, Mass.

Yaber, M.C. & Herrera, E.A. (1994). Vigilance, group size and social status in capybaras. — Anim. Behav. 48, p. 1301-1307.