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Alarm calling in yellow-bellied marmots: II. The importance of direct fitness

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Abstract. Alarm calling in sciurid rodents is often explained by inclusive fitness benefits that callers accrue. Inclusive fitness arguments imply that indirect fitness plays an important role in the evolution and maintenance of alarm calling. A more parsimonious hypothesis is that animals alarm call to increase their direct fitness by warning their offspring. Group-living animals are related to each other social group member by a coefficient of relatedness, *r*, that theoretically ranges from 0–1.0. The sum of these pair-wise coefficients, 'total *r*', reflects the magnitude of possible inclusive fitness benefits. The amount of variation in the rate of yellow-bellied marmot, *Marmota flaviventris*, alarm calling that was explained by direct parental care was compared with that variation explained by total *r*. After pups emerged, adult females with pups called more than other age/sex classes. Additionally, 42% of the variation in the rate of calling over the entire study was a function of whether the caller was a female who had pups emerge above ground that year. Total *r* explained no significant variation in the rate of alarm calling. Alarm calling in group-living yellow-bellied marmots is a form of direct parental care and inclusive fitness, broadly defined, is of little importance for the maintenance of alarm calling.

When alarmed by predators, many species produce specific vocalizations referred to as alarm calls (Klump & Shalter 1984). Alarm calling may increase the caller's probability of predation (Sherman 1977, 1985), and the question of why many social animals produce apparently altruistic alarm calls to warn group mates has puzzled biologists for some time (e.g. Maynard Smith 1965; Charnov & Krebs 1975; Smith 1986; Hoogland 1995). Several authors invoked kin selection (Hamilton 1964) as a mechanism to explain some or all of the alarm calling in sciurid rodents (e.g. Dunford 1977; Sherman 1977; Davis 1984; MacWhirter 1992; Hoogland 1983, 1995). Kin selection includes that fitness that individuals gain by helping their descendent kin (direct fitness) and non-descendent kin (indirect fitness) (Brown 1987). By invoking kin selection, sensu

lato, without distinguishing the direct and indirect components, researchers imply that indirect fitness benefits are an important driving force behind apparently altruistic behaviours such as alarm calling (but see Dunford 1977, page 784, who noted that although kin selection was important for the evolution of alarm calling, alarm calling was not an 'altruistic' behaviour because it was not risky). A more parsimonious explanation (Williams 1966) is that callers primarily produce alarm calls to warn their descendent kin, particularly vulnerable offspring who have much to gain from being warned (Maynard Smith 1965; Shields 1980). Most researchers would not consider such parental care, or more generally, behaviour patterns that increase direct fitness, to be 'altruistic', because altruism implies that non-descendants must benefit (Bertram 1982). In support of alarm calling as a way to maximize direct fitness, females of several species call relatively more within a single year, when recently emerged and presumably vulnerable offspring are present (McCarley 1966; Smith 1978; Schwagmeyer 1980; Shields 1980), and/or call more in years when emergent

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young are present than in years when there are no young (Barash 1989; Hoogland 1995).

Kin selection was invoked to explain alarm-calling behaviour when adult kin, because of their relative density and spatial distribution, were likely to hear alarm calls (Schwagmeyer 1980). Most studies of the function of anti-predator calling, however, used contingency table analyses to identify the opportunity for kin selection. These analyses frequently did not distinguish between direct, indirect and/or inclusive fitness, so we are left questioning the relative importance of indirect fitness for the maintenance of alarm calling. For instance, kin selection, or the potential for kin selection, was inferred if certain classes of callers (e.g. females with kin) called more than would be expected by their frequency in the population, and other classes of callers (e.g. males without kin) called less than expected (Dunford 1977; Table 2 in Sherman 1977 made additional specific comparisons that distinguished between direct and inclusive fitness).

Each individual living in a social group has a coefficient of relatedness, r, between themselves and each other individual that theoretically ranges between 0 and 1.0. For each individual, the sum of these pair-wise coefficients equals an individual's total coefficient of relatedness, 'total r'. If inclusive fitness, which includes both direct and indirect components, is important for the maintenance of alarm calling, individuals living in groups where there is a greater total r should call more than individuals living in groups where there is a smaller total r. Specifically, there should be a positive relationship between the frequency or rate of alarm calling and total r. If direct fitness, specifically parental care, is important for the maintenance of alarm calling, individuals with offspring should call more than individuals without offspring. If there is no effect of inclusive fitness, but there is an effect of direct fitness, then we infer that indirect fitness is relatively unimportant for the maintenance of alarm calling.

We report the results of a study of alarm calling in yellow-bellied marmots where we studied the relative importance of both direct and inclusive fitness for the maintenance of alarm-calling behaviour. With individually identified marmots and known genealogies, we compared the relative amount of variation in the rate of alarm calling explained by the presence of an individual's pups in the social group (a metric of direct fitness), the

number of non-pup offspring (a metric of direct fitness) and by the total r (a metric of inclusive fitness). We examined the broader pattern of alarm-calling behaviour by discussing the costliness of alarm calling and by discussing whether conspecifics and/or predators were the primary target of alarm calls.

METHODS

Study Sites and Subjects

Yellow-bellied marmots have been continuously studied in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, U.S.A. since 1962 (Armitage 1991). For this study, marmots were classified as pups, yearlings and adults. Marmots live in social groups consisting of a breeding female and her descendent and/or collateral kin who share extensively overlapping home ranges. Adult males immigrate into an area with one or several social groups. There they may become associated with one or more of these groups; some infrequently seen adult males are not associated with social groups (Armitage & Johns 1982). Yellow-bellied marmot habitat patches are described as 'colonial' or 'satellite' (Armitage 1991). Colonies have one or more social groups, and satellite patches have a single social group. Years of observations have suggested that alarm calling is relatively uncommon, and that to properly study its function, observers should experimentally increase the frequency of alarm calling and specifically focus on identifying calling individuals.

In 1995, to study the function of alarm calling rigorously, we focused on marmots in six social groups (10 adult females, 4 adult females with pups that emerged during the study, 5 adult males, 6 yearling females, 5 yearling males; Table I; see also Blumstein & Armitage 1997). All marmots at RMBL were individually marked and were from known genealogies. Three of the social groups had pups that emerged above-ground during our 1995 study (Calder, Mammal Lab, and Marmot Alley); these pups were from four litters. One female (at River Spruce Mound) had pups emerge above-ground on 7 August, 1 week after we terminated data collection (we estimated that these young were born about 15 July and treated her as an adult female without pups). No pups emerged above-ground in the other groups, but

Table I. Group membership, the average coefficient of relationship of group members, group reproductive success, observed alarm calls (naturally and experimentally elicited) from group residents (adult males excluded), and the total time watched for the six different marmot social groups

	Calder	Marmot alley	Mammal lab	River mound	River south	River spruce
N adult female	3	2	1	3	3	2
N yearling female	0	2	2	0	0	2
N yearling males	0	2	3	0	0	0
N adult males*	1	3	1	1	2	2
Group average *r*†	0.5	0.5	0.44	0.21	0.5	0.33
Pups emerged	13 July	30 June	1 July	No pups	No pups	No pups
N calls<‡	6	14	10	9	13	3
N calls>‡	32	22	22	2	2	0
Hours watched	87.48	74.62	73.35	89.90	80.95	80.95

*Different males observed to frequent a marmot social group. Some males' home ranges overlapped multiple groups; thus numbers sum to over 5.

†The sum of the coefficients of relationship between all pairs of a group's members (i.e. adult males excluded) divided by the number of relationships. Included here for descriptive purposes only.

‡Total number of identified calls by adult females (includes those with and those without emergent young), yearling females and yearling males before (<) or after (>) pup emergence or 1 July 1995 if no pups in the group. This total includes naturally and experimentally elicited alarm calls.

one female at River South lost her litter part way through the summer (she lactated but no litter emerged above-ground).

To test the robustness of some of our conclusions from the one-summer study, we compared the results with alarm-calling data collected in 1980, 1985 and 1991 on 60 marmots (9 adult females, 20 adult females with pups that emerged during that summer's data collection period, 6 resident adult males, 14 yearling females, 12 yearling males). One individual appeared twice, once as an adult female and once as an adult female with pups; for these analyses we assumed independence between these two observations and treated her as two individuals). These marmots lived in social groups in four different colonies (Picnic: 1980, 1985, 1991; Marmot Meadow: 1980, 1985, 1991; River: 1985, 1991; North Picnic: 1980). In all groups where pups emerged, observations included time before and after pups emerged.

Observational Methods

Marmots utter single-note whistles that may be repeated multiple times when alarmed (Waring 1966; Blumstein & Armitage 1997). We defined each whistle as an 'alarm whistle'; a 'bout' of alarm calls contained at least one alarm whistle (Blumstein & Armitage 1997). Different

individuals in the same social group sometimes called in response to an alarming stimulus; we refer to these events as a 'chorus' of calls. In this study, we used the bout as the unit of analysis, and we counted and recorded the number of bouts regardless of the number of whistles in each bout and regardless of whether the bout was part of a chorus. A previous study of the function of alarm calls reached similar conclusions, regardless of whether call precedence in a chorus was considered (Figure 3 in Sherman 1977), and other studies did not distinguish between first and subsequent callers (e.g. Dunford 1977; Schwagmeyer 1980; Davis 1984).

Most yellow-bellied marmot alarm calls are associated with potentially threatening stimuli, although we could not always identify the stimulus that elicited the call. Calls produced in social situations ('social calls') were rare and accounted for less than 3% of calls (Blumstein & Armitage 1997). In this study, our analyses included all calls from identified callers regardless of whether we could identify the stimulus that elicited the call.

When alarm calling, a marmot moves its mouth and its body visibly shakes; thus it is often possible to identify callers (cf. Hoogland 1995). To increase the frequency with which alarm calls were detected and callers identified, the 1995 observations reported here focused exclusively on

alarm-calling behaviour. Alarm calls from pups were generally easily distinguished from older animals by their higher pitch. All analyses focused on alarm calls from older animals.

Other species of marmots produced calls that could be predictably heard by neighbouring social groups (e.g. Blumstein 1995; Blumstein & Arnold 1995), and some ground squirrel species (*Spermophilus* spp.) live in dense aggregations where neighbours can hear alarm calls (e.g. Dunford 1977; Sherman 1977; Schwagmeyer 1980). Yellow-bellied marmots live in habitats where alarm calls are considerably attenuated, degraded, and have to compete with substantial background noise (Blumstein & Daniel, in press). Yellow-bellied marmots lived in much patchier habitats and at lower densities than some other marmots; thus, individuals outside a social group could not predictably hear alarm calls produced in a neighbouring social group. At times, however, we saw marmots in one social group respond to a faint whistle from an adjacent social group or from a social group in an adjacent colony. Nevertheless, and in contrast to some other highly colonial sciurids found in fairly open habitat patches, yellow-bellied marmots could not predictably produce alarm calls that could be heard outside their social group. Thus, when we quantify potential inclusive fitness benefits from calling, we use the social group as the unit of analysis.

In 1995, we conducted focal group observations and noted each alarm-call bout and all predator visits. Observations were made throughout the day from 7 June to 30 July: 76% of our observations were made during the morning active period (0600–1100 hours). For the three groups studied at RMBL in 1995 that had pups emerge above-ground, we made half of our observations before pups emerged and half after pups emerged. For the three groups without pups, we made half of our observations before 1 July and half after 1 July, an arbitrary date approximating the midpoint of the study. When there was an alarm call, when possible, we noted the identity of the caller, the eliciting stimulus, the distance of the caller to the stimulus, the distance of the caller to the nearest refuge (yellow-bellied marmots exclusively use burrows as refugia) and the response of other marmots.

Because alarm calling was uncommon, we increased the frequency with which marmots alarm called by simulating predator attacks in four ways (Blumstein & Armitage 1997). Our overriding concern was for the welfare of the marmots. Thus, we minimized the total number of manipulations and the duration of each manipulation (generally less than 5–10 min including the time walking through meadows to pick up models), and we limited the number of manipulations after pups emerged above-ground (or after 1 July). We detected no adverse effects from any of our manipulations and discuss the 'naturalness' of these experiments in more detail elsewhere (Blumstein & Armitage 1997).

Our first manipulation involved walking towards marmots at a constant rate (ca 1 m/s) and noting those subjects that called; we refer to these experiments as 'predation probes'. We did this 126 times (80 times before pups emerged, 46 after pups emerged). Each group was 'probed' an average ± SD of 21 ± 11 times (range=4–33 times), and each subject was probed an average of 5.7 ± 4.3 times (range=0–21 times). We elicited 41 alarm-call bouts by walking towards marmots (1.5 ± 1.5 bouts per marmot; range=0–7 bouts).

For the second manipulation, we used a stuffed badger mounted on a radiocontrolled chassis to simulate a terrestrial predator. We drove 'RoboBadger' towards marmots (≤ 1 m/s) and noted those subjects that called. We used the model badger on 8 days and conducted 14 experiments in five social groups. Heterogeneous terrain and the lack of a suitable trail or road prevented us from driving the model through the sixth social group. Each of these groups was exposed to the badger an average of 2.8 ± 1.9 (range=1–6 times). Ten subjects were exposed, each an average of 1.3 ± 0.6 times (range=1–3 times). We elicited nine alarm-call bouts by driving the model towards marmots (0.6 ± 0.5 bouts per marmot; range=0–1 bout).

For the third manipulation, we walked dogs through two of the social groups' home ranges to elicit alarm calls and noted those animals who called. We walked one of three dogs through three of the home ranges on 7 days. The other three home ranges were located on the RMBL property, where dogs were prohibited. Seven subjects were exposed an average of 2.1 ± 1.9 times (range=1–6 times). We elicited 12 bouts of alarm calls by walking dogs towards marmots (1.7 ± 1.9 bouts per marmot; range=0–5 bouts).

For the fourth manipulation, we used a radio-controlled model glider painted brown with a 2-m

wingspan to simulate an eagle attack and noted those animals that called (see also Noyes & Holmes 1979). Four of the social groups provided suitable habitat for glider flights. We launched the glider from a hill above target marmots and made one pass over or beside target marmots. We conducted 12 flights on 5 different days; each of the social groups was exposed an average of 3 ± 1.4 times (range=2–5). Ten subjects were exposed to the model plane an average of 1.9 ± 1.2 times (range=1–4). We elicited six bouts of alarm calls by flying the model over marmots (0.6 ± 0.5 bouts per marmot; range=0–1).

We selected observational data from 1980, 1985 and 1991, because in these years (1) bouts of alarm calling were noted and (2) it was unlikely that animals alive in one year would be alive in another year (one individual appeared twice in this data set). Marmots in 13 different social group-years (a social group that we observed during the summer period marmots were active and not hibernating) were watched for 423.5 h before pups emerged (or <1 July if no pups) and 302.5 h after pups emerged (or ≥1 July if no pups). For each individual, we tabulated the number of bouts of alarm calls heard before and after pups emerged. During this time, only 99 bouts of alarm calls could be attributed to known individuals.

Marmots were routinely live-trapped, marked and re-marked throughout the study and during the long-term studies at RMBL. When live-trapped and handled, yellow-bellied marmots occasionally alarm called. These calls were not obviously distinguishable from alarm calls elicited by free-ranging marmots (cf. Sherman 1977). Throughout the 1995 research season, we noted whether marmots trapped in and around RMBL alarm called or not while being trapped and handled.

Analyses

All analyses treat the individual as the unit of analysis. For these analyses, we assumed no dependence between individuals within a social group. Specifically, we assumed that each individual makes independent decisions whether to alarm call or not. We believe that this assumption is reasonable, because not all predator encounters elicit alarm calls, and from one to all social group members may alarm-call when predators are present.

Do Different Age–Sex Classes Alarm Call at Different Rates?

We calculated the rate of alarm calling (N calls/total time watching the social group) for the historical RMBL data (no experimentally elicited calls) and for data collected in 1995 (includes both natural and experimentally elicited calls). Some of the adult males present throughout the study moved between social groups and/or 'defended' multiple social groups. For those that moved, we calculated alarm-call rates based on the time watching for one of the social groups in which they commonly appeared (otherwise a male could be counted more than once). In 1995, we excluded two adult males from further analysis because they immigrated into the study site after our observations began and moved between different social groups, never settling in one. We tested for significant differences between mean alarm-calling rates of the different age–sex classes using a Kruskal–Wallis non-parametric one-way ANOVA. All descriptive and non-parametric tests were calculated using StatView (Abacus Concepts 1993).

What Explains Variation in Calling Rate?

For the six groups studied in 1995, and from known genealogies, we calculated the coefficient of relatedness, r, for each subject with all other social group members. The only assumption we made to calculate r was that previously unmarked adult males who immigrated into a group and bred were unrelated to group residents. Long-term observations and the long-term trapping and marking programme around RMBL suggest this is a reasonable assumption. For each individual, we summed the set of pair-wise rs with other group members (i.e. we excluded adult males) to calculate the total r. As calculated, total r reflects the potential inclusive fitness benefits from alarm calling.

We used linear models (regression, ANOVA and ANCOVA) to study factors that explained variation (adjusted R^2) in the rate of alarm calling. Linear models were fitted in SuperAnova (Abacus Concepts 1991). To meet distributional assumptions of linear models, we square-root transformed call rate.

The first set of analyses focused specifically on group-living marmots: adult females, adult females who had pups emerge during the study, yearling females and yearling males. As previously stated, adult males moved between groups and/or were not predictably associated with a single group thus we excluded them from these analyses. With a one-way ANOVA, we examined whether having one's own emergent pups at any time during the study influenced call rate. We used bivariate linear regressions to study factors that influenced call rate for all group-living marmots. Specifically, we examined the effects of (1) the number of non-pup offspring present on call rate and (2) the effect of total r on call rate.

The second set of analyses excluded females who had pups emerge at any time during our study and used another series of bivariate regressions and a one-way ANOVA to study factors that influenced call rate for group-living marmots. Here we studied the effect of (1) the number of non-pup offspring in the social group on call rate, (2) the number of other group members in the social group (i.e. adult males excluded) on call rate, (3) the number of litter-mate siblings in the social group on call rate, (4) the total r on call rate and (5) the presence or absence of pups in the group on call rate.

Is Alarm Calling Risky?

To estimate the magnitude of an action's benefits, one can estimate the magnitude of costs. Specifically, if alarm calling is a relatively risky behaviour, and assuming that alarm calling has some adaptive function, there must be substantial benefits from calling. Preliminary observations suggested that yellow-bellied marmots typically returned to their burrows before vocalizing and that callers may not expose themselves to considerable risk (see also Barash 1975). To evaluate these observations better, we noted the distance that callers were from the burrow when they called.

Who is the Target of Alarm Calls?

To study the target of alarm calls, we used results from the human predation probe experiments and compared the relative frequency of those marmots that called when other group members were in sight of a caller (N alarm calls/N predation probes when others were in sight) to the relative frequency of those that called when no marmots were in sight (N alarm calls/N predation probes when others were not in sight). Sometimes the focal marmot was the only individual above ground; thus, determining whether others were in sight or not was easy. On other occasions, we knew that other group members were in distant and visually-obstructed parts of the home range, and we scored the focal marmot as being alone. If other group members were above-ground and potentially in sight based on our estimation of what the focal marmot could see, we scored other individuals as present. When others were above-ground, and when in doubt, we scored others as present. We used a paired non-parametric Wilcoxon signed-rank test to compare the relative frequency of calling when alone versus calling when others were present.

We also noted those marmots that alarm called when live trapped and routinely handled. We include all marmots trapped around RMBL in 1995. We used the single response, or for animals trapped multiple times, the modal response, to summarize the frequency of alarm calling when trapped as a function of age/sex class.

RESULTS

Between 7 June and 30 July 1995 we observed the six marmot social groups for 415 h (Table I). Because two of the social groups could be observed simultaneously, groups were observed a total of 487 h ($\bar{X} \pm \text{SD} = 82.7 \pm 9.4$ h; $N = 6$ groups), 235 h before and 252 h after pups emerged (or after 1 July for those groups without pups). Although predation is a documented source of mortality for RMBL marmots (Andersen & Johns 1977; Armitage 1982a; Van Vuren & Armitage 1994; Blumstein & Armitage 1997), we observed no predation and saw only a few potential predators of adult marmots. Marmots alarm-called to a variety of threatening and apparently non-threatening stimuli (Blumstein & Armitage 1997). During these observations, we identified individuals who alarm called 148 times: 68 of these calls were in direct response to our manipulations. Our analyses focus on the overall rate of alarm calling.

Table II. Alarm-calling rates (bouts of alarm calls/h ± SD) before pups emerged above ground (rate<), after pups emerged above ground (rate>), and the overall seasonal average (total rate during the two periods over which marmot alarm calling was quantified: 1995 summer only, and the composite of 1980, 1985 and 1991)

	Adult female (mother)	Adult female	Adult males*	Yearling females	Yearling males
1995	$N=4$†	$N=10$	$N=3$	$N=6$	$N=5$
Rate<	0.05 (± 0.04)	0.08 (± 0.05)	0.06 (± 0.05)	0.03 (± 0.02)	0.05 (± 0.02)
Rate>	0.31 (± 0.12)	0.04 (± 0.08)	0.01 (± 0.01)	0.00 (± 0.00)	0.07 (± 0.06)
Rate (total)	0.18 (± 0.07)	0.06 (± 0.06)	0.03 (± 0.02)	0.01 (± 0.01)	0.06 (± 0.03)
1980, 1985, 1991	$N=20$	$N=9$	$N=6$	$N=14$	$N=12$
Rate<	0.02 (± 0.05)	0.04 (± 0.03)	0.05 (± 0.07)	0.02 (± 0.04)	0.01 (± 0.02)
Rate>	0.08 (± 0.10)	0.003 (± 0.01)	0.02 (± 0.03)	0.04 (± 0.11)	0.02 (± 0.04)
Rate (total)	0.05 (± 0.08)	0.01 (± 0.02)	0.03 (± 0.04)	0.02 (± 0.03)	0.01 (± 0.02)

*Because adult males often are associated with more than one social group, other analyses treat adult males as non-group members. These are calculated based on the total number of alarm calls each male produced divided by the time spent watching the social group in which he was generally associated.
†Sample sizes refer to the number of individuals in each age–sex group.

Do Different Age–Sex Classes Alarm-call at Different Rates?

Adult females with pups that emerged during the study tended to alarm call at higher rates than other age–sex classes. We analysed overall calling rate data on three time scales: before pups emerged, after pups emerged and over the entire season (Table II). Before pups emerged, there were no significant differences in calling rates between marmots in different age–sex classes (Table II; RMBL (1980–1991): Kruskal–Wallis $H=2.82$, $P=0.59$; RMBL (1995): $H=5.07$, $P=0.28$). After pups emerged, there were significant differences in calling rates between marmots in different age–sex classes (Table II; RMBL (1980–1991): $H=15.61$, $P=0.004$; RMBL (1995): $H=16.27$, $P=0.003$). Post-hoc Mann–Whitney U-tests revealed that adult females with pups that emerged during the study called at significantly higher rates than all other age–sex classes in both data sets (RMBL (1980–1991): adult female $P=0.0027$, adult male $P=0.0330$, yearling male $P=0.0096$, yearling female $P=0.0533$; RMBL (1995): adult female $P=0.0091$, adult male $P=0.0323$, yearling male $P=0.0143$, yearling female $P=0.0039$). Four of these eight significant differences disappear when we use a more rigorous critical P-value (0.05/4 post-hoc tests in each data set=0.0125) to compensate for the multiple post-hoc tests. Over the entire season, calling rates did not significantly differ between different age–sex classes in the 1980–1991 data set, but did significantly differ in the 1995 data set (Table II; RMBL (1980–1991): $H=6.17$, $P=0.19$; RMBL (1995): $H=16.25$, $P=0.003$). Post hoc Mann–Whitney U-tests again revealed that adult females with pups that emerged during the study called at significantly higher rates than all other age–sex classes (adult female $P=0.0106$, adult male $P=0.0323$, yearling male $P=0.0139$, yearling female $P=0.0083$). Two of these significant differences disappear if we use a more rigorous critical P-value (0.05/4 tests=0.0125) to compensate for the multiple post-hoc tests.

What Explains Variation in Calling Rate?

Results suggested that variation in alarm-calling rate of all group-living marmots (i.e. adult males excluded) was significantly explained by variables related to direct fitness, but not by variables related to inclusive fitness. The presence of one's own emergent pups at any time during the study, a variable reflecting direct fitness, significantly explained approximately 42% of the variation in the overall rate of alarm calling ($F_{1,23}=18.19$, $P=0.0003$; Fig. 1a). The presence of non-pup offspring, another variable reflecting direct fitness, significantly explained about 13% of variation in the overall alarm calling rate ($F_{1,23}=4.62$, $P=0.042$; Fig. 1b). Total r, a variable reflecting inclusive fitness, explained no significant variation in the overall rate of alarm calling ($F_{1,23}=0.40$, $P=0.53$; Fig. 1c).
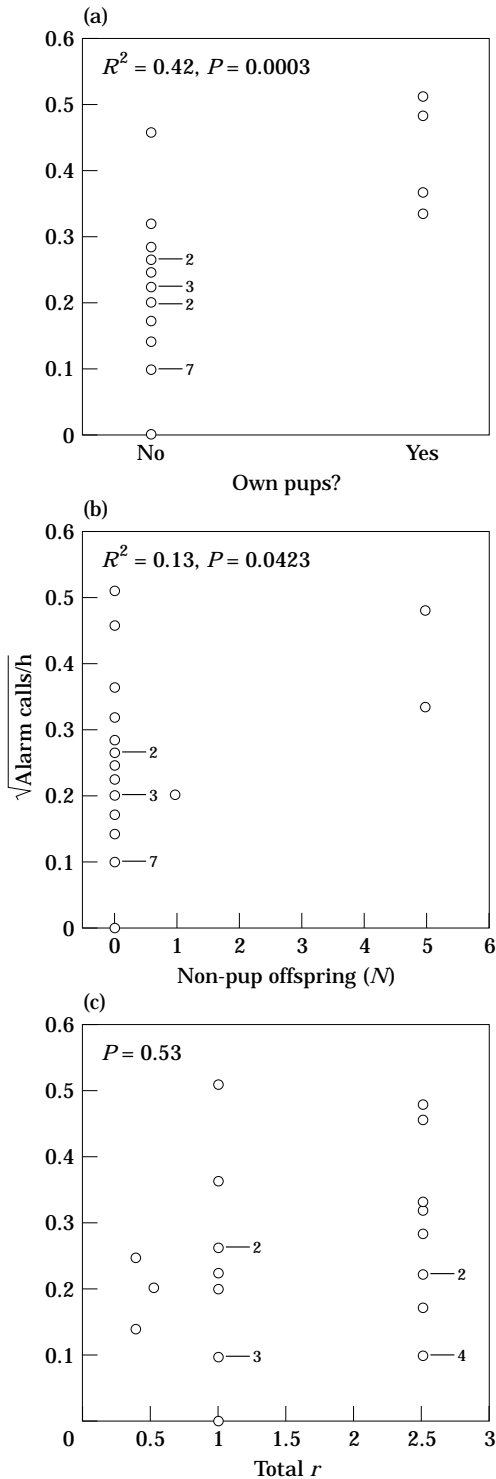
For group-living marmots who did not have young emerge during our study, no significant variation in alarm-calling rate was explained by variables reflecting direct or inclusive fitness. The number of non-pup offspring present, a variable reflecting direct fitness, did not significantly explain variation in the rate of alarm calling ($F_{1,19}=0.2$, $P=0.90$, Fig. 2a). Strictly, this comparison is questionable because we have only a single observation of a marmot with non-pup offspring present after removing the adult females who had young emerge above-ground. Nevertheless, the single observation falls in the middle of the distribution of calling rates from those without non-pup offspring, further suggesting no significant effect. The number of other social-group members, a variable reflecting inclusive fitness because all group members are kin, explains no significant variation in the rate of alarm calling ($F_{1,19}=0.10$, $P=0.77$, Fig. 2b). The number of litter-mate siblings in a social group, a variable reflecting inclusive fitness, explains no significant variation in the rate of alarm calling ($F_{1,19}=0.01$, $P=0.94$, Fig. 2c). The total r, a variable reflecting inclusive fitness, explains no significant variation in the rate of alarm calling ($F_{1,19}=0.57$, $P=0.46$, Fig. 2d). The presence or absence of pups in the social group at any time during the study, a variable reflecting inclusive fitness, explains no significant variation in the rate of alarm calling ($F_{1,19}=1.15$, $P=0.30$, Fig. 2e).

Is Alarm Calling Risky?

For all non-social alarm calls where we estimated the distance to the burrow and identified the caller, virtually all (135/141) alarm calls were uttered no more than 5 m from a burrow. In this data set, 27 marmots called an average of 5.2 ± 5.2 times (range=1–23). For each of these subjects, we calculated the proportion of calls given no more than 5 m from a burrow and

Figure 1. The effect of (a) the presence of an individual's pups, (b) the number of non-pup offspring and (c) the total r (the sum of the pair-wise coefficients of relatedness between an individual and each other group member) on the square root of the rate of alarm calling (alarm calls/h) observed during the study. $N=25$ and includes group-living marmots (i.e. adult males excluded). Identical points are plotted on top of each other; numbers identify multiple observations.
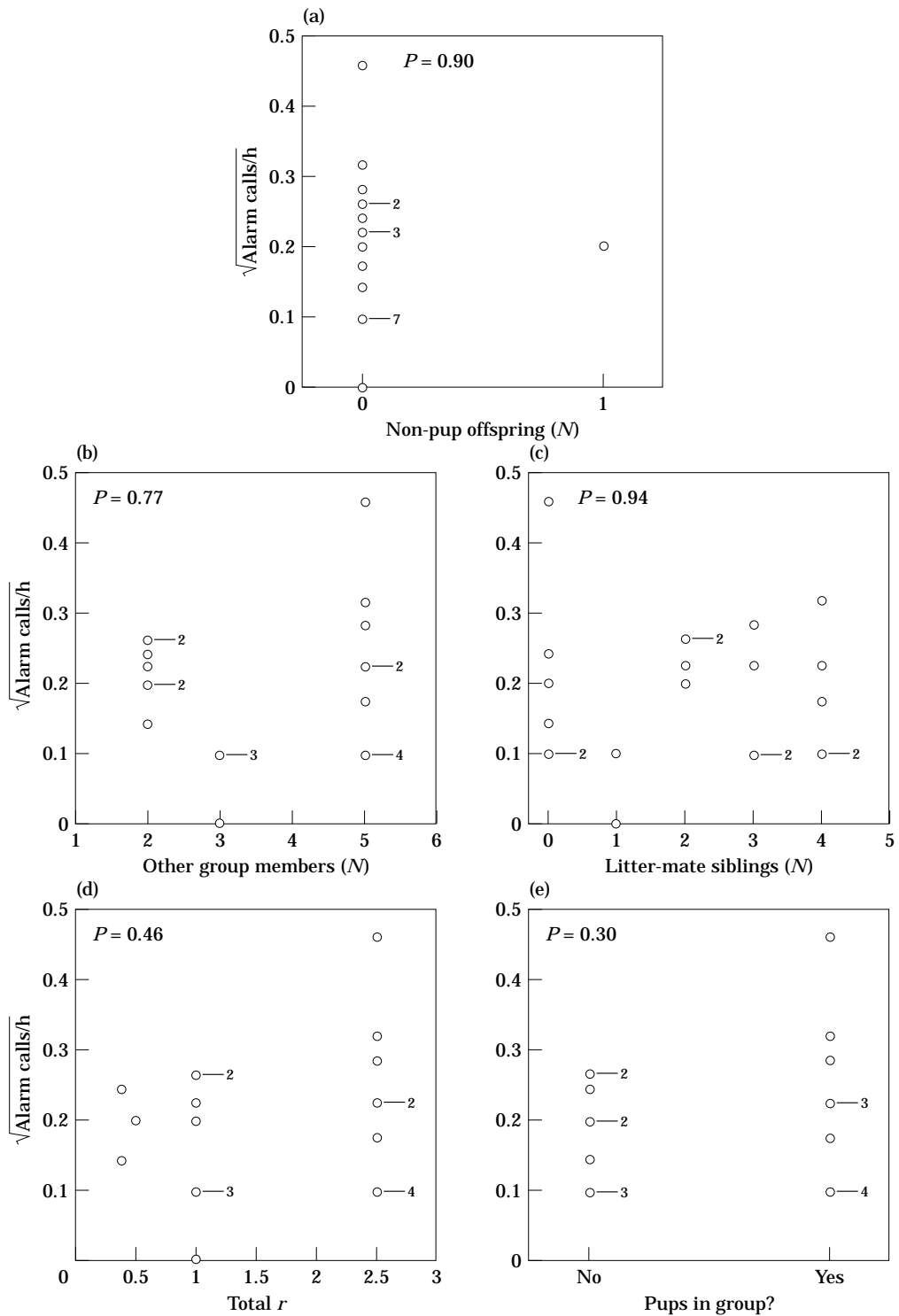
Figure 2. The effect of (a) the number of non-pup offspring in the group, (b) the number of other group members, (c) the number of litter-mate siblings, (d) the total r and (e) the presence or absence of pups in the group on the square root of the rate of alarm calling (alarm calls/h) during the entire study. $N=21$ and includes group-living marmots but excludes adult females with pups. Identical points are plotted on top of each other; numbers identify multiple observations.

averaged this non-pseudoreplicated value. An average of 97 ± 0.06 % (range=80–100%) of alarm calls were uttered within 5 m from a burrow. The six calls uttered greater than 5 m from a burrow were produced by five subjects (3 adult females, 2 yearling males). Two were produced by a mother with pups that emerged that day and were uttered as she chased a weasel, *Mustela frenata*, on two separate occasions, from her burrow area. One of the other two adult females had recently emergent pups; she called, then returned to her burrow in response to an unidentified stimulus. The other adult female called and then returned to her burrow in response to an unidentified stimulus. Both yearling males called first and then returned to their burrows; one called in response to a deer and, the other called at an unidentified stimulus.

Who is the Target of Alarm Calls?

Predation probe results suggest that the presence or absence of conspecifics above-ground did not influence the frequency of alarm calling in response to humans. There was no significant difference in the proportion of alarm calls given per predation probe when the focal marmot was alone (0.18 ± 0.28, $N=19$) versus that when other group members were in sight (0.28 ± 0.31, $N=19$) (Wilcoxon signed-ranks test $z=-1.07$, $P=0.28$).

We had data on 57 different marmots trapped in 1995. Only a single adult female called when trapped; thus we did not sub-divide adult females as a function of whether they had emergent young. Overall, there was no significant effect of age–sex class on the frequency of calling when live-trapped and handled ($\chi^2_3=4.86$, $P=0.18$). Twelve per cent of the individuals trapped tended to call when trapped (adult males: 2/12; adult females: 1/26; yearling males: 3/10; yearling females: 1/9). Overall, males were a bit more likely than females to call when trapped (males called 5/22 times, females called 2/35 times; $\chi^2_2=3.63$, $P=0.057$).

DISCUSSION

Adult female yellow-bellied marmots who had young emerge during our study periods alarm called at higher rates after their young emerged from their natal burrows than other age–sex classes (Table II), suggesting that alarm calling is a form of parental care. This pattern is similar to that found in some other sciurids (e.g. McCarley 1966; Smith 1978; Schwagmeyer 1980; Shields 1980; Hoogland 1995). In contrast, Sherman (1977, 1980) reported that the frequency of alarm calling did not change seasonally. Additionally, for group-living marmots (i.e. adult males excluded), variation in the seasonal rate of alarm calling is significantly explained by two variables associated with direct parental care (Fig. 1a, b), but no significant variation is explained by a variable reflecting the potential magnitude of inclusive fitness benefits (Fig. 1c). When we excluded adult females with young who emerged during our study period from the analysis, one variable associated with direct fitness (Fig. 2a), and four variables associated with indirect fitness (Fig. 2b–e) explained no significant variation in the rate of alarm calling.

We conclude that a primary function of alarm calling by group-living yellow-bellied marmots is the care of vulnerable offspring and that alarm-calling behaviour is maintained by its role in maximizing direct fitness. There was no relationship between alarm-calling rate and any variable we measured that reflected inclusive fitness benefits. Despite their living within earshot of each other (see also Schwagmeyer 1980), we found no evidence suggesting that individuals altered their frequency of alarm calling as a function of the magnitude of potential inclusive fitness benefits (measured as total r) from alarm calling, as is predicted if both direct and indirect fitness were important for the maintenance of alarm calling. In contrast to our findings, other studies of social sciurids found evidence that callers warned non-descendent or distant kin (e.g. Dunford 1977; Sherman 1977; Schwagmeyer 1980; Hoogland 1995). Hoogland (1995, page 178) also reported, however, that black-tailed prairie dogs, *Cynomys ludovicianus*, did not vary their calling behaviour as a function of the degree of kinship in home coteries.

Available evidence suggests that marmots expose themselves to limited risk while calling; alarm calling in yellow-bellied marmots is apparently not 'altruistic' (see also Barash 1975; Dunford 1977 for low-risk ground squirrel calling; cf. Sherman 1977). Virtually all alarm calls were given no more than 5 m from a burrow. If we assume that marmots can sprint about 3 m/s

(Blumstein 1992), then callers are virtually always within 2 s of safety. Moreover, during 38 years of marmot observations, Armitage never observed a calling marmot to be attacked. In the two cases where Armitage observed predation on non-juvenile marmots, neither alarm called immediately prior to being attacked.

Given the presumably limited risk of calling, it is surprising that we found no evidence that marmot calling rate was influenced by potential inclusive fitness benefits. With limited costs and variable benefits, we expected more calling when there was the potential for greater benefits (but see Hoogland 1995, page 178). That calling rate was not influenced by total r suggests that, for yellow-bellied marmots, indirect selection has a limited role in the maintenance of alarm calling. The limited role of indirect selection is not unexpected; amicable behaviour (Armitage & Johns 1982) and space-use overlap (Armitage 1996) occur primarily between close kin ($r=0.5$), but more distant kin are usually treated no differently than un-related individuals. Furthermore, kinship is not always the major determinant of social behaviours (Armitage 1982b, 1987). If indirect fitness benefits evolve after direct fitness benefits (Maynard Smith 1965), then we may be justified in concluding that indirect fitness played a relatively limited role in the evolution of alarm calling in yellow-bellied marmots.

Marmots alarm called whether or not con-specifics were present and presumably could have benefited from their calls. Marmots also alarm called when being live-trapped and handled, an unnatural situation where no other conspecifics were present (marmots typically retreated to their burrows when we checked traps). That marmots called regardless of whether conspecifics were present to alert is consistent with the hypothesis that predators are a potential target of alarm calls (see also Owings & Leger 1980). Both direct and inclusive fitness could theoretically be maximized by directing calls to predators. For example, predators may be 'distracted' away from other individuals (Armstrong 1965), or alarm calls may encourage the predator to 'move on' (Hasson 1991).

Kin selection, in its broadest sense, has been invoked to explain the evolution and maintenance of alarm calling. Kin selection includes direct and indirect fitness components, where both descend-ent and collateral kin benefit from an action.

Implicit in explanations invoking kin selection is the assumption that the indirect fitness component played an important role in the evolution of alarm calling. If a behaviour pattern evolved as a form of parental care, and thus maximized only direct fitness, most researchers would not emphasize that that behaviour pattern evolved through kin selec-tion (but see Sherman 1980). Because alarm calls can often be heard by several to many individuals, some of whom might be non-descendent kin (Schwagmeyer 1980), and because there is some evidence suggesting that alarm calling, in some species, is risky (Sherman 1977), kin selection and implicitly indirect fitness is commonly invoked to explain the evolution of 'altruistic' alarm calling. If individuals were concerned about maximizing their inclusive fitness, one would predict that the 'amount' of inclusive fitness a caller could com-municate to should influence the frequency or rate of alarm calling. We found no evidence that the rate at which marmots alarm called was related to the total r of their audience. Unlike J. B. S. Haldane, who once said that '. . . he was willing to lay down his life for two brothers or eight cousins' (Medawar & Medawar 1983, page 12), yellow-bellied marmots appear to care primarily about the welfare of their descendant kin.

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