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Why do yellow-bellied marmots call?

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When we see animals do things that are potentially risky, such as alarm calling around predators, we ask why. Why should an animal possibly identify itself to a predator when it could simply make a silent escape? Hamilton's (1964) inclusive fitness (kin selection) hypothesis is often used to explain the evolution and maintenance of alarm-calling behaviour (Maynard Smith 1965; and references in Hauber & Sherman 1998). Mathematically, the logic is elegant: individuals surrounded by relatives acquire a genetic benefit both from warning or otherwise protecting relatives that are descendants as well as nondescendants. If the benefit from both 'direct' and 'indirect' pathways to fitness (Brown 1987) is sufficiently large, the benefit may outweigh any costs associated with performing the seemingly risky behaviour and the behaviour will evolve and/or be maintained.

A reasonable empirical question that arises when looking at a system that may have evolved through kin selection is: do the animals have a way of assessing relatedness and modifying their behaviour appropriately, as would be predicted if they were attempting to maximize their inclusive fitness? We addressed this question indirectly by seeing if and how yellow-bellied marmot, *Marmota flaviventris*, alarm-calling behaviour was influenced by the presence or absence of both descendent and nondescendent kin (Blumstein et al. 1997). Hauber & Sherman (1998); questioned, on logical and methodological grounds, our assertion that yellow-bellied marmots respond in a way suggesting that they maximize their direct, and not indirect, component of inclusive fitness. Below we address their major criticisms and acknowledge on-going disagreement over the definition of kin selection (Sherman 1980; Shields 1980).

Is total *r* the 'simple weighted sum' that Grafen (1982, 1984) showed could not be used to calculate inclusive fitness? In a word, no. We used total *r* as a measure of the opportunity for kin selection (strictly it is the sum of the weights that could be used to calculate inclusive fitness benefits). As Hauber & Sherman (1998) noted, Creel (1990, page 230) wrote that to calculate an individual's inclusive fitness, the effect of one individual on others' reproductive success should be stripped away and the effects of the individual on others should be added after being devalued by the coefficient of relationship. Doing so would require estimates of the benefits from both giving and hearing alarm calls. Our inability to estimate these parameters prevented us from directly calculating the fitness payoff from calling or not calling. Moreover, we focused on current fitness and not future fitness: if studied, future fitness effects would have to be estimated for all individuals (cf. Hauber & Sherman 1998, page 1050). Regardless, if maximizing both direct and indirect fitness is important to marmots, we still typically expect there to be a positive association with the amount of total *r* and calling rate: we found none.

Our '. . . use of total *r* assumes that the benefit component in Hamilton's rule (b_i) is the same for each marmot that hears a call, and the cost of calling (c_i) is the same for each marmot that vocalizes . . .' (Hauber & Sherman 1998, page 1050). While yellow-bellied marmot pups utter alarm calls (Blumstein & Armitage 1997a), we focused on calling by older animals. We assume that the obvious predation costs of alarm calling are more-or-less constant for older animals. In fact, the predation risk of calling may be insignificant: marmots almost always return to the safety of a burrow before calling and we, and others, have never seen a calling marmot get killed by a predator (Barash 1989; Blumstein et al. 1997). Ultimately, we agree that in the future, more effort placed into quantifying the costs of calling might reveal variation with important explanatory power.

If alarm calling has a limited but constant cost for older individuals, then either all individuals should always call, or individuals should utter calls in proportion to the benefit they can obtain. All individuals did not always call: we have observed individuals at a burrow simply look towards a potential predator without vocalizing, and we have observed marmots away from a burrow immediately return to the burrow and look at a potential predator without vocalizing. Sometimes individuals vocalize. Alarm calls warn conspecifics, and nearly always, predators depart from the area after a call or calls. The target of the call (conspecific or predator) does not influence the ultimate payoff from calling: warning a conspecific or chasing away a predator can increase, direct, indirect and/or inclusive fitness. Overall, we found that different demographic classes of individuals called with different

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frequencies and that the frequency of calling changed after vulnerable pups emerged above-ground (Blumstein et al. 1997). Specifically we found that adult females with vulnerable pups called more after pups emerged above-ground: other age-sex classes either called less or calling rates did not change. We also found that the presence of one's own pups, and the presence of one's own nonpup offspring significantly explained variation in the rate of alarm calling, while variables broadly reflecting overall inclusive fitness did not.

Hauber & Sherman (1998) claim that our conclusions are not parsimonious. If we consider the mechanisms or rules that animals use when assessing and deciding (Bouskila & Blumstein 1992; Blumstein & Bouskila 1996) whether or not to utter an alarm call, we believe that our evolutionary conclusions are parsimonious. We maintain that a rule of thumb like 'call if vulnerable offspring are around' is both simpler and more parsimonious than an assessment and decision-making process that must be used if animals were modifying their behaviour based on maximizing inclusive, and therefore indirect, fitness. Simple rules of thumb may lead to more-or-less 'optimal' solutions (Bouskila & Blumstein 1992): on average, calling when offspring are around may, by maximizing direct fitness, ultimately maximize inclusive fitness. If inclusive fitness sensu lato were important, marmots would have to engage in a more complex assessment and decision making process that would include assessing the magnitude of benefit based on some calculation of potential direct and indirect fitness benefits, assessing the cost of an activity, and calling in proportion to the net benefit. Perhaps marmots cannot accurately assess their inclusive fitness, but can determine whether or not they are surrounded by potentially vulnerable relatives. If so, then we would expect to see all individuals in groups with pups call more than individuals in groups without pups. What we saw was that only the mother increased her calling rate when pups emerged above-ground. We maintain that a parsimonious mechanism, and therefore interpretation, for this behaviour, is that animals call if vulnerable offspring are around. This parsimonious interpretation is consistent with the evolutionary process of maximizing the direct, not the indirect, component of inclusive fitness.

Our results imply that direct fitness, not indirect fitness, is responsible for the maintenance and possibly the origin of alarm-calling behaviour. If the ancestral alarm-calling sciurid was solitary and noncolonial, alarm calling could evolve solely by the direct fitness benefits of warning vulnerable offspring or by chasing a predator away from vulnerable offspring. Woodchucks (*M. monax*), the least social marmot species (Blumstein & Armitage 1997b), rarely vocalize but may be more likely to do so when vulnerable offspring are present.

If direct fitness is important in explaining yellow-bellied marmot alarm calling, why don't adult males call? As previously discussed in Blumstein et al. (1997), adult males are not always associated with a single social group. Adult males have larger home ranges than group-living marmots (Salsbury & Armitage 1994), consequently they may not be around vulnerable young. In other more socially complex marmots (Blumstein & Armitage 1997b), males are more integrated into the social group and thus may be around vulnerable young. At this point we do not know whether adult males 'choose' not to call, or whether they are simply not around vulnerable young as much as other group-living marmots. We agree that studying why and when adult male yellow-bellied marmots call will be a fruitful line of research.

Reproductive competition (competition for direct fitness) may explain a variety of behaviours in both yellow-bellied marmots and other species. For instance, why do all marmots that see a potential predator not vocalize if alarm calling is not risky? In addition to potentially cooperating with relatives, individuals may compete with their close relatives. Previous studies showed that competition occurred among yellow-bellied marmot kin with coefficients of relationship as high as 0.5 (Armitage 1986, 1989). An alarm call has the potential of warning conspecific competitors and their offspring (sensu Dunford 1977). If there is reproductive competition, competition for direct fitness may be a cost that prevents all individuals from helping their competitors. To quantify this cost, the competitor's benefit from hearing an alarm call must be quantified. Currently, we have no idea of the relative importance of this potential cost. The benefits from warning vulnerable or descendant offspring may exceed the costs associated with incidentally warning competitors.

Competition for direct fitness may have considerable explanatory power. For instance, Hoogland (1995) explained kin-directed infanticide by female black-tailed prairie dogs, *Cynomys ludovicianus*, as a way that prairie dogs obtained direct fitness by reducing competition among close kin. Interestingly, black-tailed prairie dogs did not vary calling rates as a function of the degree of kinship in home coteries. These observations suggest that, for some animals, the quest for direct fitness may be relatively more important than the quest for indirect fitness. If so, relatives of equal *r*s are not equal; animals act as if obtaining direct fitness is more important than obtaining indirect fitness. Thus, by not distinguishing between direct and indirect pathways to fitness, we fail to understand why many animals behave the way they do. Our alarm-calling results join a list of other results that are consistent with this hypothesis (e.g. Altmann 1979; Mumme et al. 1983; Armitage 1986, 1987, 1989, 1996, in press; Emlen & Wrenge 1992; Arnold et al. 1994; Hoogland 1995).

Finally, Hauber & Sherman (1998) noted that adult males (including potential fathers) do not call that much and suggested that male calls function in a different context. We have noted previously (Blumstein et al. 1997; Blumstein & Armitage 1997a), and here, that calls may also be directed to predators. Consistent with this hypothesis is the observation that all age–sex classes utter alarm calls. Also consistent is the observation that yellow-bellied marmot alarm calls become more obvious as risk increases: marmots call faster and utter more calls (Blumstein & Armitage 1997a). This is not true for all species of marmots: both golden (*M. caudata aurea*) and alpine marmots (*M. marmota*) decrease the number of calls that are packaged into a multinote alarm call as risk increases. In doing so, these other species appear to make themselves less obvious (Blumstein 1995; Blumstein & Arnold 1995). A prediction from the hypothesis that calls are directed to the predators is that vulnerable individuals will call (FitzGibbon & Fanshawe 1988). We do not see this in yellow-bellied marmots: marmots primarily call from relatively safe locations and all individuals typically do not call when a predator is present. We would eagerly welcome any suggestions on how to better tease apart the relative importance of predators versus conspecifics in driving the evolution and maintenance of marmot alarm-calling.

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