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Spider Monkey Alarm Calls: Honest Advertisement or Warning Kin?

Many primate species give alarm calls at night in response to predators or to the alarm calls of conspecifics (Anderson 1984). Byrne (1981) proposed that alarm calls of this type may be an 'honest advertisement' (Clutton-Brock & Albon 1979), providing predators with reliable information about the number of defenders in the group. Alternatively individuals in small groups could attempt to deceive predators by calling more and mimicking larger groups ('Beau Geste tactic', Krebs 1977; Byrne 1981). Alarm calls given at night may have a greater potential for manipulation than those given during the day, since detection of cheating may be more difficult.

Here, we report experimental field data describing the responses of spider monkeys in Santa Rosa National Park, Costa Rica to recorded alarm calls played back at sleeping trees at dusk. The social unit of spider monkeys, *Ateles geoffroyi*, consists of amiably interacting subgroups, the size and composition of which change frequently. Over 5 years (1983–1988) of investigation at Santa Rosa (36 months field time), 1018 subgroups were observed and followed, the size of which averaged ($\pm$ SE) $4{\cdot}9 \pm 0{\cdot}13$ individuals (range = 1–35). Spontaneous alarm calls were infrequently heard during this period ($N = 48$), probably because spider monkeys rarely encountered predators and/or the presence of the observers may have deterred predators from approaching. Spontaneous bouts of repetitive alarm calling varied from 5 s to 46 min ($\bar{X} = 204$ s, $N = 48$) and were given by subgroups ranging in size from 1 to 18 members. Usually, it was not possible to identify the reason the animals called ($N = 31$). However, on five occasions we saw a potential predator when the calls were given, and on 12 instances calls were given when humans (other than the observers) approached the subgroup. Since in a forest environment it is impossible to state if or when a predator has left the vicinity, or to control for the actions of a predator, it is extremely difficult to relate the duration of spontaneous calling bouts to the size of the subgroups in order to test the hypotheses proposed earlier. We therefore opted for a more experimental approach.

The alarm calls of a medium-ranking adult female, responding to an unknown terrestrial predator were recorded with a Sony TC-D5 recorder. The spider monkey's alarm call is known as a 'bark' (Eisenberg 1976) and is given to a variety of terrestrial predators (Symington 1987). Observers arrived at the sleeping site well before the monkeys and placed speakers on the opposite side of the tree to which the observers were positioned. Shortly after a subgroup settled into the sleeping tree, the alarm call was played to them. Playbacks were conducted only on those occasions where the subgroup contained only known individuals and did not include the female that was recorded giving the original alarm call. This female was known to interact with all members of the subgroups. The spider monkeys often congregated at sleeping sites at night (Chapman 1989), and alarm calls were never given in response to the sudden appearance of a monkey at the sleeping tree ($N = 152$). Thus, we believe that the behaviour of the spider monkeys when the alarm call was played was a response to the playback and not to the presumed approach of other monkeys. When subgroups were comprised of known individuals ($N = 12$), we recorded the duration and type of vocalizations, and whether the animal oriented and/or travelled in the direction of the speakers. We considered the duration of the response for the subgroup as the time from when they first responded, to the time when the last animal stopped calling. Observations were continued for approximately 20 min following the playback or until the lack of light precluded observations (one occasion). In all instances the animals were no longer exhibiting any apparent reactions. To prevent familiarization with the experimental procedure and to minimize the potential of unnatural response by the monkeys, playbacks conducted at one sleeping site were separated by at least 10 days.

If alarm calls given at sleeping sites are honest advertisements, then the duration and/or intensity of the call should be proportional to the size of the subgroup. If individuals in small subgroups attempt to imitate large subgroups by calling longer, then one would expect a negative relationship between subgroup size and call duration. In addition, we have sufficient information with respect to social organization and kin affiliation in the monkeys of our study group to permit an analysis of their behaviour at sleeping sites in terms of the proximity of immediate family kin.

We conducted playbacks on 12 occasions involving subgroups that ranged in size from three to eight individuals ($\bar{X} = 5{\cdot}7$). On 18 other occasions, spider monkeys did not come to the sleeping site we had chosen, and on four occasions, subgroups contained unknown individuals. All subgroups

responded to the recorded alarm call by vocalizing (range in duration = 30 s–11 min). All individuals, with the exception of some infants, oriented in the direction of the speakers. Individuals in 10 out of the 12 subgroups approached the speaker and occasionally travelled well past its location. There was no difference between the size of subgroups that approached the speaker and those that did not approach (approach: $\bar{X}=5{\cdot}4$; no approach: $\bar{X}=7{\cdot}0$, $t=1{\cdot}25$, $P=0{\cdot}289$), nor between the number of known related individuals in the subgroup that approached the speaker and those that did not (approach: $\bar{X}=2{\cdot}4$; no approach: $\bar{X}=1{\cdot}0$; $t=1{\cdot}21$, $P=0{\cdot}255$). In a multiple regression, subgroup size and the number of immediate family kin accounted for 77% of the variation in the duration of the vocal response to the playback ($R_2=0{\cdot}766$, $P=0{\cdot}0014$). Partial correlation coefficients were then examined to isolate the independent effects of these two variables. As the number of known kin in a subgroup increased, there was a strong tendency for the duration of the response to increase (partial correlation coefficient = 0·87, $P=0{\cdot}0005$) when the effects of subgroup size were held constant. When the size of the subgroups increased independent of the number of kin they contained, there was a weak tendency for the duration of the vocal response to decrease (partial correlation coefficient = −0·52, $P=0{\cdot}098$).

Contrary to the prediction of the honest advertisement hypothesis, the duration of the vocal response given to alarm calls did not increase with subgroup size. In fact, the opposite effect was observed; individuals in small subgroups tended to give longer responses than individuals in larger subgroups, although this effect did not reach traditional levels of statistical significance ($P=0{\cdot}098$). It may be that spider monkeys in small subgroups are using the Beau Geste tactic, calling longer in order to deceive predators by mimicking a larger group with more defenders. However, we observed no additional behaviour (such as monkeys moving positions silently between calling) that would further support a deception explanation of the Beau Geste type. In addition, before a deception hypothesis can be accepted, it must be demonstrated that such behaviour can actually deceive predators, and that a simpler functional explanation is not more likely to explain the observed responses. For example, it is possible that spider monkeys in small subgroups are in more danger than those in large subgroups, either because they are less likely to detect a predator, or because they are less capable of defending themselves (van Schaik 1983). Thus, they may call longer to maintain a higher level of vigilance. We suggest, as has been shown for ground squirrels, *Spermophilus beecheyi* (Loughry & McDonough 1988), that the repetitive calling of monkeys in response to predators may function to maintain visual vigilance and thus increase the probability of detecting a predator should it return.

Our main results suggest that spider monkeys alter the duration of their alarm calls in response to the number of kin in the vicinity. This suggests that the intensity of responses given by spider monkeys to a potential predator depends on the social context, and that they act in such a way to preferentially benefit kin.

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