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Selfish or Altruistic? An Analysis of Alarm Call Function in Wild Capuchin Monkeys (*Cebus apella nigritus*)

Running Headline: Wheeler Alarm call function in tufted capuchin monkeys

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Word count of the text: 8,425

ABSTRACT

Alarm calls facilitate some anti-predatory benefits of group-living but may endanger the caller by attracting the predator's attention. A number of hypotheses invoking kin selection and individual selection have been proposed to explain how such behaviour could evolve. This study tests eight hypotheses for alarm call evolution by examining the responses of tufted capuchin monkeys (*Cebus apella nigritus*) to models of felids, perched raptors, and vipers. Specifically, this study examines: 1) differences among individuals in their propensity to call in response to different threat types, 2) whether or not there is an audience effect for alarm calling, and 3) the response of conspecifics to alarms. Results indicate that the benefits likely afforded to the caller vary with stimulus type. Alarm calling in response to felids is most likely selfish, with calls apparently directed towards both the predator and potential conspecific mobbers. Alarm calling in response to vipers attracts additional mobbers as well, but also appears to be driven by kin selection in the case of males and parental care benefits in the case of females. Alarm responses to perched raptors are rare, but seem to be selfish with callers benefiting by recruiting additional mobbers.

Keywords: anti-predatory behaviour, predator model experiments, mobbing, audience effect, tufted capuchin, *Cebus apella*

Alarm calls are ubiquitous among birds and mammals and facilitate proposed anti-predatory benefits of group-living including the many-eyes effect (Lima 1995) and cooperative defense (Curio 1978). However, the benefits afforded to the caller need to be explained because vocalizing in the presence of a predator may attract the predator's attention (e.g. Ivins & Smith, 1983). Several hypotheses invoking kin selection (Maynard Smith 1965) and individual selection (*e.g.* Charnov & Krebs 1975) have been developed to explain how this apparently costly behaviour can evolve (see Klump & Shalter, 1984; Hauser, 1996, Caro 2005 for reviews). Many tests of these hypotheses have been conducted in avian and rodent taxa (e.g. Sherman 1985; Smith 1978; Hoogland 1996; Davis 1984; Taylor et al. 1990; Neudorf & Sealy 2002; Shelly & Blumstein 2005) but only two studies have appropriately tested some of these hypotheses among primates (Cheney & Seyfarth 1981, 1985; Zuberbühler et al. 1999). Furthermore, few studies have differentiated between alarms given to different predator types, although this has been shown to affect the selective pressures that act on alarm calling (Sherman 1985; Zuberbühler et al. 1999). This study tests predictions associated with eight hypotheses (see table 1) for the evolution of alarm calls in tufted capuchin monkeys (*Cebus apella nigritus*) in Iguazú National Park, Argentina by examining their reactions to models of felids, raptors, and venomous snakes.

The earliest hypothesis developed to explain the evolution of alarm calls was based on kin selection; alarm calling may be selected for if calling decreases the predation risk of relatives of the caller and thereby increases the caller's indirect fitness (Maynard Smith 1965). Several additional hypotheses explain how alarm calling can evolve through individual selection. First, similar to the kin selection hypothesis, alarm callers may benefit by alerting offspring to the predator's presence ("parental care": Williams 1966). Whether costly parental behaviour should be considered kin selection or individual selection is a matter of contention (c.f. Dawkins 1976; Bertram 1982), but these are here tested separately. Second, an alarm may decrease predation risk for potential mates ("mate protection": Witken & Ficken 1979). Under a polygamous mating system, this hypothesis predicts that adult males will call more often than will females or non-mating males (Hauser 1996). Third, an alarm caller may benefit via a "selfish herd" effect (Hamilton 1971) if group-mates coalesce around the caller. Fourth, it may be beneficial for an individual to call if protecting group members increases the caller's direct fitness ("group maintenance": Smith 1986), for example through the dilution effect (Bertram 1978; but see Zuberbühler & Byrne, 2006) or as the result of between group feeding competition (Wrangham, 1980). Under this scenario, dominant individuals should be more likely to call than subordinates if the former receive more benefits and face fewer costs with increasing group size than do the latter (Alatalo & Helle 1990; see also Cheney & Seyfarth 1985). Fifth, an alarm call may manipulate the behaviour of conspecifics in a way that confuses the predator and allows the caller a chance to escape ("predator confusion"; Charnov & Krebs 1975). Sixth, alarm calls may elicit mobbing of the predator by conspecifics ("mobbing recruitment"; see Curio 1978). Finally, an alarm call may cause "ambush" predators to give up their hunt ("pursuit deterrence"; Woodland *et al*. 1980). Of these eight hypotheses only the latter predicts a lack of a conspecific audience effect; the presence of conspecifics is necessary for the caller to benefit under all other scenarios (Gyger 1990).

The parental care and pursuit deterrence hypotheses have thus far found the most widespread support. Evidence in favor of these hypotheses has been found in each of birds, rodents, and primates, while other hypotheses have found support only within one of the three taxa (see table 1; see also Caro 2005 for more complete review). However, a lack of support for other hypotheses may be due to the fact that most previous studies did not test all possible hypotheses (e.g. Zuberbühler et al. 1999).

This study tests the predictions of the eight hypotheses listed in table 1. Because the selective pressures acting on alarm calls have been shown to vary with predator type (*e.g.* Sherman, 1985), every hypothesis is evaluated separately for detections of each of the model types used in this study: felids, vipers, and raptors. However, the selfish herd, predator confusion, and pursuit deterrence hypotheses are not considered for vipers since these hypotheses assume a strict predator-prey relationship; venomous snakes are not known to prey on capuchins although they do pose a mortal threat to individuals that approach too closely (see Methods).

METHODS

Study Site and Subjects

The study was conducted from August - September 2003, July – September, 2004, and May 2005- December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W). The site is part of the South American Atlantic Forest and is characterized by humid, semi-deciduous, sub-tropical forest (Crespo 1982). The study area has been logged in the past and is in various stages of secondary growth (see Di Bitetti et al. 2000 for further description of the study site).

Tufted capuchins are small (2.5-3.6 kg; Smith & Jungers 1997), diurnal primates that feed primarily on fruits but spend a large proportion of time searching for insect prey by specialized destructive foraging (Terborgh 1983; Brown & Zunino 1990). The species is highly arboreal, inhabiting primarily the mid to lower canopy and the understory (Fleagle & Mittermier 1980). Approximately 3% of their active time is spent on the ground, although this varies considerably by season (Wheeler unpublished data). Groups are multimale-multifemale, typically consist of 7-30 individuals (Di Bitetti 2001b), and are characterized by female philopatry and male dispersal (Di Bitetti 1997). Dominance hierarchies are linear and dominant individuals benefit from contests over food and spatial position (Janson 1985; Di Bitetti & Janson 2001). In addition, although the dominant male likely sires the majority of offspring (Escobar-Páramo 1999), subdominant adult males obtain some matings (Janson 1994). All adult males but one were observed mating during the course of the current study, while only one copulation involving a natal (juvenile) male was observed. In addition, because all observed male takeovers at the study site have been the result of subdominant males within the group rising in rank (Janson, unpublished data), all adult males have the potential to sire offspring.

The species produces at least three distinct calls in association with predator encounters (Wheeler in prep.). Two of these, the “hiccup” and “peep”, are given in response to both felids and vipers and are often produced together during a single predator encounter. The “hiccup” is also given in non-predatory contexts (including aggressive interactions and when foraging in a precarious position; Di Bitetti 2001a, Wheeler in prep.), has been shown to be an indicator of stress (Boinski et al. 1999), and may be best classified as a general “disturbance call” (Emmons et al. 1997). The third call, the “bark”, is a functionally referential aerial predator alarm given only in response to flying stimuli or large perched birds (Wheeler in prep.). A similar alarm call system has been described for white-faced capuchins (*C. capucinus*; Digweed et al. 2005).

Among the predators of capuchin monkeys at the site are three species of felids (jaguars, *Panthera onca*; pumas, *Felis concolor*; and ocelots, *Leopardus pardalis*), tayras (*Eira barbara*), and two species of raptors (hawk-eagles: *Spizaetus ornatus* and *S. tyrannus*; see Hirsch 2002; Di Bitetti et al. 2006 for further descriptions of predators at the study site). In approximately 400 weeks of observation, one predation attempt by a felid has been recorded (Di Bitetti 2001a); although several additional monkey-felid encounters have been observed, it is unclear if any of these were actual predation attempts. There have been two observed predation attempts by raptors at the study site, one of which was successful (Di Bitetti 2001a). Capuchins in Iguazú also face threats from three species of vipers (*Bothrops neuwiedii, B. jararaca,* and *Crotalus durissus*; Martinez et al. 1992). While these snakes are not known to be capuchin predators, their presence nevertheless evokes a strong reaction in the capuchins, likely because of the mortal threat they pose to individuals who approach too closely.

Data were collected on three separate groups (“Macuco”: 23-45 individuals; “Gundolf”: 15 individuals; “Guenon”: 9 individuals). The two latter groups split off from the former during the initial period of data collection to form new groups. For the majority of the study period, the Macuco group consisted of 23-28 individuals, with variation due to births. Maternal relationships for all individuals are known and all individuals were recognizable based on facial characteristics.

Observational and Experimental Protocols

Data were collected using models of ocelots, vipers, and hawk-eagles (see fig. 1) and playbacks of puma vocalizations. Models were placed in front of the group while they were traveling or foraging. One observer went ahead of the group to place the model while one or more observers remained with the group to ensure that they did not approach too closely before the model was placed. Ocelot and snake models were placed at least 50m ahead and raptor models were placed 150m in front of the group. In all cases, the distance chosen was sufficient to prevent the study subjects from cueing in on the model placement. Viper models were always placed on the ground while ocelot models were placed on the ground or in trees at a height of 2 to 5m. Raptor models were suspended from tree branches at a height of 4 to 12m by a rope thrown over the branch. In most cases, the model remained stationary for the duration of the experiment. For a few experiments, snake (N=7) and ocelot (N=5) models were moved a short distance (less than 15cm) once every two minutes until a detection occurred. Although this movement sometimes caused individuals to detect the models when they otherwise would not have, there was no discernable difference in the way that they reacted to moving models relative to stationary ones. To avoid habituation, a given model type (e.g. felid, snake, raptor) was not used for seven days following a detection, while a specific model was not used for at least fifteen days; in most cases each model was used only once with each group in a thirty day period. Three exemplars of each of model type were used. The capuchins did not appear to habituate to the models, given that responses to the models remained consistent throughout the study period.

Continuous focal sampling (Martin & Bateson 2007) was used simultaneously by three observers to record whether or not individuals gave an alarm upon detecting a model. A detection was defined as an instance in which a focal animal suddenly ceased the behaviour in which it was engaged and began to stare attentively at the model. Individuals that approached to within 15m of the model were chosen as focal animals. A distance of 15m was chosen because detections of models are very unlikely from greater distances, even when visibility is relatively high (Janson 2007). Focal animals were followed until detecting or moving farther than 15m from the model.

Upon the detection, the focal animal's vocal behaviour (or lack thereof) was noted, as was whether or not the detector performed any other conspicuous anti-predator behaviours (e.g. flee or display). If an alarm call was given by the detector, all-occurrence sampling (Martin & Bateson 2007) was used to note if, immediately following the call, conspecifics reacted with: 1) a sudden burst of movement and/or vocalizations or ("pandemonium"; Sherman 1977), 2) mobbing of the predator model (i.e. aggressive displays towards the model). In addition, a scan sample (Martin & Bateson 2007) was conducted 30 seconds after the first alarm to record neighbor density (the number of conspecifics within 3m) for all individuals in the group, including the caller. These experimental scan samples were compared to scans conducted in non-experimental contexts at 30 minute intervals throughout the day. Only non-experimental scans which were taken when the group was traveling or foraging were included in the analysis since experiments were always conducted in this behavioural context.

Experiments were also conducted with individuals who had become separated from the group (hereafter "solitary") to test for audience effects on alarm calling. An individual was considered solitary if there were no conspecifics within 150m for at least 15 minutes. In most cases, the animal had been separated from conspecifics for at least several hours. These experiments used either an ocelot model or a playback of a puma vocalization and followed a protocol similar to that described for non-solitary individuals. Puma calls were deemed appropriate to use for solitary but not non-solitary individuals; non-solitary individuals may withhold alarms since all prey individuals simultaneously become aware of the predator's presence (see Arnold et al. 2008). Playbacks conducted with non-solitary individuals confirm that capuchins do typically call in response to this stimulus (Wheeler unpublished data). The calls used for playbacks were recorded at the study site during an encounter with a vocalizing puma. Recordings were made with a Marantz PMD-660 recorder and a Sennheiser ME67/K6 microphone at a sampling rate of 44.1 kHz. Recordings were played from a Saul Mineroff AFS speaker connected to a portable CD player at an intensity of 80-90 dB (measured by a Radio Shack 33-2055 digital sound level meter placed 1 meter from the speaker). The speaker was placed in dense vegetation at a height of 1m. Each playback consisted of a single vocalization played four times at 5 second intervals and began when the solitary individual approached to within 25m of the speaker. The individual was scored as alarm calling if it produced an alarm at any point from the initiation of the playback until 40 seconds after the last call was played.

All dyadic agonistic interactions (including aggression, submission, and spatial displacements) were noted *ad libitum*, entered into a dominance matrix, and analyzed using MatMan™ (Vers. 1.1.4; De Vries *et al*. 1993). Because the hierarchy of the Macuco group was significantly linear, the ordering procedure within MatMan immediately provides an ordinal dominance rank for each individual with the "inconsistencies and strength of inconsistencies" (I&SI) method (De Vries 1998). A sufficient number of interactions were recorded only for the Macuco group; the "group maintenance" hypothesis was therefore tested using only data from this group.

All methods conformed to the guidelines for use of animals in research outlined by the ABS. The study was conducted with the permission of the Argentine Administration of National Parks and IACUC Stony Brook University (ID numbers 2003-1218, 2004-1218, 2005-1448, and 2006-1448).

Data selection and statistical methods

An individual's response was included in the analysis only if it was the first detector during that particular experiment or if previous detectors did not call or perform any other conspicuous anti-predator behaviours which would allow subsequent detectors to cue in on the model's presence. It is thus unlikely that any individual's reaction was confounded by the behaviours of previous detectors. For individuals whose detections met these criteria on more than one occasion, the first such detection of a particular model type was selected for inclusion in the analysis. To ensure that all data points were independent, only a single detection from each experiment was used. Only detections by juveniles and adults were included in the analysis because, although juveniles readily recognize predators as dangerous, infants do not appear to have yet fully developed this recognition (Wheeler in prep.). The number of individuals of different age and sex categories which were included in the analysis is shown in table 2.

Binary logistic regressions were used to determine if total maternal *r*, number of offspring, dominance rank, or "sire potential" predicts whether or not an individual produced a vocalization upon detecting a particular model type. "Total *r*" was calculated for each detector by summing the coefficient of relatedness (Wright 1922) between the detector and all other individuals present at the time of detection. An individual was considered present if it had been seen in the group during the day of the experiment unless it was otherwise known to be absent from the group during the experiment; misclassification of an individual as present was unlikely given the rarity in which individuals separated from the group. Because paternity for many individuals is unknown, *r* values were based solely on maternal relationships (e.g. mother-offspring dyads = 0.50, maternal siblings = 0.25, aunt-nephew dyads = 0.13, etc.). Offspring (of any age) were excluded when calculating an individual's total maternal *r* since this study examines the kin selection and parental care hypotheses separately. Due to the lack of paternity data, only females were included in tests of the parental care hypothesis. The sire potential variable divided individuals into two categories, adult males vs. all other individuals (i.e. adult females plus all juveniles). Logistic regressions were performed by examining each independent variable both alone and in a multivariate analysis including several independent variables simultaneously. In addition, because different selective pressures may act on male and female alarm calling (e.g. Alatalo & Helle 1990), the interaction between sex and each predictor variable was examined in a univariate logistic regression. If the interaction variable was found to be significant, that variable was tested separately for males and females. Two multivariate logistic regressions were run for each predator model type. The first of these was based on all detections (i.e. by both males and females) and included the following predictor variables: total maternal *r*, dominance rank, sire potential, and the interaction between sex and each of these three independent variables. The second was based on detections by females only and included total maternal *r*, dominance rank, and number of offspring as predictor variables. Males were not included in this model because paternity is unknown in many cases.

Binomial tests were used to test whether mobbing of the model by conspecifics or "pandemonium" followed the production of alarm calls more often than expected. An expected value of 37.5% was chosen because this is the frequency in which conspecifics mobbed the models when no alarm call had been given by a previous detector (12 of 32 cases). Although this does not reflect the expected baseline values of "pandemonium" behaviour, a value of 37.5% is conservative since such behaviours were rare. To determine if the sex of the caller predicted the reactions of conspecifics, a binary logistic regression was used. A Wilcoxon signed ranks test was used to determine whether or not individuals achieved a higher neighbor density subsequent to producing an alarm than those same individuals had in non-experimental contexts. To determine if overall group cohesion was greater in experimental than non-experimental contexts, the mean number of neighbors within 3m for all individuals was calculated for each scan in both contexts, was square root transformed, and compared using a one-tailed t-test. Finally, a Fisher's exact test was used to test for differences between solitary and non-solitary individuals in the probability of calling following a felid detection. Significance levels were set at $p<0.05$ for all tests; a result was considered to show a trend in the predicted direction if $p<0.10$. Regressions, signed ranks tests, and t-tests were conducted using SPSS 15.0 (SPSS Inc., Chicago, IL, USA). The binomial tests and Fisher's exact test were calculated by hand.

RESULTS

Felid experiments

Twenty-three of the 25 individuals who detected an ocelot model gave an alarm call upon detecting the model (92.0%; fig. 2). The individuals who did not call included a low-ranking juvenile female and an alpha male. Whether or not an individual called upon detecting the ocelot model was not predicted by its total maternal *r*, number of offspring, dominance rank, or sire potential in the univariate analyses, and no variables showed a significant interaction with sex (see table 3). Likewise, the multivariate logistic regressions were non-significant (whole group: $\chi^2_6=9.28$, N=16, p=0.158; females only: $\chi^2_3=6.03$, N=8, p=0.11). Pandemonium by conspecifics did not occur following any alarms (0 of 20 documented cases), but groupmates mobbed the model following an alarm call significantly more often than expected (15 of 20 documented cases; binomial test: $p<0.001$). The sex of the caller did not predict whether or not conspecifics mobbed the ocelot model (binary logistic regression: $\beta=-0.81$, N=20, p=0.44). Finally, callers did not achieve a greater number of neighbors within three meters in experimental contexts (mean ± SE = 0.67 ± 0.20 neighbors) than they averaged in non-experimental contexts (mean ± SE = 0.59 ± 0.04 neighbors; Wilcoxon signed ranks test: N=18; Z=-0.04, p=0. 97). However, when neighbor densities for all group members were averaged, there was a non-significant trend towards an increase in neighbor density in experimental contexts (mean ± SE = 1.05 ± 0.16 neighbors) relative to non-experimental contexts (mean ± SE = 0.72 ± 0.02 neighbors; one-tailed t-test on square root transformed data: $t_{28}=1.69$, $N_1=28$, $N_2=641$, p=0.10).

Four experiments with a model ocelot and four using a puma call playback were conducted with solitary individuals. Six of eight (75%) solitary detectors called, including all four detections of the ocelot model and following two of the four playbacks (fig. 2). This probability of calling per detection does not differ significantly from that of non-solitary individuals (Fisher's Exact test: p=0.21). In addition, three of the four detectors mobbed the ocelot model, while both individuals who called in response to the puma call approached the speaker.

Viper experiments

Thirteen of 28 (46.4%) individuals called upon detecting a viper model (fig. 2). Whether or not an individual called in this context was not predicted by its total maternal *r*, dominance rank, or its sire potential in the univariate analyses (see table 4). Among females, there was a non-significant trend (p=0.10) for the number of offspring to predict the response to viper models (see table 4, fig. 3). In addition, tests of the interaction between sex and each of the independent variables indicated a significant interaction between sex and total maternal *r* as well as sex and sire potential (see table 4). Further analysis showed that kinship was a nearly significant predictor of whether or not males, but not females, gave an alarm upon detecting a viper model (see table 4, fig. 4). The sire potential variable approached significance in the case of males, although with a trend for non-potential sires to be more likely to alarm (see table 4). The latter variable was not tested for females because all females are assigned to the non-potential sire category. Neither the multivariate logistic regression for the whole group (χ^2_6=7.02, N=22, p=0.32) or for females (χ^2_3=7.14, N=11, p=0.07) was significant; although the latter model approached significance, none of the individual predictor variables was significant. Finally, additional conspecifics approached and mobbed the model in nine of 13 documented cases, significantly more often than expected (binomial test: p=0.02); the sex of the caller did not predict whether or not conspecifics mobbed the model viper (binary logistic regression: β=-0.41, N=13, p=0.77).

Perched eagle experiments

Five of 22 individuals (22.7%) alarm called following the detection of a raptor model (fig. 2). Callers included a subdominant adult male and four mid to low ranking adult and juvenile females. All five individuals who called as well as 7 of 17 (41.2%) non-callers approached and mobbed the predator model. None of the independent variables or the interaction variables were significant in the univariate analyses (see table 5). Likewise, the multivariate analyses were also nonsignificant (whole group: χ^2_6=3.63, N=16, p=0.73; females only: χ^2_3=2.08, N=10, p=0.55). Sudden "pandemonium" did not follow any of the alarms, while additional group members mobbed the model following all five alarm calls, a value significantly greater than expected (binomial test: p=0.01). Insufficient data were collected to test whether or not intragroup spacing decreased following the alarms.

DISCUSSION

While alarm calls given to each of felids, vipers, and snakes can be explained by the mobbing recruitment hypothesis, no other single hypothesis for the evolution of alarm calling seems to apply to tufted capuchins across all contexts (table 6). However, each of the kin selection, parental care, mobbing recruitment, and pursuit deterrence hypotheses received some support for at least one stimulus type. The selfish herd, group maintenance, conspecific manipulation, and mate protection hypotheses were not supported for any stimulus type. Because of the small percentage of perched hawk-eagle detections which resulted in alarms, it is difficult to determine which hypothesis may best explain the evolution of alarms given in this context although the observed trends allow some hypotheses to be eliminated. While the low observed rate of calls given to perched raptors may be a result of insufficiently realistic models, this seems unlikely given that most detectors mobbed the models. Less intense reactions to perched relative to flying raptors have been noted in several previous studies of prey species (e.g. Marler 1955; Macedonia & Evans, 1993; Digweed et al. 2005).

The kin selection hypothesis was not supported for alarms given for felids or raptors but found mixed support for those given in response to vipers (table 6). Immigrant males, unlikely to have kin in the group, consistently alarmed in response to felids and were among the few individuals who called in during raptor detections. In contrast, total *r* was a nearly significant predictor of whether or not males called in response to the viper models. The lack of significance in this case may be due to the small number of males who were tested (N=14). In addition, the lack of data on paternity may obscure paternal kinship effects (but see Perry et al. 2008). Support for the kin selection hypothesis for alarm calling has been primarily limited to rodent taxa (see table 1) with only weak support among primates (Tenaza & Tilson 1977; Chapman et al. 1990).

Parental care also received some support for alarms given in response to vipers (table 6). In this case, there is a positive trend (albeit nonsignificant) for females with more offspring to be more likely to call in response to a viper than those females with fewer offspring. Again, the lack of significance in the regression model may be a result of a small sample size (N=14). This adds to the taxonomically widespread support for this hypothesis (see table 1).

The mate protection hypothesis was not supported for alarms given in any context (table 6). In fact, among the viper detections by males, there was a nonsignificant trend for potential sires were to be less likely to alarm. This trend is likely due to the fact that, among males, only juveniles are not potential sires, and juvenile males are more likely than adult males to have kin in the group. While considerable support for this hypothesis has been found in several avian taxa (see table 1), there is only weak evidence suggesting that such selective pressures act on mammalian prey (Cheney & Seyfarth 1985).

The selfish herd hypothesis was not supported (table 6) because individuals who called upon detecting the ocelot model did not achieve a higher neighbor density than in non-experimental contexts. A lack of support for this hypothesis is not surprising given that the short distances in which the capuchins tend to detect predators (Janson 2007) provide a small amount of time to employ a proper anti-predator defense. The constraints of an arboreal environment make it unlikely that a caller could attract enough individuals quickly enough to protect itself from an immediate attack (see Terborgh 1990). Indeed, the only support for a selfish herd benefit for alarm calling has been found among avian taxa in an open environment (Owens & Goss-Custard 1976). Not only are such taxa more likely to detect predators from long distances, but they can also become a cohesive group much more quickly than can arboreal primates.

The predator confusion hypothesis was not supported for alarms given in response to ocelots or perched eagles (table 6) because alarm calls did not cause a response in conspecifics that would be predicted to confuse the predator. Support for this hypothesis has been found in studies of redshanks (*Tringa totanus*; Cresswell 1994) and Belding's ground squirrels (*Spermophilus beldingi*; Sherman 1985). However, there is no evidence indicating that arboreal mammals use the confusion effect to reduce predation risk (Terborgh 1990).

The group maintenance hypothesis was not supported (table 6) because no significant relationship between dominance rank and call production was found for any model type. This hypothesis has found support in only one previous study of vervet monkeys (*Chlorocebus aethiops*; Cheney & Seyfarth 1981, 1985),wherein the loss of a groupmate is likely costly to dominants and beneficial to subordinates. Because such variation in costs and benefits between dominants and subordinates is also expected in capuchins (see Janson 1985, 1990), this may explain why dominant capuchins alarm in response to dangerous stimuli, but it does not explain why subordinates also do so.

Mobbing recruitment was supported for all three stimulus types (table 6). Because alarm callers normally approached and mobbed the models, it is possible that conspecifics were reacting to this non-vocal cue rather than to the call; however, this seems unlikely given that forest density greatly limits the effectiveness of non-vocal communication. This is supported by the fact that playbacks of alarm calls often caused others to approach the speaker (Wheeler, in prep.). Mobbing behaviour is well-documented in capuchin monkeys (*C. apella*: van Schaik & van Noordwijk, 1989; *C. capucinus*: Chapman 1986; Boinski 1988; Perry et al. 2003) and it has been suggested that their alarms may recruit conspecifics to mob (Digweed et al. 2005). Such behaviour by conspecifics may be beneficial if it deters the predator and/or if it allows immatures to learn to identify dangerous stimuli (Curio 1978; Srivastava 1991). The latter may increase the caller's inclusive fitness but can also directly benefit the caller if the younger individual later recognizes a predator and alarms, thereby warning the original caller (Curio 1978).

The pursuit deterrence hypothesis was supported for calls given to felids (table 6). The lack of an audience effect in this context indicates that alarm calls may serve to communicate to the predator itself in addition to conspecifics (i.e. to recruit mobbers). Since most forest-dwelling felids depend largely on surprise in order to ambush their prey (see Terborgh 1990; Treves and Palmqvist 2007), capuchin monkeys should benefit by communicating to such a predator that it has been detected. This hypothesis is further supported by two additional lines of evidence. First, nearly all detections of ocelots resulted in alarm calls, indicating that nearly all detectors likely benefit by calling. This may in fact obscure other benefits for the caller, including the decreased predation risk for mates and/or kin. Second, capuchin monkeys more often respond to playbacks of terrestrial predator-associated alarms by approaching the speaker than by fleeing to safety

(Wheeler in prep.). The latter behaviour suggests that an individual likely benefits by locating the potential predator even if it must move closer to do so. Previous studies have indicated mixed support for the pursuit deterrence hypothesis. Support has been found in a study of six sympatric Old World monkeys, wherein more alarm calls were given in response to the vocalizations of ambush predators than to those that pursue their prey (Zuberbühler et al. 1999). Likewise, several studies of birds and ungulates have demonstrated a lack of a conspecific audience effect for the production of anti-predator signals (Woodland et al. 1980; Reby et al. 1999; Haftorn 2000; Murphy 2006; see also Ostreiher 2003). The strongest evidence favoring this hypothesis comes from studies showing that ambush predators give up their hunt when prey produce anti-predator signals (e.g. Clark 2005; Zuberbühler et al. 1999) . In contrast, the hypothesis is not supported by a number of studies among primates and birds which demonstrate a conspecific audience effect for alarm calling (Sullivan 1985; Karakashian et al. 1988; Cheney & Seyfarth 1990; Wich & Sterck 2003; Krams et al. 2006). Such findings indicate that the lack of an audience effect in the current study is unlikely due to cognitive constraints.

Future directions

In sum, the mobbing recruitment hypothesis for alarm calling is supported for calls given to each of felids, vipers, and raptors, while the kin selection, parental care and pursuit deterrence hypotheses receive more limited support. Future studies of alarm call function in capuchin monkeys should examine calls given in response to flying raptors. Several studies have indicated that alarm calling behaviour in response to flying raptors differs considerably from that which occurs in response to perched raptors (e.g. Marler 1955; Macedonia & Evans 1993). The behaviour of predators should be examined to determine whether or not alarm calling affects their hunting behaviour. Finally, possible within-species variation in alarm call function based on habitat type (e.g. open vs. closed) should be examined to determine if predator detection distances affect alarm calling behaviour.

ACKNOWLEDGEMENTS

I wish to thank A. Koenig and C. Janson for the many hours of input they offered throughout this project. D. Blumstein, S. Boinski, T. Caro, M. Di Bitetti , J. Fleagle, B. Hirsch, and two anonymous reviewers also offered many helpful comments on previous versions of this manuscript. I thank the Argentine Administration of National Parks and the Delegación Tecnica for permission to live and work in the park. This project benefited from the assistance of many individuals in the field, especially E. Acevedo, M. Bischoff , P. Cooper , C. Janson, C. Scarry , F. Silva, B. Tiddi , and M.E. Vidal. C. Janson and J. Warwick kindly provided permission to use photographs of the live predators in figure 1. Funding was provided by the American Society of Primatologists, the Wenner-Gren Foundation (Grant #7244), the National Science Foundation (DDIG # 0550971 and BCS-0515007 to C. Janson), and the National Geographic Society Committee on Research and Exploration (grant to C. Janson).

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Table 1. Proposed hypotheses, associated predictions, and taxa in which they have been previously supported.

Hypothesis[a]	Prediction(s)[b]	Previous support in[c]:
Kin selection	Individuals with higher total *r* are more likely to call	rodents[1]
Parental care	Individuals with more offspring are more likely to call	primates[2], rodents[3], birds[4]
Mate protection	Mating males more likely to call than others	birds[5]
Selfish herd[d]	Neighbor density for caller is higher after an alarm call	birds[6]
Predator confusion[d]	Alarms cause a sudden burst of movement and/or vocalizations by conspecifics	rodents[7], birds[8]
Group maintenance	Dominants more likely to call than subordinates	primates[9]
Mobbing recruitment	Conspecifics more likely to mob predator following an alarm	birds[910,]
Pursuit deterrence[d]	No conspecific audience effect for calling	primates[11], rodents[12], birds[13]

a. Sources for each hypothesis are listed in the text.

b. Additional predictions may be applicable. Only those tested in this study are listed.

c. Not an exhaustive list of hypothesis support. See Caro (2005) for extensive review.

d. Hypotheses which assume a strict predator-prey relationship and are therefore not applicable to detections of vipers in the present study.

1. Sherman 1977; Smith 1978; Schwagmeyer 1980; Hoogland 1983, 1996; 2. Cheney & Seyfarth 1985; 3. Shields 1980; Blumstein et al. 1997; 4. Griesser & Eckman 2004; 5.Witkin & Ficken,1979; Gyger et al. 1986; Taylor et al. 1990; Hogstad 1995; 6. Owens & Goss-Custard 1976; 7. Sherman 1985; 8. Cresswell 1994; 9. Cheney & Seyfarth 1985; 10. Rohwer et al. 1976; 11. Zuberbühler et al. 1999; 12. Shelley & Blumstein 2005; Clark, 2005; 13. Woodland et al. 1980; Clark 2005; Murphy 2006.

Table 2. Sample sizes by age and sex for each of the four experiment types.

	solitary (felid)	ocelot	viper	raptor
juvenile males	3	5	10	3
adult males	1	7	4	4
juvenile females	2	9	8	6
adult females	2	4	6	9

Table 3. Results of univariate binary logistic regression analyses for detections of ocelot models

predictor variable	β	p	N
whole group			
maternal *r*	0.20	0.85	25
dominance rank	-0.08	0.44	16
sire potential	-0.29	0.83	25
sex*maternal *r*	112.18	0.99	25
sex*rank	0.48	0.40	16
sex*sire potential	19.47	0.99	25
females			
# of offspring	17.70	0.99	13

Table 4. Results of univariate binary logistic regression analyses for detections of viper models

predictor variable	β	p	N
whole group			
maternal *r*	0.43	0.50	28
dominance rank	0.07	0.32	22
sire potential	1.10	0.37	28
sex*maternal *r*	3.21	0.03	28
sex*rank	0.13	0.09	22
sex*sire potential	2.34	0.02	28
females			
# of offspring	0.98	0.10	14
maternal *r*	-1.95	0.85	14
males			
maternal *r*	3.40	0.06	14
sire potential	2.49	0.08	14

683 Table 5. Results of univariate binary logistic regression analyses for detections of raptor models.

predictor variable	β	p	N
whole group			
maternal *r*	1.66	0.12	22
dominance rank	-0.01	0.90	16
sire potential	0.15	0.91	22
sex*maternal *r*	-69.94	0.99	22
sex*rank	-0.14	0.51	16
sex*sire potential	-20.17	0.99	22
females			
# of offspring	0.07	0.87	15

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Table 6. Summary of hypothesis support for each stimulus type.

	felids	vipers	perched raptors
Kin selection	-*	+	-
Parental care	-*	+	-
Mate protection	-*	-	-
Selfish herd	-	n/a	U
Predator confusion	-	n/a	-
Group maintenance	-*	-	-
Mobbing recruitment	+	+	+
Pursuit deterrence	+	n/a	-

+ = hypothesis supported

- = hypothesis not supported

* = hypothesis not supported but effects may be obscured by communication to predator

n/a = hypothesis not applicable for vipers

U = not tested, but unlikely to be supported

Figure legends

Figure 1. Photographs of predator models (top) and the live animals (bottom): A. *Leopardus pardalis*. B. *Bothrops neuwiedi*. C. *Spizaetus ornatus*. Photograph of live ocelot copyright James Warwick. Photographs of live snake and raptor courtesy Charles Janson.

Figure 2. Percent of detectors alarm calling in relation to model type. The first column represents the percent of solitary individuals who called to felid models.

Figure 3. Boxplots representing the number of offspring present in the group for females who did and did not call upon detecting a model viper. Boxplots show median (dark line), 1st and 3rd quartiles (box), range (whiskers), and extreme values (open circles).

Figure 4. Maternal relatedness values for males and females and responses when detecting a model viper. Note that total maternal *r* values do not include an individual's offspring. Boxplots as in fig. 3.

Figure 1

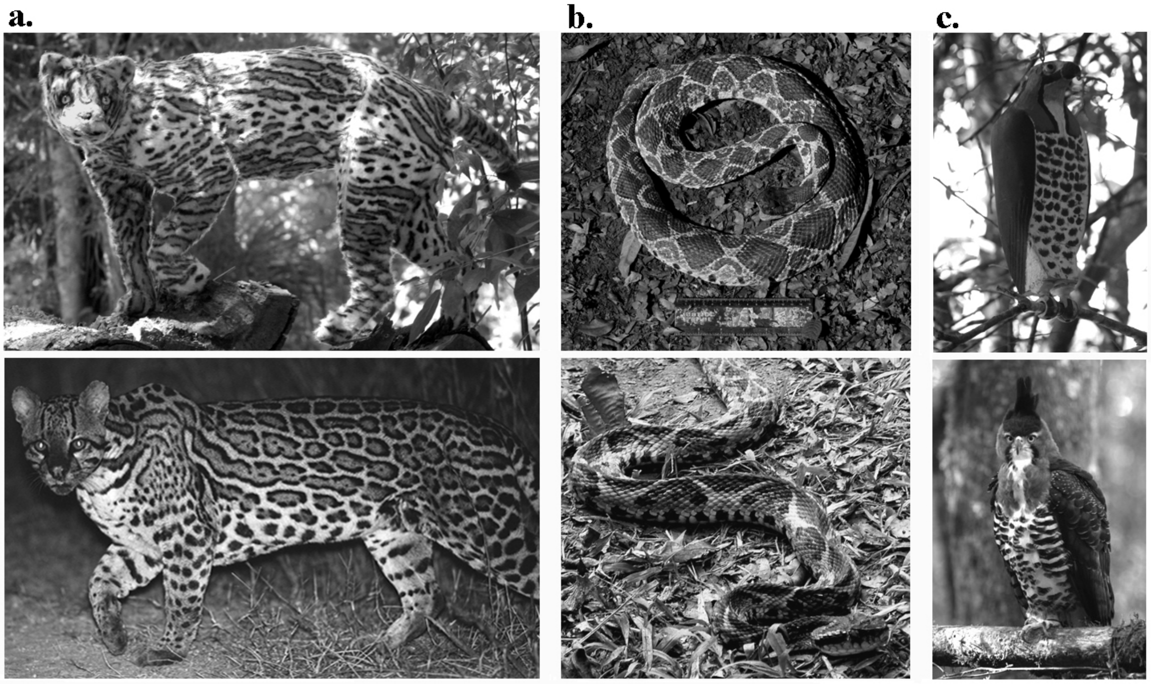

Figure 2

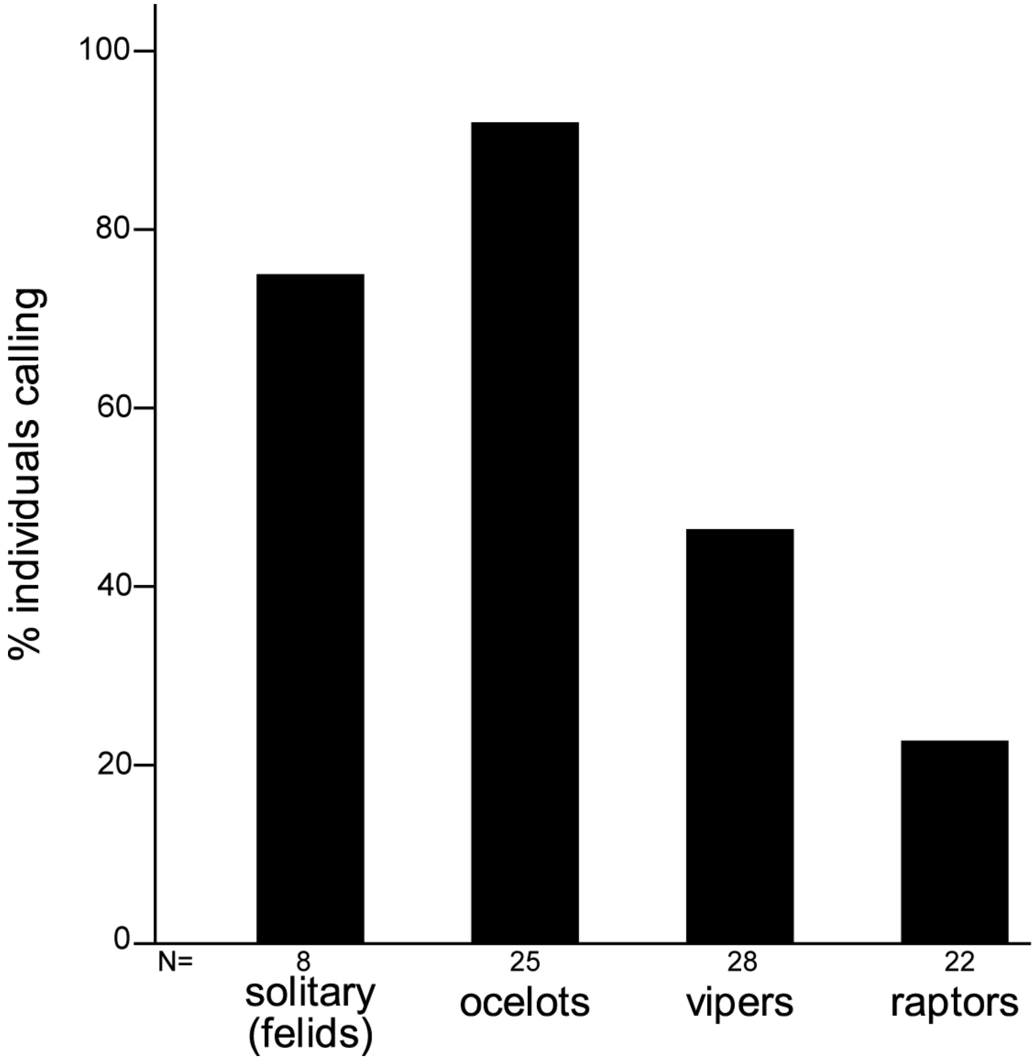
% individuals calling
100
80
60
40
20
0
N=
8
25
28
22
solitary (felids)
ocelots
vipers
raptors

Figure 3

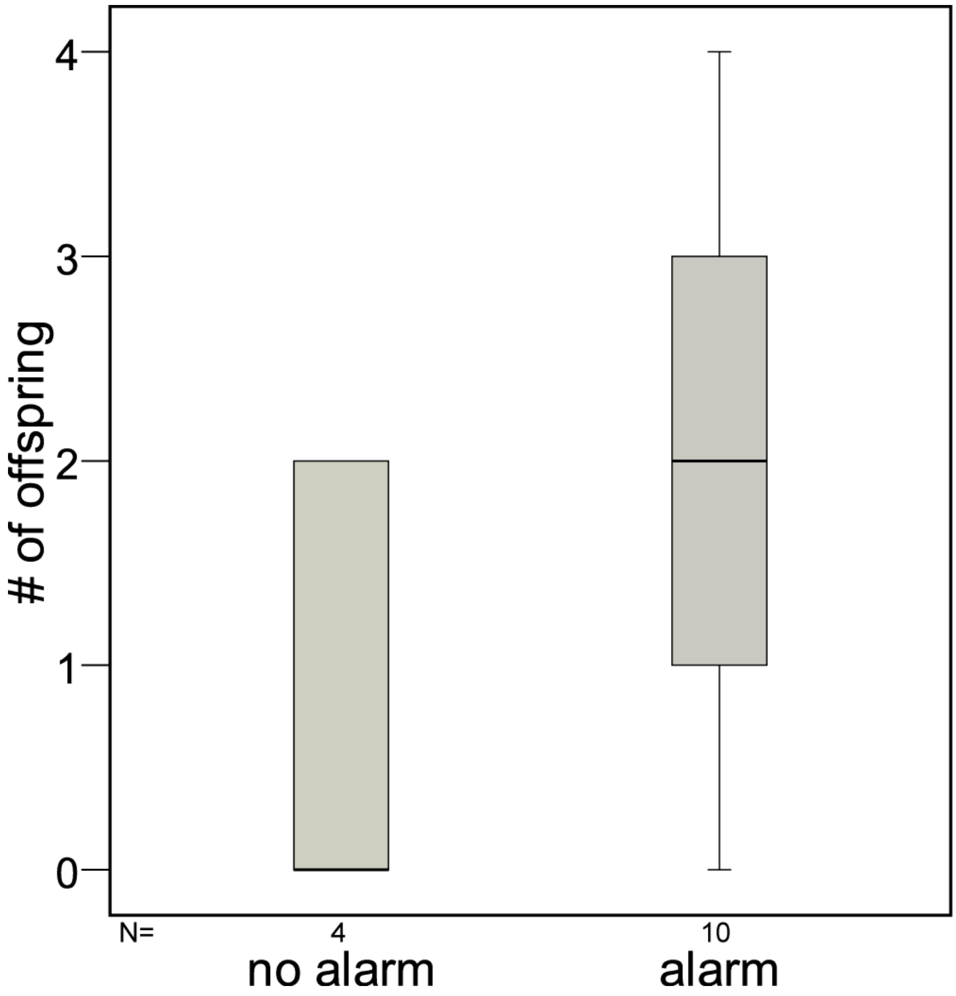

Figure 4