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2 **Selfish or Altruistic? An Analysis of Alarm Call Function in**

3 **Wild Capuchin Monkeys (*Cebus apella nigritus*)**

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5 Running Headline: Wheeler Alarm call function in tufted capuchin monkeys

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24   **ABSTRACT**

25

26   Alarm calls facilitate some anti-predatory benefits of group-living but may endanger the caller by

27   attracting the predator's attention. A number of hypotheses invoking kin selection and individual

28   selection have been proposed to explain how such behaviour could evolve. This study tests eight

29   hypotheses for alarm call evolution by examining the responses of tufted capuchin monkeys

30   (*Cebus apella nigritus*) to models of felids, perched raptors, and vipers. Specifically, this study

31   examines: 1) differences among individuals in their propensity to call in response to different

32   threat types, 2) whether or not there is an audience effect for alarm calling, and 3) the response of

33   conspecifics to alarms. Results indicate that the benefits likely afforded to the caller vary with

34   stimulus type. Alarm calling in response to felids is most likely selfish, with calls apparently

35   directed towards both the predator and potential conspecific mobbers. Alarm calling in response

36   to vipers attracts additional mobbers as well, but also appears to be driven by kin selection in the

37   case of males and parental care benefits in the case of females. Alarm responses to perched

38   raptors are rare, but seem to be selfish with callers benefiting by recruiting additional mobbers.

39

40   **Keywords:** anti-predatory behaviour, predator model experiments, mobbing, audience effect,

41   tufted capuchin, *Cebus apella*

42

43   Alarm calls are ubiquitous among birds and mammals and facilitate proposed anti-predatory

44   benefits of group-living including the many-eyes effect (Lima 1995) and cooperative defense

45   (Curio 1978). However, the benefits afforded to the caller need to be explained because

46   vocalizing in the presence of a predator may attract the predator's attention (e.g. Ivins & Smith,

47   1983). Several hypotheses invoking kin selection (Maynard Smith 1965) and individual selection

48   (*e.g.* Charnov & Krebs 1975) have been developed to explain how this apparently costly

49   behaviour can evolve (see Klump & Shalter, 1984; Hauser, 1996, Caro 2005 for reviews). Many

50   tests of these hypotheses have been conducted in avian and rodent taxa (e.g. Sherman 1985;

51   Smith 1978; Hoogland 1996; Davis 1984; Taylor et al. 1990; Neudorf & Sealy 2002; Shelly &

52   Blumstein 2005) but only two studies have appropriately tested some of these hypotheses among

53   primates (Cheney & Seyfarth 1981, 1985; Zuberbühler et al. 1999). Furthermore, few studies

54   have differentiated between alarms given to different predator types, although this has been

55   shown to affect the selective pressures that act on alarm calling (Sherman 1985; Zuberbühler et

56   al. 1999). This study tests predictions associated with eight hypotheses (see table 1) for the

57   evolution of alarm calls in tufted capuchin monkeys (*Cebus apella nigritus*) in Iguazú National

58   Park, Argentina by examining their reactions to models of felids, raptors, and venomous snakes.

59

60   The earliest hypothesis developed to explain the evolution of alarm calls was based on

61   kin selection; alarm calling may be selected for if calling decreases the predation risk of relatives

62   of the caller and thereby increases the caller's indirect fitness (Maynard Smith 1965). Several

63   additional hypotheses explain how alarm calling can evolve through individual selection. First,

64   similar to the kin selection hypothesis, alarm callers may benefit by alerting offspring to the

65   predator's presence ("parental care": Williams 1966). Whether costly parental behaviour should

66   be considered kin selection or individual selection is a matter of contention (c.f. Dawkins 1976;

67   Bertram 1982), but these are here tested separately. Second, an alarm may decrease predation risk

68   for potential mates ("mate protection": Witken & Ficken 1979). Under a polygamous mating

69   system, this hypothesis predicts that adult males will call more often than will females or non-

70   mating males (Hauser 1996). Third, an alarm caller may benefit via a "selfish herd" effect

71   (Hamilton 1971) if group-mates coalesce around the caller. Fourth, it may be beneficial for an

72   individual to call if protecting group members increases the caller's direct fitness ("group

73   maintenance": Smith 1986), for example through the dilution effect (Bertram 1978; but see

74   Zuberbühler & Byrne, 2006) or as the result of between group feeding competition (Wrangham,

75   1980). Under this scenario, dominant individuals should be more likely to call than subordinates

76   if the former receive more benefits and face fewer costs with increasing group size than do the

77   latter (Alatalo & Helle 1990; see also Cheney & Seyfarth 1985). Fifth, an alarm call may

78   manipulate the behaviour of conspecifics in a way that confuses the predator and allows the caller

79   a chance to escape ("predator confusion"; Charnov & Krebs 1975). Sixth, alarm calls may elicit

80   mobbing of the predator by conspecifics ("mobbing recruitment"; see Curio 1978). Finally, an

81   alarm call may cause "ambush" predators to give up their hunt ("pursuit deterrence"; Woodland

82   *et al*. 1980). Of these eight hypotheses only the latter predicts a lack of a conspecific audience

83   effect; the presence of conspecifics is necessary for the caller to benefit under all other scenarios

84   (Gyger 1990).

85

86   The parental care and pursuit deterrence hypotheses have thus far found the most

87   widespread support. Evidence in favor of these hypotheses has been found in each of birds,

88   rodents, and primates, while other hypotheses have found support only within one of the three

89   taxa (see table 1; see also Caro 2005 for more complete review). However, a lack of support for

90   other hypotheses may be due to the fact that most previous studies did not test all possible

91   hypotheses (e.g. Zuberbühler et al. 1999).

92

93   This study tests the predictions of the eight hypotheses listed in table 1. Because the

94   selective pressures acting on alarm calls have been shown to vary with predator type (*e.g.*

95   Sherman, 1985), every hypothesis is evaluated separately for detections of each of the model

96   types used in this study: felids, vipers, and raptors. However, the selfish herd, predator confusion,

97   and pursuit deterrence hypotheses are not considered for vipers since these hypotheses assume a

98   strict predator-prey relationship; venomous snakes are not known to prey on capuchins although

99   they do pose a mortal threat to individuals that approach too closely (see Methods).

100

101   **METHODS**

102

103   Study Site and Subjects

104   The study was conducted from August - September 2003, July – September, 2004, and May

105   2005- December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W). The site is part of

106   the South American Atlantic Forest and is characterized by humid, semi-deciduous, sub-tropical

107   forest (Crespo 1982). The study area has been logged in the past and is in various stages of

108   secondary growth (see Di Bitetti et al. 2000 for further description of the study site).

109

110   Tufted capuchins are small (2.5-3.6 kg; Smith & Jungers 1997), diurnal primates that

111   feed primarily on fruits but spend a large proportion of time searching for insect prey by

112   specialized destructive foraging (Terborgh 1983; Brown & Zunino 1990). The species is highly

113   arboreal, inhabiting primarily the mid to lower canopy and the understory (Fleagle & Mittermier

114   1980). Approximately 3% of their active time is spent on the ground, although this varies

115   considerably by season (Wheeler unpublished data). Groups are multimale-multifemale, typically

116   consist of 7-30 individuals (Di Bitetti 2001b), and are characterized by female philopatry and

117   male dispersal (Di Bitetti 1997). Dominance hierarchies are linear and dominant individuals

118   benefit from contests over food and spatial position (Janson 1985; Di Bitetti & Janson 2001). In

119   addition, although the dominant male likely sires the majority of offspring (Escobar-Páramo

120   1999), subdominant adult males obtain some matings (Janson 1994). All adult males but one were

121   observed mating during the course of the current study, while only one copulation involving a

122   natal (juvenile) male was observed. In addition, because all observed male takeovers at the study

123   site have been the result of subdominant males within the group rising in rank (Janson,

124   unpublished data), all adult males have the potential to sire offspring.

125

126   The species produces at least three distinct calls in association with predator encounters

127   (Wheeler in prep.). Two of these, the "hiccup" and "peep", are given in response to both felids

128   and vipers and are often produced together during a single predator encounter. The "hiccup" is

129   also given in non-predatory contexts (including aggressive interactions and when foraging in a

130   precarious position; Di Bitetti 2001a, Wheeler in prep.), has been shown to be an indicator of

131   stress (Boinski et al. 1999), and may be best classified as a general "disturbance call" (Emmons et

132   al. 1997). The third call, the "bark", is a functionally referential aerial predator alarm given only

133   in response to flying stimuli or large perched birds (Wheeler in prep.). A similar alarm call

134   system has been described for white-faced capuchins (*C. capucinus*; Digweed et al. 2005).

135

136   Among the predators of capuchin monkeys at the site are three species of felids (jaguars,

137   *Panthera onca*; pumas, *Felis concolor*; and ocelots, *Leopardus pardalis*), tayras (*Eira barbara*),

138   and two species of raptors (hawk-eagles: *Spizaetus ornatus* and *S. tyrannus*; see Hirsch 2002; Di

139   Bitetti et al. 2006 for further descriptions of predators at the study site). In approximately 400

140   weeks of observation, one predation attempt by a felid has been recorded (Di Bitetti 2001a);

141   although several additional monkey-felid encounters have been observed, it is unclear if any of

142   these were actual predation attempts. There have been two observed predation attempts by raptors

143   at the study site, one of which was successful (Di Bitetti 2001a). Capuchins in Iguazú also face

144   threats from three species of vipers (*Bothrops neuwiedii, B. jararaca,* and *Crotalus durissus*;

145   Martinez et al. 1992). While these snakes are not known to be capuchin predators, their presence

146   nevertheless evokes a strong reaction in the capuchins, likely because of the mortal threat they

147   pose to individuals who approach too closely.

148

149   Data were collected on three separate groups ("Macuco": 23-45 individuals; "Gundolf":

150   15 individuals; "Guenon": 9 individuals). The two latter groups split off from the former during

151   the initial period of data collection to form new groups. For the majority of the study period, the

152   Macuco group consisted of 23-28 individuals, with variation due to births. Maternal relationships

153   for all individuals are known and all individuals were recognizable based on facial characteristics.

154

155   <u>Observational and Experimental Protocols</u>

156   Data were collected using models of ocelots, vipers, and hawk-eagles (see fig. 1) and playbacks

157   of puma vocalizations. Models were placed in front of the group while they were traveling or

158   foraging. One observer went ahead of the group to place the model while one or more observers

159   remained with the group to ensure that they did not approach too closely before the model was

160   placed. Ocelot and snake models were placed at least 50m ahead and raptor models were placed

161   150m in front of the group. In all cases, the distance chosen was sufficient to prevent the study

162   subjects from cueing in on the model placement. Viper models were always placed on the ground

163   while ocelot models were placed on the ground or in trees at a height of 2 to 5m. Raptor models

164   were suspended from tree branches at a height of 4 to 12m by a rope thrown over the branch. In

165   most cases, the model remained stationary for the duration of the experiment. For a few

166   experiments, snake (N=7) and ocelot (N=5) models were moved a short distance (less than 15cm)

167   once every two minutes until a detection occurred. Although this movement sometimes caused

168   individuals to detect the models when they otherwise would not have, there was no discernable

169   difference in the way that they reacted to moving models relative to stationary ones. To avoid

170   habituation, a given model type (e.g. felid, snake, raptor) was not used for seven days following a

171   detection, while a specific model was not used for at least fifteen days; in most cases each model

172   was used only once with each group in a thirty day period. Three exemplars of each of model

173   type were used. The capuchins did not appear to habituate to the models, given that responses to

174   the models remained consistent throughout the study period.

175

176   Continuous focal sampling (Martin & Bateson 2007) was used simultaneously by three

177   observers to record whether or not individuals gave an alarm upon detecting a model. A detection

178   was defined as an instance in which a focal animal suddenly ceased the behaviour in which it was

179   engaged and began to stare attentively at the model. Individuals that approached to within 15m of

180 the model were chosen as focal animals. A distance of 15m was chosen because detections of

181 models are very unlikely from greater distances, even when visibility is relatively high (Janson

182 2007). Focal animals were followed until detecting or moving farther than 15m from the model.

183

184 Upon the detection, the focal animal's vocal behaviour (or lack thereof) was noted, as

185 was whether or not the detector performed any other conspicuous anti-predator behaviours (e.g.

186 flee or display). If an alarm call was given by the detector, all-occurrence sampling (Martin &

187 Bateson 2007) was used to note if, immediately following the call, conspecifics reacted with: 1) a

188 sudden burst of movement and/or vocalizations or ("pandemonium"; Sherman 1977), 2) mobbing

189 of the predator model (i.e. aggressive displays towards the model). In addition, a scan sample

190 (Martin & Bateson 2007) was conducted 30 seconds after the first alarm to record neighbor

191 density (the number of conspecifics within 3m) for all individuals in the group, including the

192 caller. These experimental scan samples were compared to scans conducted in non-experimental

193 contexts at 30 minute intervals throughout the day. Only non-experimental scans which were

194 taken when the group was traveling or foraging were included in the analysis since experiments

195 were always conducted in this behavioural context.

196

197 Experiments were also conducted with individuals who had become separated from the

198 group (hereafter "solitary") to test for audience effects on alarm calling. An individual was

199 considered solitary if there were no conspecifics within 150m for at least 15 minutes. In most

200 cases, the animal had been separated from conspecifics for at least several hours. These

201 experiments used either an ocelot model or a playback of a puma vocalization and followed a

202 protocol similar to that described for non-solitary individuals. Puma calls were deemed

203 appropriate to use for solitary but not non-solitary individuals; non-solitary individuals may

204 withhold alarms since all prey individuals simultaneously become aware of the predator's

205 presence (see Arnold et al. 2008). Playbacks conducted with non-solitary individuals confirm that

206   capuchins do typically call in response to this stimulus (Wheeler unpublished data). The calls

207   used for playbacks were recorded at the study site during an encounter with a vocalizing puma.

208   Recordings were made with a Marantz PMD-660 recorder and a Sennheiser ME67/K6

209   microphone at a sampling rate of 44.1 kHz. Recordings were played from a Saul Mineroff AFS

210   speaker connected to a portable CD player at an intensity of 80-90 dB (measured by a Radio

211   Shack 33-2055 digital sound level meter placed 1 meter from the speaker). The speaker was

212   placed in dense vegetation at a height of 1m. Each playback consisted of a single vocalization

213   played four times at 5 second intervals and began when the solitary individual approached to

214   within 25m of the speaker. The individual was scored as alarm calling if it produced an alarm at

215   any point from the initiation of the playback until 40 seconds after the last call was played.

216

217   All dyadic agonistic interactions (including aggression, submission, and spatial

218   displacements) were noted *ad libitum*, entered into a dominance matrix, and analyzed using

219   MatMan™ (Vers. 1.1.4; De Vries *et al*. 1993). Because the hierarchy of the Macuco group was

220   significantly linear, the ordering procedure within MatMan immediately provides an ordinal

221   dominance rank for each individual with the "inconsistencies and strength of inconsistencies"

222   (I&SI) method (De Vries 1998). A sufficient number of interactions were recorded only for the

223   Macuco group; the "group maintenance" hypothesis was therefore tested using only data from

224   this group.

225

226   All methods conformed to the guidelines for use of animals in research outlined by the

227   ABS. The study was conducted with the permission of the Argentine Administration of National

228   Parks and IACUC Stony Brook University (ID numbers 2003-1218, 2004-1218, 2005-1448, and

229   2006-1448).

230

231   Data selection and statistical methods

232   An individual's response was included in the analysis only if it was the first detector during that

233   particular experiment or if previous detectors did not call or perform any other conspicuous anti-

234   predator behaviours which would allow subsequent detectors to cue in on the model's presence. It

235   is thus unlikely that any individual's reaction was confounded by the behaviours of previous

236   detectors. For individuals whose detections met these criteria on more than one occasion, the first

237   such detection of a particular model type was selected for inclusion in the analysis. To ensure that

238   all data points were independent, only a single detection from each experiment was used. Only

239   detections by juveniles and adults were included in the analysis because, although juveniles

240   readily recognize predators as dangerous, infants do not appear to have yet fully developed this

241   recognition (Wheeler in prep.). The number of individuals of different age and sex categories

242   which were included in the analysis is shown in table 2.

243

244   Binary logistic regressions were used to determine if total maternal r, number of

245   offspring, dominance rank, or "sire potential" predicts whether or not an individual produced a

246   vocalization upon detecting a particular model type. "Total r" was calculated for each detector by

247   summing the coefficient of relatedness (Wright 1922) between the detector and all other

248   individuals present at the time of detection. An individual was considered present if it had been

249   seen in the group during the day of the experiment unless it was otherwise known to be absent

250   from the group during the experiment; misclassification of an individual as present was unlikely

251   given the rarity in which individuals separated from the group. Because paternity for many

252   individuals is unknown, r values were based solely on maternal relationships (e.g. mother-

253   offspring dyads = 0.50, maternal siblings = 0.25, aunt-nephew dyads = 0.13, etc.). Offspring (of

254   any age) were excluded when calculating an individual's total maternal r since this study

255   examines the kin selection and parental care hypotheses separately. Due to the lack of paternity

256   data, only females were included in tests of the parental care hypothesis. The sire potential

257   variable divided individuals into two categories, adult males vs. all other individuals (i.e. adult

258   females plus all juveniles). Logistic regressions were performed by examining each independent

259   variable both alone and in a multivariate analysis including several independent variables

260   simultaneously. In addition, because different selective pressures may act on male and female

261   alarm calling (e.g. Alatalo & Helle 1990), the interaction between sex and each predictor variable

262   was examined in a univariate logistic regression. If the interaction variable was found to be

263   significant, that variable was tested separately for males and females. Two multivariate logistic

264   regressions were run for each predator model type. The first of these was based on all detections

265   (i.e. by both males and females) and included the following predictor variables: total maternal r,

266   dominance rank, sire potential, and the interaction between sex and each of these three

267   independent variables. The second was based on detections by females only and included total

268   maternal r, dominance rank, and number of offspring as predictor variables. Males were not

269   included in this model because paternity is unknown in many cases.

270

271   Binomial tests were used to test whether mobbing of the model by conspecifics or

272   "pandemonium" followed the production of alarm calls more often than expected. An expected

273   value of 37.5% was chosen because this is the frequency in which conspecifics mobbed the

274   models when no alarm call had been given by a previous detector (12 of 32 cases). Although this

275   does not reflect the expected baseline values of "pandemonium" behaviour, a value of 37.5% is

276   conservative since such behaviours were rare. To determine if the sex of the caller predicted the

277   reactions of conspecifics, a binary logistic regression was used. A Wilcoxon signed ranks test was

278   used to determine whether or not individuals achieved a higher neighbor density subsequent to

279   producing an alarm than those same individuals had in non-experimental contexts. To determine

280   if overall group cohesion was greater in experimental than non-experimental contexts, the mean

281   number of neighbors within 3m for all individuals was calculated for each scan in both contexts,

282   was square root transformed, and compared using a one-tailed t-test. Finally, a Fisher's exact test

283   was used to test for differences between solitary and non-solitary individuals in the probability of

284   calling following a felid detection. Significance levels were set at $p<0.05$ for all tests; a result was

285   considered to show a trend in the predicted direction if $p<0.10$. Regressions, signed ranks tests,

286   and t-tests were conducted using SPSS 15.0 (SPSS Inc., Chicago, IL, USA). The binomial tests

287   and Fisher's exact test were calculated by hand.

288

289   **RESULTS**

290

291   Felid experiments

292   Twenty-three of the 25 individuals who detected an ocelot model gave an alarm call upon

293   detecting the model (92.0%; fig. 2). The individuals who did not call included a low-ranking

294   juvenile female and an alpha male. Whether or not an individual called upon detecting the ocelot

295   model was not predicted by its total maternal r, number of offspring, dominance rank, or sire

296   potential in the univariate analyses, and no variables showed a significant interaction with sex

297   (see table 3). Likewise, the multivariate logistic regressions were non-significant (whole group:

298    $\chi^2_6=9.28$, N=16, p=0.158; females only: $\chi^2_3=6.03$, N=8, p=0.11). Pandemonium by conspecifics

299   did not occur following any alarms (0 of 20 documented cases), but groupmates mobbed the

300   model following an alarm call significantly more often than expected (15 of 20 documented

301   cases; binomial test: $p<0.001$). The sex of the caller did not predict whether or not conspecifics

302   mobbed the ocelot model (binary logistic regression: $\beta=-0.81$, N=20, p=0.44). Finally, callers did

303   not achieve a greater number of neighbors within three meters in experimental contexts (mean $\pm$

304   SE = 0.67 $\pm$ 0.20 neighbors) than they averaged in non-experimental contexts (mean $\pm$ SE = 0.59

305    $\pm$ 0.04 neighbors; Wilcoxon signed ranks test: N=18; Z=-0.04, p=0. 97). However, when neighbor

306   densities for all group members were averaged, there was a non-significant trend towards an

307   increase in neighbor density in experimental contexts (mean $\pm$ SE = 1.05 $\pm$ 0.16 neighbors)

308   relative to non-experimental contexts (mean $\pm$ SE = 0.72 $\pm$ 0.02 neighbors; one-tailed t-test on

309   square root transformed data: $t_{28}=1.69$, $N_1=28$, $N_2=641$, p=0.10).

310

311   Four experiments with a model ocelot and four using a puma call playback were

312   conducted with solitary individuals. Six of eight (75%) solitary detectors called, including all four

313   detections of the ocelot model and following two of the four playbacks (fig. 2). This probability

314   of calling per detection does not differ significantly from that of non-solitary individuals (Fisher's

315   Exact test: p=0.21). In addition, three of the four detectors mobbed the ocelot model, while both

316   individuals who called in response to the puma call approached the speaker.

317

318   Viper experiments

319   Thirteen of 28 (46.4%) individuals called upon detecting a viper model (fig. 2). Whether or not an

320   individual called in this context was not predicted by its total maternal r, dominance rank, or its

321   sire potential in the univariate analyses (see table 4). Among females, there was a non-significant

322   trend (p=0.10) for the number of offspring to predict the response to viper models (see table 4,

323   fig. 3). In addition, tests of the interaction between sex and each of the independent variables

324   indicated a significant interaction between sex and total maternal r as well as sex and sire

325   potential (see table 4). Further analysis showed that kinship was a nearly significant predictor of

326   whether or not males, but not females, gave an alarm upon detecting a viper model (see table 4,

327   fig. 4). The sire potential variable approached significance in the case of males, although with a

328   trend for non-potential sires to be more likely to alarm (see table 4). The latter variable was not

329   tested for females because all females are assigned to the non-potential sire category. Neither the

330   multivariate logistic regression for the whole group (χ^2_6=7.02, N=22, p=0.32) or for females

331   (χ^2_3=7.14, N=11, p=0.07) was significant; although the latter model approached significance,

332   none of the individual predictor variables was significant. Finally, additional conspecifics

333   approached and mobbed the model in nine of 13 documented cases, significantly more often than

334   expected (binomial test: p=0.02); the sex of the caller did not predict whether or not conspecifics

335   mobbed the model viper (binary logistic regression: β=-0.41, N=13, p=0.77).

336

337   Perched eagle experiments

338   Five of 22 individuals (22.7%) alarm called following the detection of a raptor model (fig. 2).

339   Callers included a subdominant adult male and four mid to low ranking adult and juvenile

340   females. All five individuals who called as well as 7 of 17 (41.2%) non-callers approached and

341   mobbed the predator model. None of the independent variables or the interaction variables were

342   significant in the univariate analyses (see table 5). Likewise, the multivariate analyses were also

343   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).

344   Sudden "pandemonium" did not follow any of the alarms, while additional group members

345   mobbed the model following all five alarm calls, a value significantly greater than expected

346   (binomial test: p=0.01). Insufficient data were collected to test whether or not intragroup spacing

347   decreased following the alarms.

348

349   **DISCUSSION**

350

351   While alarm calls given to each of felids, vipers, and snakes can be explained by the mobbing

352   recruitment hypothesis, no other single hypothesis for the evolution of alarm calling seems to

353   apply to tufted capuchins across all contexts (table 6). However, each of the kin selection,

354   parental care, mobbing recruitment, and pursuit deterrence hypotheses received some support for

355   at least one stimulus type. The selfish herd, group maintenance, conspecific manipulation, and

356   mate protection hypotheses were not supported for any stimulus type. Because of the small

357   percentage of perched hawk-eagle detections which resulted in alarms, it is difficult to determine

358   which hypothesis may best explain the evolution of alarms given in this context although the

359   observed trends allow some hypotheses to be eliminated. While the low observed rate of calls

360   given to perched raptors may be a result of insufficiently realistic models, this seems unlikely

361   given that most detectors mobbed the models. Less intense reactions to perched relative to flying

362   raptors have been noted in several previous studies of prey species (e.g. Marler 1955; Macedonia

363   & Evans, 1993; Digweed et al. 2005).

364

365   The kin selection hypothesis was not supported for alarms given for felids or raptors but

366   found mixed support for those given in response to vipers (table 6). Immigrant males, unlikely to

367   have kin in the group, consistently alarmed in response to felids and were among the few

368   individuals who called in during raptor detections. In contrast, total r was a nearly significant

369   predictor of whether or not males called in response to the viper models. The lack of significance

370   in this case may be due to the small number of males who were tested (N=14). In addition, the

371   lack of data on paternity may obscure paternal kinship effects (but see Perry et al. 2008). Support

372   for the kin selection hypothesis for alarm calling has been primarily limited to rodent taxa (see

373   table 1) with only weak support among primates (Tenaza & Tilson 1977; Chapman et al. 1990).

374

375   Parental care also received some support for alarms given in response to vipers (table 6).

376   In this case, there is a positive trend (albeit nonsignificant) for females with more offspring to be

377   more likely to call in response to a viper than those females with fewer offspring. Again, the lack

378   of significance in the regression model may be a result of a small sample size (N=14). This adds

379   to the taxonomically widespread support for this hypothesis (see table 1).

380

381   The mate protection hypothesis was not supported for alarms given in any context (table

382   6). In fact, among the viper detections by males, there was a nonsignificant trend for potential

383   sires were to be less likely to alarm. This trend is likely due to the fact that, among males, only

384   juveniles are not potential sires, and juvenile males are more likely than adult males to have kin in

385   the group. While considerable support for this hypothesis has been found in several avian taxa

386   (see table 1), there is only weak evidence suggesting that such selective pressures act on

387   mammalian prey (Cheney & Seyfarth 1985).

388

389   The selfish herd hypothesis was not supported (table 6) because individuals who called

390   upon detecting the ocelot model did not achieve a higher neighbor density than in non-

391   experimental contexts. A lack of support for this hypothesis is not surprising given that the short

392   distances in which the capuchins tend to detect predators (Janson 2007) provide a small amount

393   of time to employ a proper anti-predator defense. The constraints of an arboreal environment

394   make it unlikely that a caller could attract enough individuals quickly enough to protect itself

395   from an immediate attack (see Terborgh 1990). Indeed, the only support for a selfish herd benefit

396   for alarm calling has been found among avian taxa in an open environment (Owens & Goss-

397   Custard 1976). Not only are such taxa more likely to detect predators from long distances, but

398   they can also become a cohesive group much more quickly than can arboreal primates.

399

400   The predator confusion hypothesis was not supported for alarms given in response to

401   ocelots or perched eagles (table 6) because alarm calls did not cause a response in conspecifics

402   that would be predicted to confuse the predator. Support for this hypothesis has been found in

403   studies of redshanks (*Tringa totanus*; Cresswell 1994) and Belding's ground squirrels

404   (*Spermophilus beldingi*; Sherman 1985). However, there is no evidence indicating that arboreal

405   mammals use the confusion effect to reduce predation risk (Terborgh 1990).

406

407   The group maintenance hypothesis was not supported (table 6) because no significant

408   relationship between dominance rank and call production was found for any model type. This

409   hypothesis has found support in only one previous study of vervet monkeys (*Chlorocebus*

410   *aethiops*; Cheney & Seyfarth 1981, 1985),wherein the loss of a groupmate is likely costly to

411   dominants and beneficial to subordinates. Because such variation in costs and benefits between

412   dominants and subordinates is also expected in capuchins (see Janson 1985, 1990), this may

413   explain why dominant capuchins alarm in response to dangerous stimuli, but it does not explain

414   why subordinates also do so.

415

416   Mobbing recruitment was supported for all three stimulus types (table 6). Because alarm

417   callers normally approached and mobbed the models, it is possible that conspecifics were reacting

418   to this non-vocal cue rather than to the call; however, this seems unlikely given that forest density

419   greatly limits the effectiveness of non-vocal communication. This is supported by the fact that

420   playbacks of alarm calls often caused others to approach the speaker (Wheeler, in prep.).

421   Mobbing behaviour is well-documented in capuchin monkeys (*C. apella*: van Schaik & van

422   Noordwijk, 1989; *C. capucinus*: Chapman 1986; Boinski 1988; Perry et al. 2003) and it has been

423   suggested that their alarms may recruit conspecifics to mob (Digweed et al. 2005). Such

424   behaviour by conspecifics may be beneficial if it deters the predator and/or if it allows immatures

425   to learn to identify dangerous stimuli (Curio 1978; Srivastava 1991). The latter may increase the

426   caller's inclusive fitness but can also directly benefit the caller if the younger individual later

427   recognizes a predator and alarms, thereby warning the original caller (Curio 1978).

428

429   The pursuit deterrence hypothesis was supported for calls given to felids (table 6). The

430   lack of an audience effect in this context indicates that alarm calls may serve to communicate to

431   the predator itself in addition to conspecifics (i.e. to recruit mobbers). Since most forest-dwelling

432   felids depend largely on surprise in order to ambush their prey (see Terborgh 1990; Treves and

433   Palmqvist 2007), capuchin monkeys should benefit by communicating to such a predator that it

434   has been detected. This hypothesis is further supported by two additional lines of evidence. First,

435   nearly all detections of ocelots resulted in alarm calls, indicating that nearly all detectors likely

436   benefit by calling. This may in fact obscure other benefits for the caller, including the decreased

437   predation risk for mates and/or kin. Second, capuchin monkeys more often respond to playbacks

438   of terrestrial predator-associated alarms by approaching the speaker than by fleeing to safety

439   (Wheeler in prep.). The latter behaviour suggests that an individual likely benefits by locating the

440   potential predator even if it must move closer to do so. Previous studies have indicated mixed

441   support for the pursuit deterrence hypothesis. Support has been found in a study of six sympatric

442   Old World monkeys, wherein more alarm calls were given in response to the vocalizations of

443   ambush predators than to those that pursue their prey (Zuberbühler et al. 1999). Likewise, several

444   studies of birds and ungulates have demonstrated a lack of a conspecific audience effect for the

445   production of anti-predator signals (Woodland et al. 1980; Reby et al. 1999; Haftorn 2000;

446   Murphy 2006; see also Ostreiher 2003). The strongest evidence favoring this hypothesis comes

447   from studies showing that ambush predators give up their hunt when prey produce anti-predator

448   signals (e.g. Clark 2005; Zuberbühler et al. 1999) . In contrast, the hypothesis is not supported by

449   a number of studies among primates and birds which demonstrate a conspecific audience effect

450   for alarm calling (Sullivan 1985; Karakashian et al. 1988; Cheney & Seyfarth 1990; Wich &

451   Sterck 2003; Krams et al. 2006). Such findings indicate that the lack of an audience effect in the

452   current study is unlikely due to cognitive constraints.

453

454   <u>Future directions</u>

455   In sum, the mobbing recruitment hypothesis for alarm calling is supported for calls given to each

456   of felids, vipers, and raptors, while the kin selection, parental care and pursuit deterrence

457   hypotheses receive more limited support. Future studies of alarm call function in capuchin

458   monkeys should examine calls given in response to flying raptors. Several studies have indicated

459   that alarm calling behaviour in response to flying raptors differs considerably from that which

460   occurs in response to perched raptors (e.g. Marler 1955; Macedonia & Evans 1993). The

461   behaviour of predators should be examined to determine whether or not alarm calling affects their

462   hunting behaviour. Finally, possible within-species variation in alarm call function based on

463   habitat type (e.g. open vs. closed) should be examined to determine if predator detection distances

464   affect alarm calling behaviour.

465

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467

479

480 **REFERENCES**

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658

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

660 previously supported.

661

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[9,10,]
Pursuit deterrence[d]	No conspecific audience effect for calling	primates[11], rodents[12], birds[13]

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

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

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

665   d. Hypotheses which assume a strict predator-prey relationship and are therefore not applicable to

666   detections of vipers in the present study.

667   1. Sherman 1977; Smith 1978; Schwagmeyer 1980; Hoogland 1983, 1996; 2. Cheney & Seyfarth

668   1985; 3. Shields 1980; Blumstein et al. 1997; 4. Griesser & Eckman 2004; 5.Witkin &

669   Ficken,1979; Gyger et al. 1986; Taylor et al. 1990; Hogstad 1995; 6. Owens & Goss-Custard

670   1976; 7. Sherman 1985; 8. Cresswell 1994; 9. Cheney & Seyfarth 1985; 10. Rohwer et al. 1976;

671   11. Zuberbühler et al. 1999; 12. Shelley & Blumstein 2005; Clark, 2005; 13. Woodland et al.

672   1980; Clark 2005; Murphy 2006.

673

674   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

675

676

677   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

678

679

680   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

681

682

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

684

685

686   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	-

687   + = hypothesis supported

688   - = hypothesis not supported

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

690   n/a = hypothesis not applicable for vipers

691   U = not tested, but unlikely to be supported

692

693   **Figure legends**

694

695   **Figure 1.** Photographs of predator models (top) and the live animals (bottom): A. *Leopardus*

696   *pardalis*. B. *Bothrops neuwiedi*. C. *Spizaetus ornatus*. Photograph of live ocelot copyright James

697   Warwick. Photographs of live snake and raptor courtesy Charles Janson.

698

699   **Figure 2.** Percent of detectors alarm calling in relation to model type. The first column represents

700   the percent of solitary individuals who called to felid models.

701

702   **Figure 3.** Boxplots representing the number of offspring present in the group for females who did

703   and did not call upon detecting a model viper. Boxplots show median (dark line), 1st and 3rd

704   quartiles (box), range (whiskers), and extreme values (open circles).

705

706   **Figure 4.** Maternal relatedness values for males and females and responses when detecting a

707   model viper. Note that total maternal r values do not include an individual's offspring. Boxplots

708   as in fig. 3.

709

710   **Figure 1**

a.

b.

c.
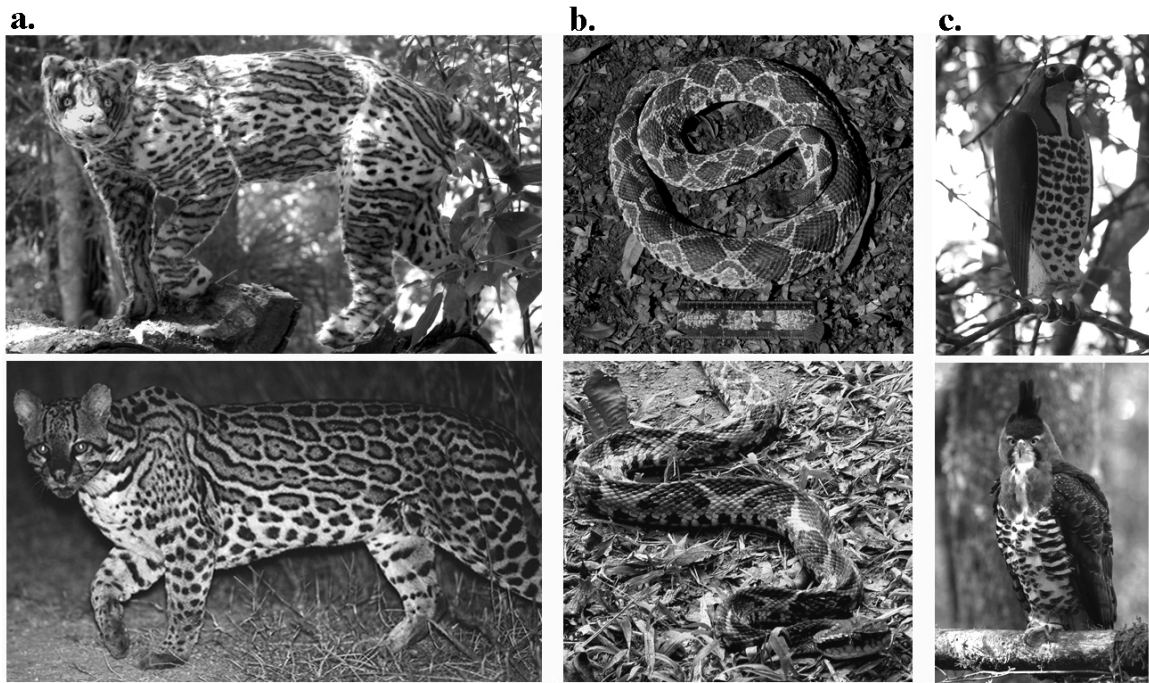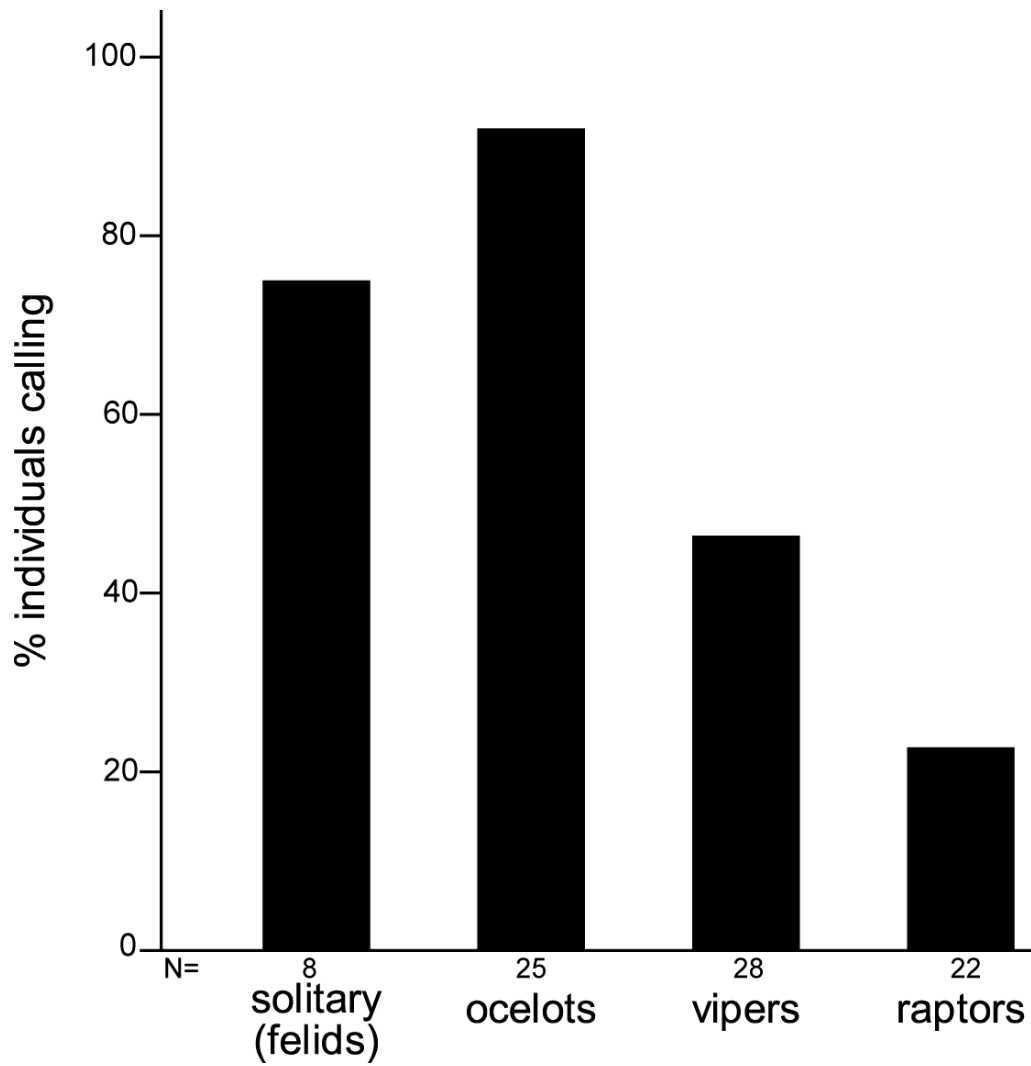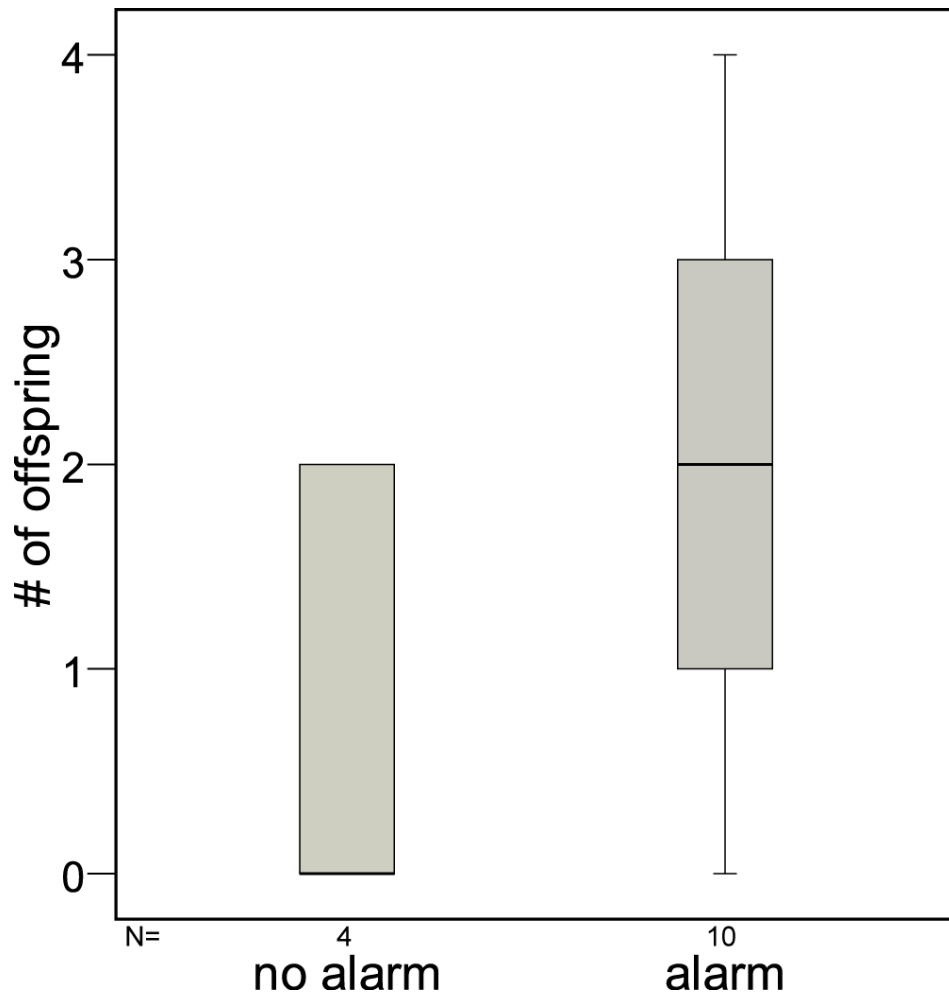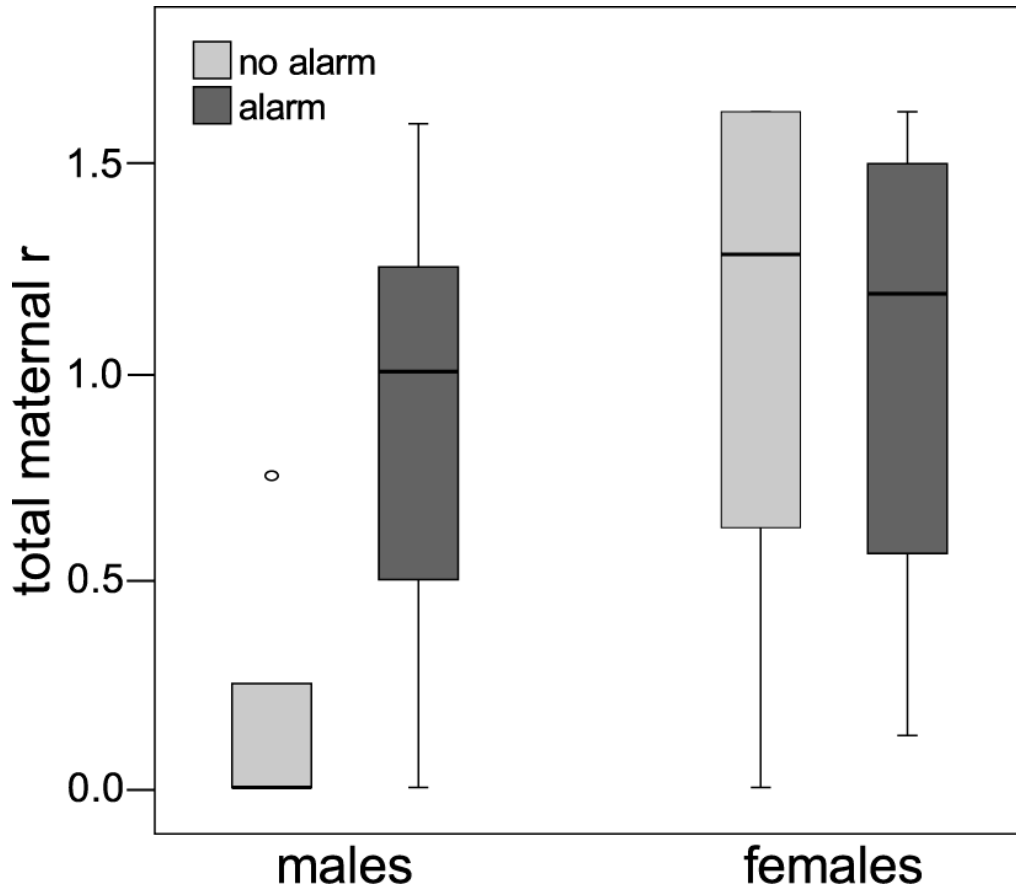

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713   **Figure 2**

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716   **Figure 3**

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719 **Figure 4**

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