

1     **TITLE: Socioecological correlates of social play in adult mantled howler monkeys**

## 2    **ABSTRACT**

3    The study of animal play is highly complex since its potential functions vary with social and  
4    environmental circumstances. Although play is generally characteristic of immature animals, it  
5    may persist in adults in its social form, particularly when interacting with young individuals,  
6    and less often with other adult playmates. We measured the amount of social play in 62 wild  
7    adult howler monkeys belonging to seven different groups in Mexico and Costa Rica. Overall,  
8    adult play represented a small mean proportion of observation time across all groups (0.6% of  
9    1884 hours), but it was present in all study groups. Generalized linear mixed models revealed  
10    that group size correlated with both adult-adult play and adult-immature play, supporting that  
11    more individuals provide more play opportunities. While play between adults decreased with  
12    increases in immature-to-adult ratio, we did not find a clear preference for adults to play with  
13    immatures, emphasising the importance of playing with other adult peers. Conversely, adults  
14    played more with immatures as immature-to-adult ratio increased, which may correspond  
15    with the role adult-immature play may have in the socialization process of young individuals.  
16    More time dedicated to foraging on fruits corresponded with more adult-adult play. This  
17    finding, aside from being associated with more energy being available to engage at play,  
18    supports the hypothesis that play is a mechanism for solving conflicts associated with contest  
19    competition by either reducing social tension and/or fighting for a limited resource. The range  
20    of factors affecting social play indicates that this behaviour in adult howler monkeys is  
21    facultative, having affiliative, socializing and competitive roles, depending on the socio-  
22    ecological context.

23

24    **Keywords:** adult-adult play, adult behaviour, adult-immature play, *Alouatta palliata*, Costa  
25    Rica, Mexico

## 26    **HIGHLIGHTS**

- 27        •    Adult play correlated positively with group size and fruit consumption
- 28        •    Adult play correlated negatively with immature to adult ratio.
- 29        •    Adult females played more than adult males.
- 30        •    Adults of both sexes had no preference for playing with immatures over other adults.
- 31        •    Social play may have different functions while exhibiting the same behavioural
- 32        structure.

## 33 INTRODUCTION

34 The perennial question of why animals play has been debated since the earliest detailed  
35 studies of behaviour began (Darwin, 1871; Groos, 1898; Spencer, 1872). Darwin (1871) wrote  
36 “happiness is never better exhibited than by young animals, such as puppies, kittens, lambs,  
37 and company, when playing together, like our own children”. Spencer (1872) believed that  
38 play occurs when excess energy builds up in an animal’s brain, which leads to play that  
39 imitates more functional behaviour. Since play has elements from other behaviors, including  
40 aggression and affiliation, it can have a wide variety of causes and functions (Bekoff & Byers,  
41 1998; Breuggeman, 1978; Pellis et al., 2019; Smith, 1982). Accordingly, the role of play might  
42 respond to specific social and environmental circumstances that fluctuate across contexts.  
43 This makes the study of play highly complex and many questions remain unanswered about  
44 the evolution and function of this intriguing behaviour (Cenni & Fawcett, 2018; Graham &  
45 Burghardt, 2010; Pellis et al., 2015; Richter et al., 2016; Schank et al., 2018).

46 For many species, including humans, play is a conspicuous phenomenon in young  
47 individuals (herein after ‘immatures’), who spend large proportions of their time playing  
48 (Bekoff & Byers, 1981; Fagen, 1981; 1992; Fairbanks, 2000; Martin & Caro, 1985). Accordingly,  
49 the main function given to explain animal play is the rehearsal of behaviours individuals will  
50 assume later in adult life. These behaviours include mating, foraging, and fighting (Burghardt,  
51 2010; Fagen, 1981; Groos, 1898; Naples & Rothschild, 2015; Lafreniere, 2011; Palagi &  
52 Mancini, 2011; Pellis et al., 2015) in addition to facilitating the development of relationships  
53 with other group members (Bekoff, 1984; Cafazzo et al., 2018; Cordoni et al., 2018; Eifermann,  
54 1971; Mackey et al., 2014; Merrick, 1977; Paquette, 1994; Pellis et al., 2010; Poirier & Smith,  
55 1974; Shimada & Sueur, 2018). Nevertheless, play can also endure beyond sexual maturity in  
56 many species (e.g. otters: Beckel, 1991; birds: Diamond & Bond, 2003; wolves: Essler et al.,  
57 2016; kangaroos: Ganslosser, 1993; humans: Johnson et al., 2015; non-human primates: Pellis

58 & Iwaniuk, 2000a), suggesting that it may be a relevant functional behaviour across the entire  
59 life span of social animals.

60         Studies suggest that when adults participate in social play (i.e., an interaction in which  
61 two or more individuals play with each other), the behaviour can serve multiple compatible  
62 functions depending on the nature of the context and the participants (Bekoff & Byers, 1981;  
63 Dolhinow, 1999; Yamanashi et al., 2018). In this sense, when adults play with immatures (the  
64 most frequent type of adult play described; Fagen, 1981, 1992), it might serve as a means to  
65 'educate' them about the social rules that govern groups (Bekoff & Byers, 1998; Carpenter,  
66 1934; Fagen, 1992; Pellegrini & Smith, 2005; Poirier & Smith, 1974; Zahavi, 1977). During play,  
67 adults aid immatures with forming existing relationships, creating new ones, and allowing  
68 them to test social boundaries via pulling, biting, tugging, or hitting, that in other contexts  
69 would not be tolerated by others. Social play only amongst adults may have similar roles, i.e.,  
70 strengthening social networks and promoting cooperation between participants (Baldwin  
71 1982; Pellis et al. 1993). In primates in particular, play between adults, might have an  
72 affiliative function similar to grooming as it provides ways to interact with others (Merrick,  
73 1977; Palagi et al., 2006). That is, it allows individuals to establish and maintain social bonds  
74 (Baldwin & Baldwin, 1973; Enomoto, 1990; Goodall, 1986) and limit aggression, reduce  
75 tension, and increase tolerance when stressful situations, such as food competition, arise  
76 (Breuggeman, 1978; Gray, 2009; Martin & Caro, 1985; Norscia & Palagi, 2011). For example,  
77 play among adult bonobos (*Pan paniscus*) is more frequent before and during feeding than in  
78 any other context, which supports the idea that adults use it to cope with competition and  
79 social tension (Palagi et al., 2006).

80         As social play is a particularly elaborate and energy-consuming behaviour that often  
81 resembles fighting (Aldis, 1975), it can also assume a competitive function – assessing the  
82 abilities, the strengths and the weaknesses of playmates as well as showing competitive skills

83 in a 'safe' context (Breuggeman, 1978; Montgomery, 2014; Palagi, 2018; Paquette 1994; Pellis  
84 & Iwaniuk, 2000a, 2000b, 2002; Palagi et al., 2004, 2006, 2007; Cordoni, 2009; Smuts, 2014).  
85 This function becomes particularly important in social species without rigid dominance  
86 hierarchies or with social uncertainty (Ciani et al., 2012; Palagi et al., 2016; Pellis & Iwaniuk,  
87 2000a). Thus, adult individuals can use play as a tool to negotiate social relationships,  
88 maintain alliances, reduce social tension, and foster cooperation between group members  
89 (Antonacci et al., 2010; Ciani et al., 2012; Norscia & Palagi, 2011; Elisabetta Palagi et al., 2006).

90 Previous research on social play in howler monkeys (genus *Alouatta*) has mostly  
91 described developmental aspects of infants and juveniles of the *A. palliata* species (Baldwin &  
92 Baldwin, 1978; Gennuso et al., 2018; Jasso del Toro et al., 2020; Zucker et al., 1992). Play in  
93 howler monkeys starts around the age of three months, when the infant starts moving more  
94 autonomously, and it reaches a peak during the juvenile period (between 12-36 months), then  
95 it drastically reduces as they approach adulthood (>40 months). Adult howler monkeys have a  
96 highly folivorous diet, which makes them comparatively inactive primates, spending most of  
97 their time resting for cellulose digestion (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Dunn  
98 et al., 2010; Milton, 1980; 1998). Howler play decreases with age according to increasing  
99 demand for energy in digestion as mothers wean juveniles (Baldwin & Baldwin, 1978).  
100 Correspondingly, in a review of play by Pellis & Iwaniuk (2000b), *A. palliata* adults were  
101 reported to not engage in social play. Nonetheless, several authors have observed social play  
102 in adult howler monkeys (Fontaine, 1994; Garcia, 2001; Zucker & Clarke, 1992). Zucker &  
103 Clarke (1992) further suggested that social play should be more common in mantled howler  
104 monkeys (*A. palliata*) than in other howler species, (e.g. *A. seniculus*), as they live in groups  
105 with several adult males and females. Correspondingly, Garcia (2001) observed 59 dyadic  
106 interactions of social play in adult mantled howler (*A. p. mexicana*) males in Agaltepec island,  
107 Mexico, during 840 hours of focal observations.

108           The objective of the present study was to examine the social and ecological variables  
109 affecting adult social play in howler monkeys and shed further light on the potential function  
110 of this behaviour in natural populations. This study encompassed two subspecies of howler  
111 monkeys, from seven different groups in Mexico (*A. p. mexicana*) and Costa Rica (*A. p.*  
112 *palliata*). We first examined how social play varied with age. Then, we tested the effect of  
113 several socio-ecological factors on the amount of time adult howler monkeys spend playing  
114 with other adults (adult-adult play) and immatures (adult-immature play), including: group  
115 size, immature-to-adult-ratio, sex, howler density, study area, percentage of time dedicated to  
116 foraging on fruit, and percentage of time dedicated to travelling.

117

## 118   **METHODS**

### 119   *Study sites*

120   We studied social play in howler monkeys at two different sites: Los Tuxtlas Biosphere  
121 Reserve, Mexico, where the subspecies *A. p. mexicana* lives, and the Sector Santa Rosa in  
122 Guanacaste Conservation Area in Costa Rica where *A. p. palliata* lives (Table 1).

123           The vegetation in the Los Tuxtlas Biosphere Reserve consists of tropical forest  
124 fragments that vary in size and degree of isolation (Arroyo-Rodríguez et al., 2008; Cristóbal-  
125 Azkarate et al., 2005). The climate is warm and humid, with a mean annual temperature of  
126 25°C and rainfall between 3000 and 4600 mm (Estrada et al., 1997). The vegetation in Santa  
127 Rosa is comprised of relatively continuous tropical dry forest with patches of semi-evergreen  
128 forest at various stages of succession and an annual rainfall of approximately 1,500 mm  
129 (Fedigan & Jack, 2012). In the Los Tuxtlas Biosphere Reserve, we studied three howler monkey  
130 groups inhabiting three different forest fragments of different size, whereas in Santa Rosa we  
131 studied four groups that lived in a continuous dry forest (Table 1). We could identify all

132 individuals by natural markings (skin pigmentation on the hands and feet and sometimes  
133 scars).

134 We classified individuals as adult males, adult females, juveniles and infants following  
135 Domingo-Balcells and Veà (2009), which we validated based on the behaviour and appearance  
136 of 37 individuals (20 adults and 17 immatures) for which we knew the exact age. In order to  
137 simplify analyses, we grouped juveniles and infants into a single category of immatures (Table  
138 1).

139

#### 140 ***Behavioural data sampling***

141 Observations covered the whole day from dawn to dusk when possible. However, the total  
142 observation time and sampling period (month/year) varied between groups and study sites  
143 (Table 1). While following howler monkeys, we continuously recorded all occurrences and  
144 durations of social play in seconds using a stopwatch, along with the identities of the  
145 individuals involved. Observations occurred at distances between 20 and 30 meters using both  
146 naked eye and binoculars. We recorded field data in a notebook at the moment of  
147 observation, and later transcribed these into a database. The total observation time was 1884  
148 hours across the 7 groups (Table 1). We could usually observe all the individuals of the study  
149 groups simultaneously, except for in AGA, as this group has atypical dynamics for the species;  
150 the AGA group presents fission-fusion dynamics by which individuals often separate into  
151 subgroups (Dias & Rodriguez-Luna, 2006). Therefore, although the total observation time in  
152 AGA was 415 hours, the observation time for each individual was not equal for all members,  
153 because we never observed all individuals together simultaneously. Thus, to estimate play  
154 percentages at AGA, we divided the time spent playing per individual by its individual  
155 observation time to control for variation in individual observation effort. We did this by



156 recording the individuals' presence in the observed subgroup at 30 minute-scan intervals.  
157 Mean observation time ( $\pm$ SD) of individuals in AGA was 82.2 ( $\pm$ 38.5 hr) per adult individual.

158 We followed Burghardt's five criteria (2005) to identify social play in howler monkeys.  
159 First, play was functionally incomplete as there was no evident logical survival outcome for  
160 players in the context in which it appeared. Second, social play was spontaneous and  
161 voluntary, and it was perceived by observers as pleasurable to the players. Third, social play  
162 was different from other more 'serious' behaviors such as aggression which included severe  
163 contact and had a clear role of attacker and defender. Instead, during a single play bout, there  
164 were frequent role reversals among play partners. Fourth, it was repeated, but not  
165 stereotyped, i.e., it did not repeatedly occur in the same sequence of actions. Fifth, to our  
166 knowledge, it never occurred in the presence of severe stress, such as a loud noises or during  
167 threats from conspecifics or predators. We further defined social play as a non-aggressive  
168 interaction between two or more individuals through an unordered combination of one or  
169 more of the following actions, which were never preceded or followed by any sign of social  
170 distress: biting, chasing, wrestling/grappling, pushing, pulling, baring teeth, and/or chasing  
171 (Braza, 1980). A play bout could occur with individuals hanging from their tails and often  
172 included typical play signals such as 'shaking the head' or 'play face' (Fagen, 1981). We  
173 identified an adult-adult play bout as when two or more adult individuals played together  
174 without any immature being involved; an adult-immature play bout as when at least one adult  
175 played with at least one immature individual; and finally, mixed play as when two or more  
176 adults played with at least one immature. We recorded that an individual had stopped playing  
177 when the activity was discontinued for at least ten seconds. Thus, a play bout ended when all  
178 players stopped playing for at least ten seconds. We also recorded the time spent foraging on  
179 fruit, resting and travelling using scan sampling at five-minute intervals. Data were collected  
180 by one observer in Mexico and five observers in Costa Rica. During the first two weeks in

181 Costa Rica, field observers undertook a training period to become skilled at individual  
182 identification and distinguishing social play in howler monkeys. This allowed data collection to  
183 be comparable between sites and increased interobserver reliability. Only when there was a  
184 consensus between observers identifying social play during training was an observer deemed  
185 to be independent and allowed to collect data in the field.

186

### 187 ***Statistical analyses***

188 We used the R platform (R Core Team, 2021) for all statistical analyses. A non-parametric  
189 analysis of variance (Kruskal Wallis ANOVA) was used to test for significant differences in the  
190 amount of social play measured in seconds among the 62 individuals across age classes  
191 (infants = 18, juveniles = 10, subadults = 5, adults = 57), the seven groups, and the two  
192 subspecies. We also used a Friedman test to examine whether adults played differently across  
193 the three social play types (adult-adult, adult-immature or mixed play). In addition, we fitted a  
194 generalized linear model (GLM) adjusted for a binomial distribution to determine the  
195 influence of age in months on the percentage of social play of 37 individuals (infants = 11,  
196 juveniles = 6, adults = 21) with known age in months. The GLM included 'cbind (seconds  
197 playing, seconds not playing)' in the formula to normalize the response variable by  
198 observation time (Gardener, 2012). This is, the seconds playing and the seconds not playing  
199 were entered in the GLM as a two vector response variable (e.g. Ceccarelli et al., 2020; Dias et  
200 al., 2020). We introduced the quadratic term of age (months<sup>2</sup>) in the GLM to test for its non-  
201 linear effect on play.

202 We ran two generalized linear mixed effects models (GLMMs) that assessed the  
203 influence of all predictors (i.e., we ran two full models) on both adult-adult play and adult-  
204 immature play (n = 62: 40 adult females, 22 adult males): group size, howler monkey density

(ind/ha), percentage of observation time spent foraging on fruit and travelling, study area (ha), sex, and immature-to-adult-ratio (number of immatures/number of adults of both sexes). Instead of total group size, we only entered the number of adults in the group when modelling adult-adult play. If subspecies or study group significantly affected adult-adult play via the Kruskal Wallis ANOVA, then we controlled for these effects by setting these variables as random factors in the model selection analyses described below. The time spent by adults in social play was entered as the response variable (normalized by observation time by including the 'cbind' function in the GLMM formula), adjusted for a binomial distribution. We transformed study area to its natural logarithm, and all continuous factors were standardized by subtracting the mean of each observation and dividing it by the standard deviation before GLMM analyses. We implemented GLMMs using the 'glmer' function in the 'lme4' package (Bates et al., 2015). We calculated the variance inflate factor (VIF) to check potential multicollinearity among parameters for the two full models (Miles, 2014), which revealed no concerns (VIF < 3). Models conformed to assumption of normality of residuals when inspecting quantile-quantile plots, and to homogeneity when residuals were plotted against predicted values.

221

## 222 ***Adult play preferences***

223 To analyse the preference of adults to play with other adults versus play with immatures, we  
224 calculated the play preference using log ratios (Elston et al., 1996) for each adult individual:

$$225 \quad \text{play preference ratio} = \ln \left( \frac{A_o/I_o}{A_a/I_a} \right)$$

226 where  $A_o$  and  $I_o$  are the observed numbers of times focal adults played with other adult  
227 individuals and immature individuals, respectively, considering all play bouts each adult  
228 participated in; and  $A_a$  and  $I_a$  correspond to the number of available adult and immature

229 players. Play preference ratios  $> 0$  indicate a preference toward playing with other adults,  
230 whereas ratios  $< 0$  indicate a preference toward immatures, and values around 0 indicate no  
231 preference toward either of the two age classes. We performed  $t$ -tests to determine whether  
232 preference ratios were significantly different from zero; that is, whether individual choices to  
233 play with other adults or immatures were non-random concerning the available number of  
234 adult and immature individuals in the corresponding group. The available number of adult and  
235 immature individuals for each adult of AGA corresponded to the total number of adult and  
236 immature individuals observed in the group scans, respectively. We removed the individuals  
237 from the SE group from the preference analysis as the only immature in the group  
238 disappeared during the sampling period.

239

#### 240 ***Ethical note***

241 Our study was non-invasive and exclusively observational, carried out with the permission of  
242 the corresponding authorities in Mexico and Costa Rica. The research adheres to the  
243 ASAB/ABS Guidelines for the Use of Animals in Research, the American Society of  
244 Primatologists Principles for the Ethical Treatment of Non-Human Primates, and follows and  
245 the American Society of Mammologists' Guidelines on wild mammals in research.

246

#### 247 ***Data accessibility***

248 The data sets in CSV (comma separated values) and reproducible R scripts used for this study  
249 are available at <https://github.com/norberello/social-play-in-adult-howler-monkeys> or from  
250 the corresponding author on reasonable request.

251

## 252     **RESULTS**

### 253     ***Age and play***

254     We observed social play in all age classes of howler monkeys (Figure 1), although infants  
255     (mean $\pm$ SD = 1.4 $\pm$ 1.27%) and juveniles (2.16 $\pm$ 1.19%) had larger percentages of observation  
256     time playing than subadults (0.84 $\pm$ 0.48%) and adults (0.62 $\pm$ 0.55%). Both the ANOVA across  
257     age classes (Kruskal Wallis  $H = 18.9$ ,  $df = 3$ ,  $P < 0.001$ ; Fig 1a) and the GLM (Figure 1b) as the  
258     predictor confirmed that social play decreased in adulthood in howler monkeys. Both the  
259     linear ( $b = 4.57\text{e-}03$ ,  $SE = 3.26\text{e-}04$ ,  $P < 0.001$ ) and quadratic ( $b = -2.773\text{e-}04$ ,  $SE = 3.681\text{e-}06$ ,  $P$   
260      $< 0.001$ ) age GLM terms were significant. However, even the oldest individuals still engaged in  
261     some social play (Figure 1).

262

### 263     ***Social play categories across groups and subspecies***

264             Overall, adults played for a mean( $\pm$ SD) of 0.61( $\pm$ 0.55) percentage of observation time.  
265     There were differences in the percentage of time adults dedicated to social play across study  
266     sites (Figure 2a), but these differences were not significant (Kruskal Wallis  $H_6 = 10.5$ ,  $P =$   
267     0.103). There were differences between subspecies in adult social play (Kruskal Wallis  $H =$   
268     13.8,  $df = 1$ ,  $P < 0.001$ , Figure 2b).

269             Adults spent more time playing with other adults (adult-adult play), followed by adults  
270     playing with immatures (adult-immature play), and adults playing with other adults and  
271     immatures simultaneously (mixed play, Figure 2c). These differences were significant  
272     (Friedman test  $\chi^2 = 39.9$ ,  $df = 1$ ,  $P < 0.001$ ).

273

274

275 ***Adult-adult play and adult-immature play***

276 There were no differences between subspecies in adult-adult play (Kruskal Wallis  $H = 0.11$ ,  $df =$   
277  $1$ ,  $P = 0.73$ ) or adult-immature play (Kruskal Wallis  $H = 0.51$ ,  $df = 1$ ,  $P = 0.47$ ). There were,  
278 however, significant differences in the percentage of time that adults dedicated to adult-adult  
279 play (Kruskal Wallis  $H = 28.9$ ,  $df = 6$ ,  $P < 0.001$ , Figure 3a) and adult-immature play (Kruskal  
280 Wallis  $H = 19.1$ ,  $df = 6$ ,  $P < 0.005$ , Figure 3b) across study groups.

281

282 ***Factors explaining adult-adult social play***

283 The number of adults in the group and the percentage of time spent foraging on fruit both  
284 positively affected social play, whereas immature to adult ratio affected it negatively (Table 2,  
285 Figure 4). The percentage of time spent travelling had a positive effect on social play, but it  
286 has an estimate close to 0, and thus has a very weak effect. Adult females played more with  
287 other adults than adult males (Table 2). The density of howler monkeys and the study area did  
288 not have a significant effect on social play.

289

290 ***Factors explaining adult-immature social play***

291 Group size, immature to adult ratio and the percentage of time spent travelling all positively  
292 affected adult-immature social play (Table 3, Figure 5). The percentage of time spent foraging  
293 on fruit had a low estimate and a high standard error and the density of howler monkeys and  
294 study area did not have a significant effect on adult-immature play. Adult females played with  
295 immatures more than adult males.

296

297

## 298 ***Adult social play preferences***

299 We observed a total of 1261 social play bouts: 40% (499 bouts) occurred only between adults,  
300 whereas 60% (762 bouts) occurred between adults and immatures. However, adult howler  
301 monkeys did not show a significant preference to play with immatures over other adults ( $t =$   
302  $0.78$ ,  $df = 46$ ,  $P = 0.44$ , Fig 6). When studying these adult play preferences by sex, neither adult  
303 females ( $t = 0.99$ ,  $df = 35$ ,  $P = 0.47$ ) nor adult males ( $t = 0.17$ ,  $df = 20$ ,  $P = 0.86$ ) showed a  
304 preference to play with immatures over adults, as preference values were close to 0 (Figure  
305 6).

306

## 307 **DISCUSSION**

308 Despite play occupying a low proportion of overall observation time (0.61% of 1884 total  
309 observation hours) in adult howler monkeys in this study, it did not disappear during  
310 adulthood and even the oldest known individuals engaged in social play. The amount of time  
311 dedicated to social play in howler monkeys negatively correlated with their age, which is the  
312 general rule amongst animals (Fagen, 1981). The peak in play occurred around the weaning  
313 age of howlers monkeys (Baldwin & Baldwin, 1978) and was followed by steady decline as  
314 they age (Fagen, 1981; Pellegrini & Smith, 2005). Adult play was sensitive to several socio-  
315 ecological factors, which offer insight into the role of this behaviour in adult howler monkeys.

316 In terms of the social predictors of adult play, both adult-adult play and adult-  
317 immature play increased with the number of adults and overall group size, respectively. This is  
318 consistent with other studies showing that play increases with the number of potential  
319 playmates, and therefore there being more opportunities to play in a larger social group  
320 (Fagen, 1981). Our study also supports that immatures constitute an important stimulus for  
321 adult play (Fagen, 1981, 1992) as adult-immature play increased with the proportion of

322 immatures in the group. Play in this context has been discussed to have an  
323 educational/socialization function, helping immatures learn social rules and create and  
324 develop relationships (Bekoff, 1984; Enders & Carpenter, 1934; Fagen, 1992; Pellegrini &  
325 Smith, 2005; Poirier & Smith, 1974). However, we did not find a preference for adults to play  
326 with immatures, and adult-adult play was relatively common in the different study groups.  
327 This suggests that adult-adult play may fulfil important functions in howler monkey society.

328         Having more individuals in a group may favour play as a mechanism to facilitate both  
329 group cohesiveness and tension reduction (Palagi et al., 2006; Shimada & Sueur, 2018;  
330 Yamanashi et al., 2018) in the same way grooming behaviour does (Grueter et al., 2013; Kudo  
331 & Dunbar, 2001). It is noteworthy that individuals of *A. palliata* very rarely groom each other  
332 (Crockett & Eisenberg, 1987). Moreover, howler monkeys exhibit bisexual dispersal and  
333 groups are thus usually formed of unfamiliar individuals that immigrated from other groups  
334 (Arroyo-Rodríguez et al., 2008; Clarke & Glander, 2010; Cristóbal Azkarate et al., 2015). This  
335 may increase the necessity of interacting with other members of the group to strengthen  
336 group cohesion. Therefore, in the absence of other obvious affiliative behaviours in howler  
337 monkeys, play may be occupying at least part of the role that grooming would in other  
338 primate species. This idea is supported by the observation that the percentage of time  
339 dedicated to foraging on fruits positively correlated with adult-adult play. Fruit is a defensible  
340 resource that generates contest competition (Clutton-Brock & Harvey, 1977; Emlen & Oring,  
341 1977) and Palagi et al. (2004) found a peak in the frequencies of both grooming and social play  
342 time among adult chimpanzees, particularly before feeding – a period that creates high stress  
343 in the species. These behavioural peaks during an apprehensive context suggest that play and  
344 grooming share a mechanism to deal with social conflicts. Although predominantly folivorous,  
345 howler monkeys can be frugivorous when fruit are available (Asensio et al., 2007; Cristóbal-  
346 Azkarate & Arroyo-Rodríguez, 2007; Dunn et al., 2010), and Bergman et al. (2016) suggested



347 that across *Alouatta* species, *A. palliata* has the highest levels of intragroup contest  
348 competition. However, howler monkeys do not possess a fixed social hierarchy to navigate  
349 this potential competitive setting and rarely show aggression to each other (but see Cristóbal-  
350 Azkarate et al., 2004), and Pellis and Iwaniuk (2000) argued that social play is a substitute for  
351 codified and structured social rules. This aligns with the possibility that in species with social  
352 uncertainty, social play could serve to assess social relationships (Ciani et al., 2012; Elisabetta  
353 Palagi et al., 2016). Garcia (2001) suggested that social play among howler monkeys of AGA is  
354 used as a way of testing and establishing social hierarchies without engaging in an open fight.  
355 Regardless of whether play has a competitive or an affiliative role in adult howler monkeys (or  
356 both), our findings support the idea that adult social play might be used as a tool for  
357 regulating social relationships within howler monkey groups.

358         An alternative hypothesis for the positive effect of fruit consumption on adult-adult  
359 play could be that a fruit based diet provides more energy in comparison to that of leaves  
360 (Milton, 1980). However, if this was the case, we should have also observed a positive effect  
361 of over adult-immature play. Such a difference is likely due to immature animals not being  
362 direct competitors of adults at fruit trees yet, as they are not fully dependent on plant-eating  
363 to obtain energy (Baldwin & Baldwin, 1978). On the other hand, the proportion of time  
364 dedicated to travelling did not have an effect on adult-adult play, however it was  
365 unexpectedly positively correlated with adult-immature play. Perhaps, more movement in the  
366 group as a result of travelling creates opportunities for adults to encounter immatures, and  
367 vice versa (Dunn et al., 2010, 2013), and thus, this situation triggers adult-immature play.  
368 However, the same effect was not found in adult-adult play, for which we could not find  
369 another reasonable explanation.

370         Adult females played more both with other adults and immatures than adult males  
371 did. In principle, adult females are predicted to play less overall, as they are more constrained

372 by the energy requirements of reproduction (Fagen, 1981). This effect might be particularly  
373 strong in energy-conservative howler monkeys (Milton, 1998). However, this gives further  
374 weight to the possibility that females, who are more vulnerable to within-group food  
375 competition than males (Isbell, 1991), may use play to solve conflicts over access to food  
376 resources (Palagi et al. 2004).

377         Two of the study groups (SE and AGA) live in very small forest fragments with high  
378 howler density and are exposed to the strong negative effects of fragmentation, such as edge  
379 effects and low fruit availability (Marsh, 2003). In other studies, play behaviour has been  
380 shown to decrease or disappear entirely under food shortage or other stressful situations  
381 (Held & Špinka, 2011; Sharpe et al., 2002; Sommer & Mendoza-Granados, 1995). However,  
382 neither the size of the study area nor howler density were correlated with adult social play.  
383 Adults from SE and AGA exhibited play at similar or higher percentages than adults living in  
384 larger study sites and under lower howler densities. Perhaps the known plasticity of howler  
385 monkeys to adjust to the negative conditions of fragmentation, such as associated energetic  
386 constraints (Bicca-Marques et al., 2020), did not put them in an extreme situation that  
387 exempts them from engaging in play. Moreover, in the case of the AGA group, due to virtually  
388 living in complete isolation on an island, there exists socioecological circumstances that might  
389 trigger adult play for other reasons. The lack of ability to emigrate elsewhere for AGA  
390 individuals has also created a particularly large and related group, which provides more  
391 playmate availability and higher chances of playing with kin. Animals tend to play most  
392 frequently with kin and allies (Fagen, 1981; Pellegrini & Smith, 2005; Tomasello et al., 1990),  
393 and the unusual familiarity among individuals in AGA may boost the largest adult-adult play  
394 percentages of all study sites (but see Biben, 2010). Moreover, AGA's feature of being a group  
395 with fission-fusion dynamics (Dias & Rodríguez-Luna, 2006), highly atypical for the species,  
396 may have created the necessity to regulate social relationships through play at the potentially

397 tense subgroup fusions. This possibility suggests further research studying whether play  
398 occurs at fusion events on this group.

399

## 400 **Conclusions**

401         Howler monkeys generally have an inactive lifestyle to save the energy needed for  
402 plant digestion from their highly folivorous diet (Milton, 1998). Thus, our results of adult social  
403 play seem to align with the expectations of how an energy-conservative species should  
404 behave regarding an energy-costly activity such as play (Martin & Caro, 1985), and the idea  
405 that social play is mainly present in primate species with a dynamic social organization such as  
406 *Ateles*, *Cacajao* and *Pan*, but not *Alouatta* (Pellis & Iwaniuk, 2000a). Still, our findings indicate  
407 that adult play in howler monkeys is not atypical in their social behavioural repertoire.

408         We found that several socioecological parameters structure social play in adult howler  
409 monkeys: age, sex, group size, immature-to-adult ratios, travelling and frugivory. Moreover,  
410 the effect of immature-to-adult ratios and frugivory varied depending on whether adults  
411 played with other adults or immatures in a group. When adult play is directed to immatures, it  
412 reasonably should have the function of socializing/educating them. However, when play is  
413 directed towards adults, this suggests that it may act as a tool that regulates social  
414 relationships, which may be either competitive or affiliative.

415         These findings imply that play is a behaviour that may have a role that varies  
416 depending on the sex of the adult, the context adults face in each group, and whether the  
417 interaction is with other adults or immatures. Considering the potential variation in both  
418 contextual use and function of play, and its cooperative and competitive elements (Bateson &  
419 Barrett, 2008; Bauer & Smuts, 2007; Breuggeman, 1978; Cordoni et al., 2021), it seems likely

420 that the same social behaviour has the facultative role of adjusting to different situations, and  
421 thus functions, 'disguised' in the same behavioural structure.

422 We suggest that despite its overall form, and the general perception of what play  
423 means, this behaviour may not necessarily be associated with education, joy or frivolity, but it  
424 may serve other roles that are not so obvious, such as reducing social tension during  
425 competition.

426

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705



Table 1. Group composition, observation time and sampling periods at study sites.

Site and Subspecies	Group id	Group Composition	Obs. Time (hr)	Sampling period	Geographical coordinates	Study area (ha)	Howler density (ind/ha)
<b>Los Tuxtlas Biosphere Reserve, Mexico</b>	AGA	21F 19M 19I	415	Aug 1997 - Jun 1998	18°27'N, 95°02'W	8.3	9.5
	LIZ	2F 2M 1I	300	Aug 2000 - Jun 2001	18°41'N, 95°11'W	1.3	4.6
<b><i>A. p. mexicana</i></b>	PLA	2F 2M 3I	300	Aug 1997 - Jun 1998	18°27'N, 95°03'W	40	0.48 <sup>a</sup>
<b>Santa Rosa Sector, Guanacaste Conservation Area, Costa Rica</b> <i>A. p. palliata</i>	CH	9F 4M 6I	274	Apr - Oct 2005	10°50'N, 85°38'W	10800	0.56 <sup>b</sup>
	CP	11F 2M 4I	207	Apr - Oct 2005	10°50'N, 85°38'W	10800	0.56 <sup>b</sup>
	SN	5F 2M 2I	278	Apr - Oct 2005	10°50'N, 85°38'W	10800	0.56 <sup>b</sup>
	SE	4F 1M	110	Apr - Oct 2005	10°50'N, 85°38'W	10800	0.56 <sup>b</sup>

**AGA: Agaltepec Island, LIZ: Arrollo Liza, PLA: Playa Escondida, CH: Charly, CP: Cerco de Piedra, SN: Sendero Natural, SE: San Emilio.**

F: Adult female, M: Adult male, I: Immature (infant >3mo and juveniles).

<sup>a</sup>(Serio-Silva & Rico-Gray, 2002) <sup>b</sup>(Fedigan & Jack, 2012)

706

Table 2. Summary of GLMM estimates explaining the variation of adult-adult play among *Alouatta palliata* adult individuals.

Parameter	Estimate	Std. error	z value	<i>P</i>
<i>(Intercept)</i>	-6.43	0.42	-15.11	< 0.001
<i>immature to adult ratio</i>	-1.32	0.029	-44.96	< 0.001
<i>number of adults</i>	0.52	0.023	22.19	< 0.001
<i>%feeding fruit</i>	0.15	0.014	10.74	< 0.001
<i>%travel</i>	0.01	0.003	3.09	< 0.001
<i>howler density</i>	-0.8	0.70	-1.19	0.23086
<i>sex(male)</i>	-0.37	0.008	-44.9	< 0.001
<i>study area</i>	-0.64	0.53	-1.20	0.2297

707

708

Table 3. Summary of GLMM estimates explaining variation of adult-immature play among *Alouatta palliata* adult individuals.

Parameter	Estimate	Std. Error	z value	<i>P</i>
<i>(Intercept)</i>	-7.39	1.02	-7.23	< 0.001
<i>immature to adult ratio</i>	0.35	0.03	10.79	< 0.001
<i>group size</i>	0.63	0.04	12.72	< 0.001
<i>%feeding</i>	-0.22	0.02	-9.34	< 0.001
<i>%travelling</i>	0.51	0.004	108.23	< 0.001
<i>howler density</i>	-0.85	1.68	-0.50	< 0.001
<i>sex (male)</i>	-0.33	0.009	-35.07	< 0.001
<i>study area</i>	-1.07	1.27	-0.84	0.4

710 **FIGURE LEGENDS**

711

712 Figure 1. (a) Changes in social play in howler monkeys according to age-class (I: immatures, J:  
713 Juveniles, SA: subadults, A: adults). Solid lines and crosses within the box indicate the median  
714 and mean, respectively. The boundary of the box closest to 0 indicates the 25th percentile  
715 (first quartile), and the boundary of the box farthest from zero indicates the 75th percentile  
716 (fourth quartile). The whiskers denote the minimum and maximum values.

717 (b) Relationship between age (months) and social play; 95% confidence intervals are shown in  
718 grey dotted lines around the solid regression line.

719

720 Figure 2. Percentage of observation time in social play by adult howler monkey individuals  
721 across: (a) study groups; (b) *Alouatta* subspecies; and (c) play bout composition: adult-adult  
722 play (ad-ad), adult-immature play (ad-im), mixed play (mix). Solid lines and crosses within the  
723 box mark the median and mean, respectively. The boundary of the box closest to 0 indicates  
724 the 25th percentile (first quartile), and the boundary of the box farthest from zero indicates  
725 the 75th percentile (fourth quartile). The whiskers denote the minimum and maximum values.

726

727 Figure 3. Percentage of observation time employed in adult-adult play (a) and adult-immature  
728 play (b) by adult individuals across different groups. Solid lines and crosses within the box  
729 mark the median and mean, respectively. The boundary of the box closest to 0 indicates the  
730 25<sup>th</sup> percentile (first quartile), and the boundary of the box farthest from zero indicates the  
731 75<sup>th</sup> percentile (fourth quartile). The whiskers denote the minimum and maximum values.

732

733 Figure 4. a) Coefficients (dots) and 95% confidence intervals (horizontal lines) of the GLMM  
734 explaining adult-adult play; b) Mean fitted responses for the time engaged in adult-adult  
735 social play (expressed as the percentage of observation time) by howler monkeys according to  
736 the number of adults in the group, immature to adult ratio, percentage of time feeding on  
737 fruit, and sex, by random factor (group identification = AGA: Agaltepec Island, LIZ: Arroyo Liza,  
738 PLA: Playa Escondida, CP: Cerco de piedra, CH: Charlie, SE: San Emilio, SN: Sendero Natural) as  
739 random factors.

740

741 Figure 5. a) Coefficients (dots) and 95% confidence intervals (horizontal lines) of the GLMM  
742 explaining adult-immature play; b) Averaged fitted responses for time engaged in adult-  
743 immature social play (expressed as percentage of observation time) by howler monkeys  
744 according to group size, immature to adult ratio, and sex; and considering group ID (AGA:  
745 Agaltepec Island, LIZ: Arroyo Liza, PLA: Playa Escondida, CP: Cerco de piedra, CH: Charlie, SE:  
746 San Emilio, SN: Sendero Natural) as a random factor.

747

748 Figure 6. Play preference index of adult female (f) and male (m) howler monkeys for other  
749 adults and immatures. Values over 0 (solid point-up triangles) indicate a preference to play  
750 with adults whereas those under 0 (empty point-down triangles) a preference to play with  
751 immatures. Solid lines and crosses within the box marks the median and mean, respectively.  
752 The boundary of the box closest to 0 indicates the 25th percentile (first quartile), and the  
753 boundary of the box farthest from zero indicates the 75th percentile (fourth quartile). The  
754 whiskers denote the minimum and maximum values.

Figure 1

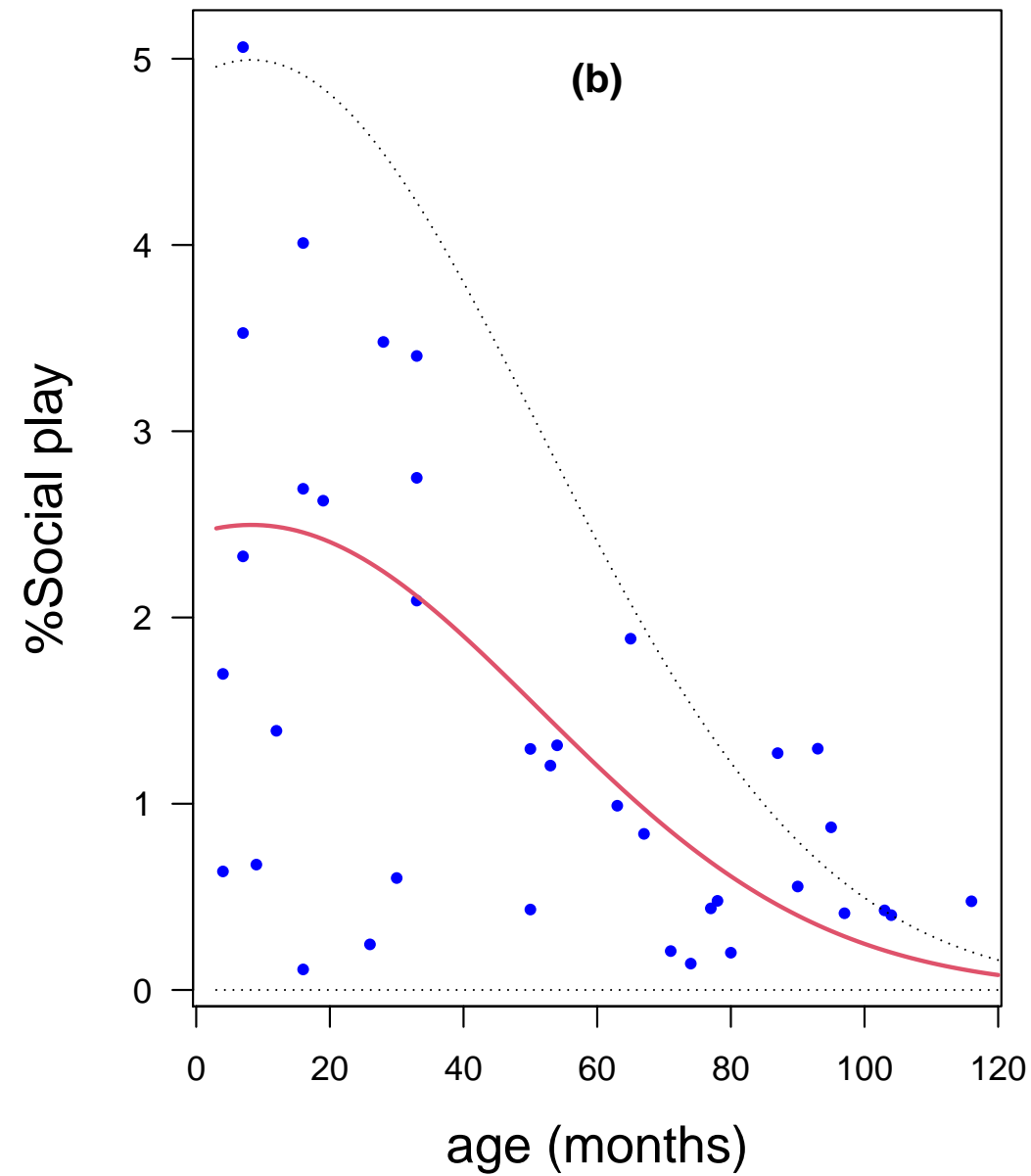
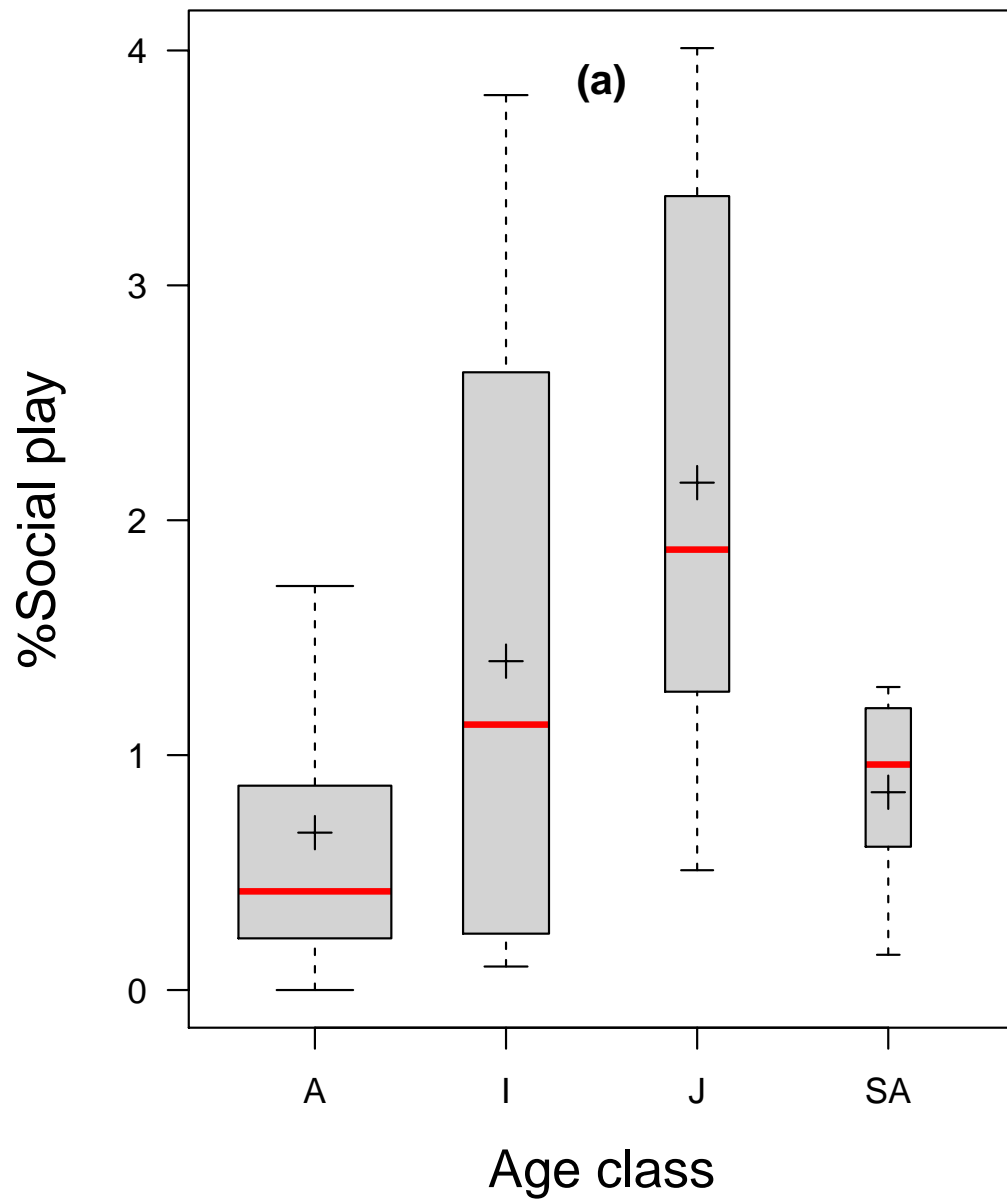


Figure 2

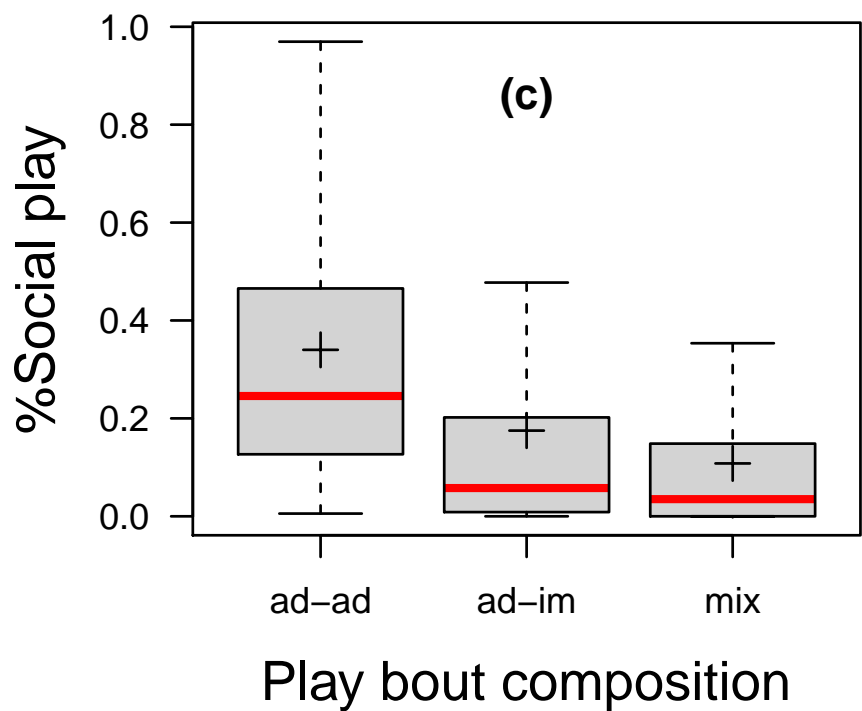
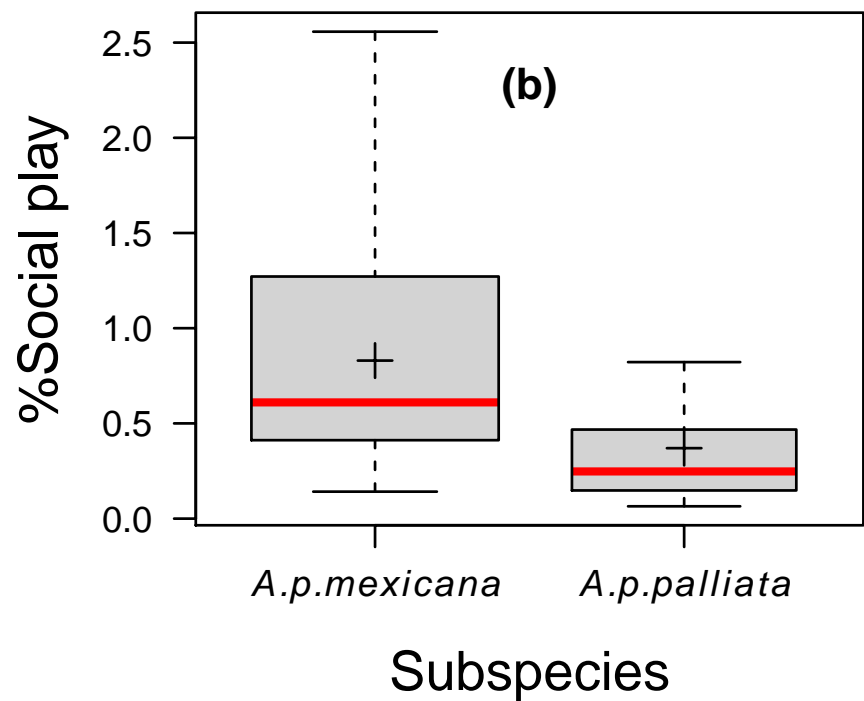
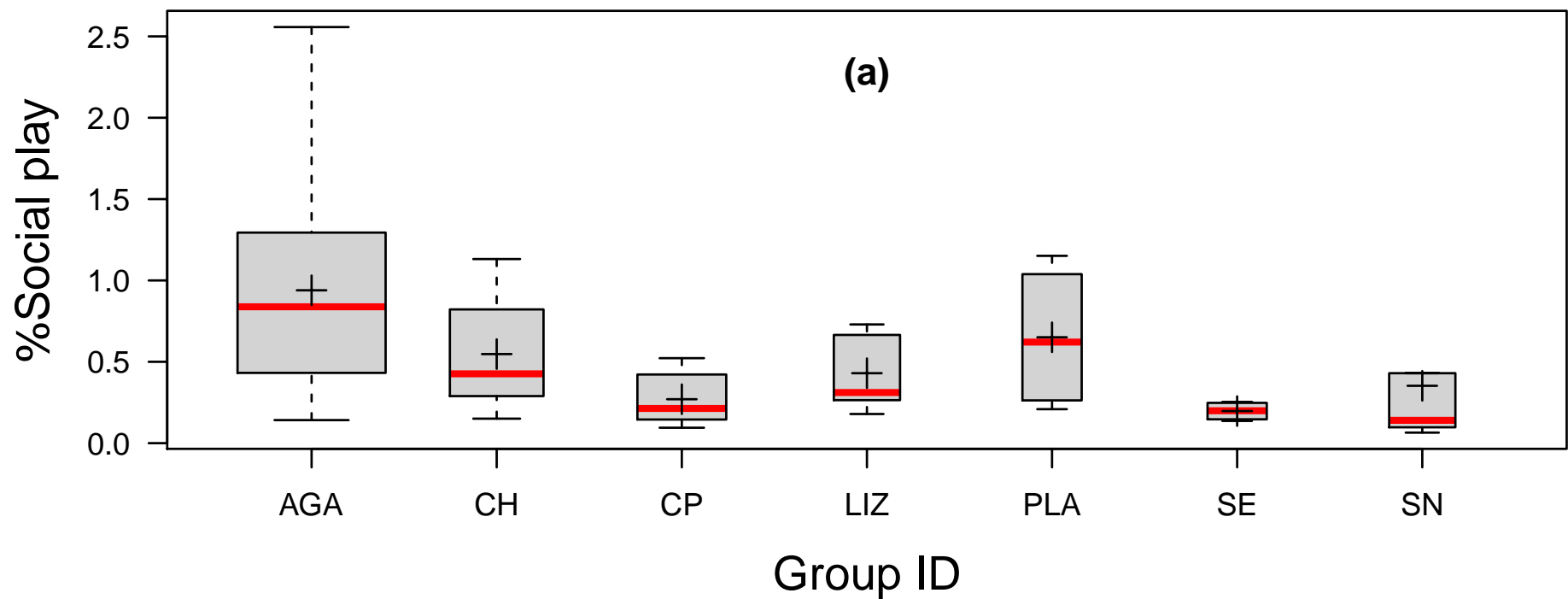


Figure 3

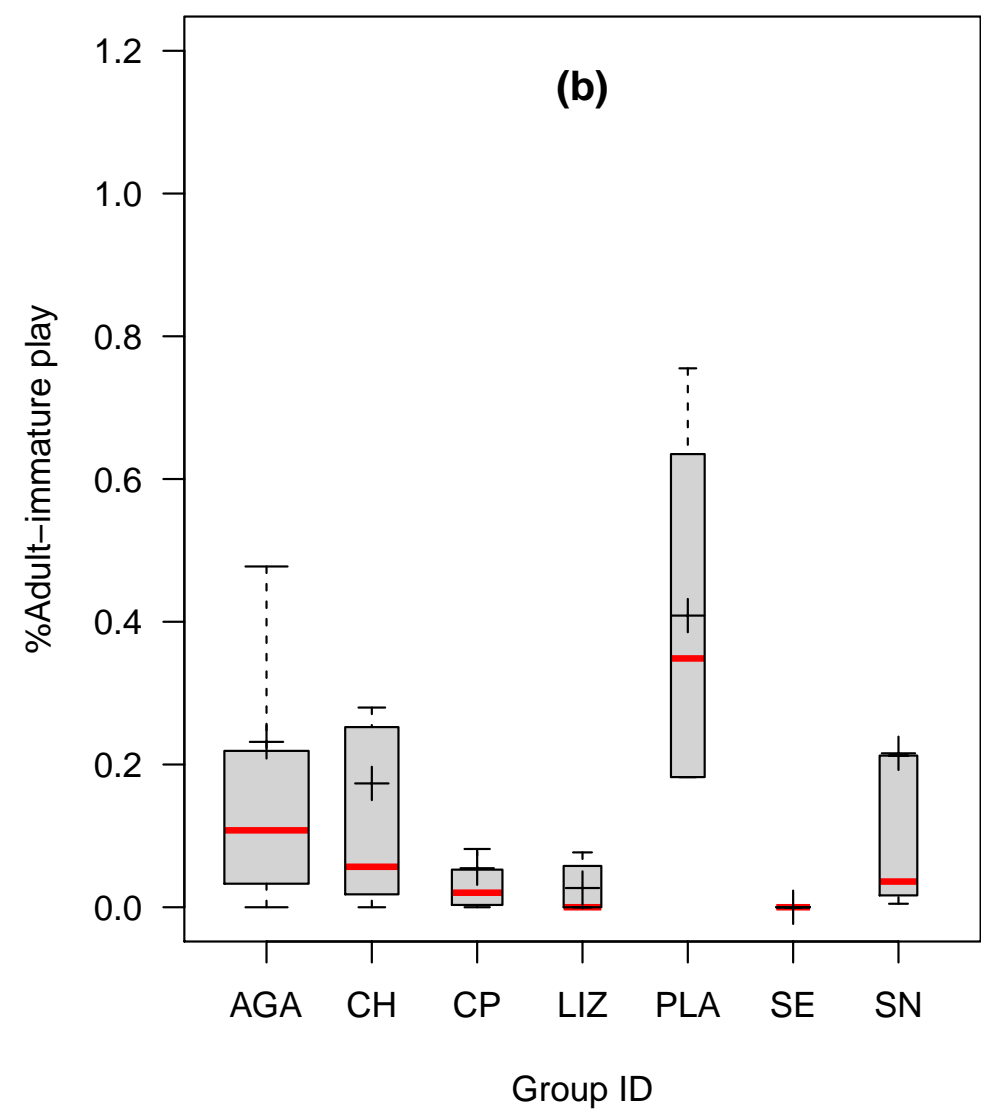
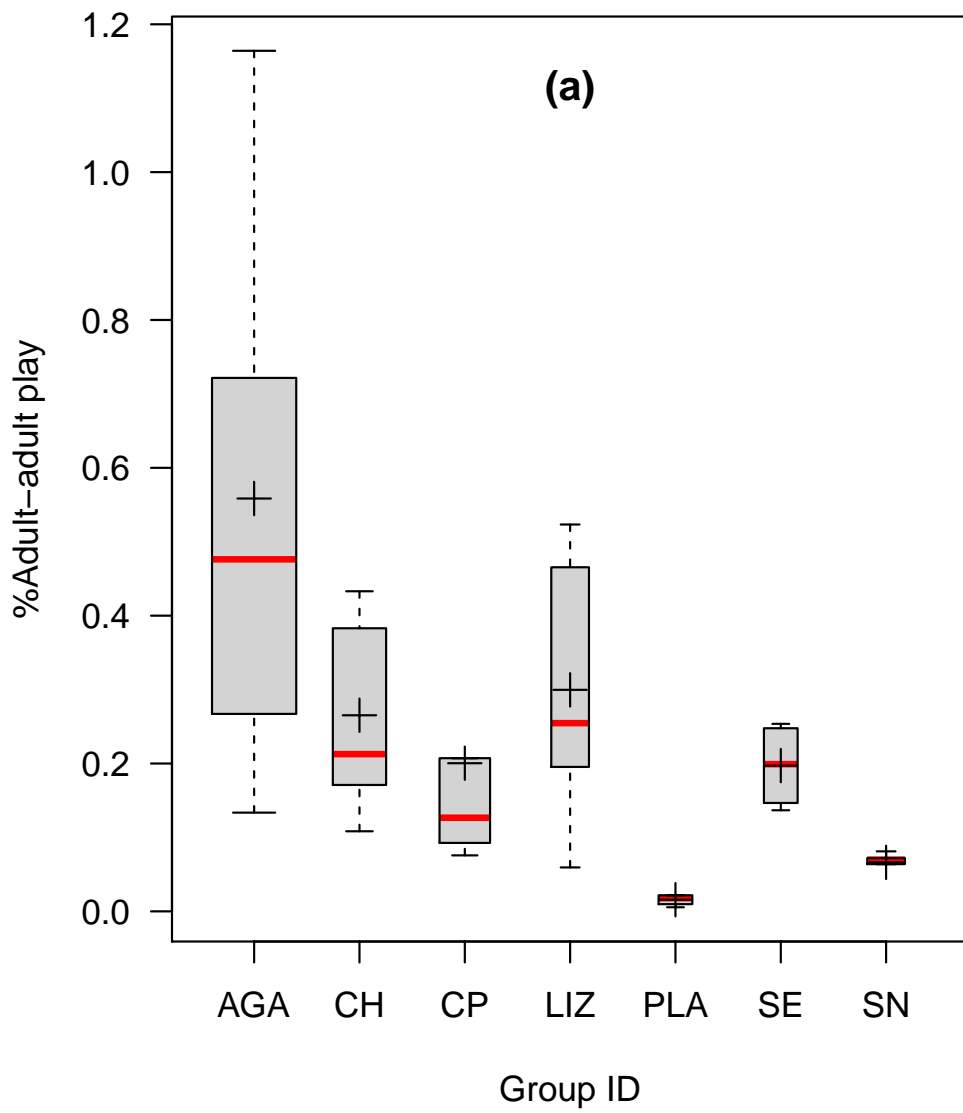




Figure 4

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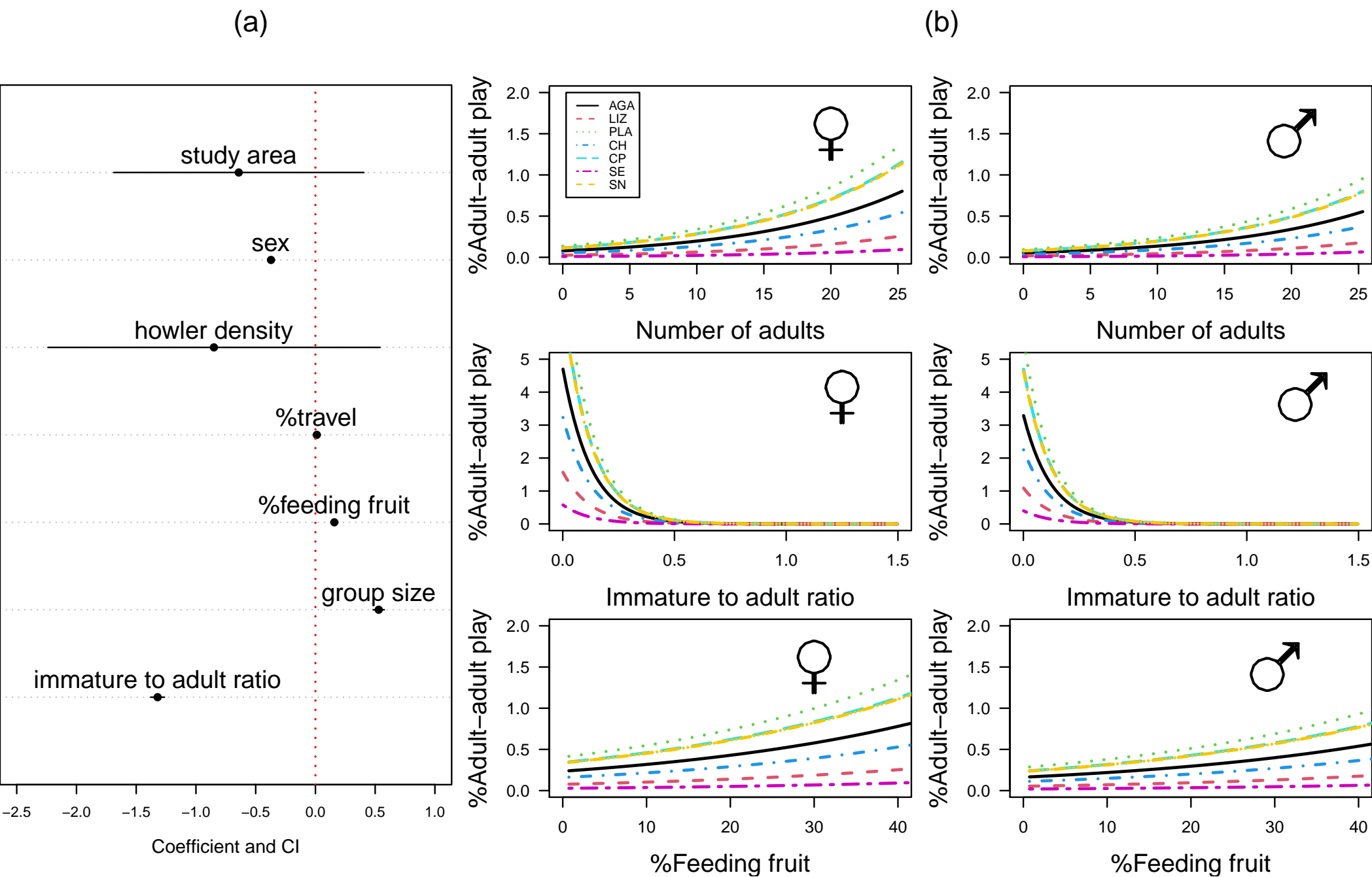
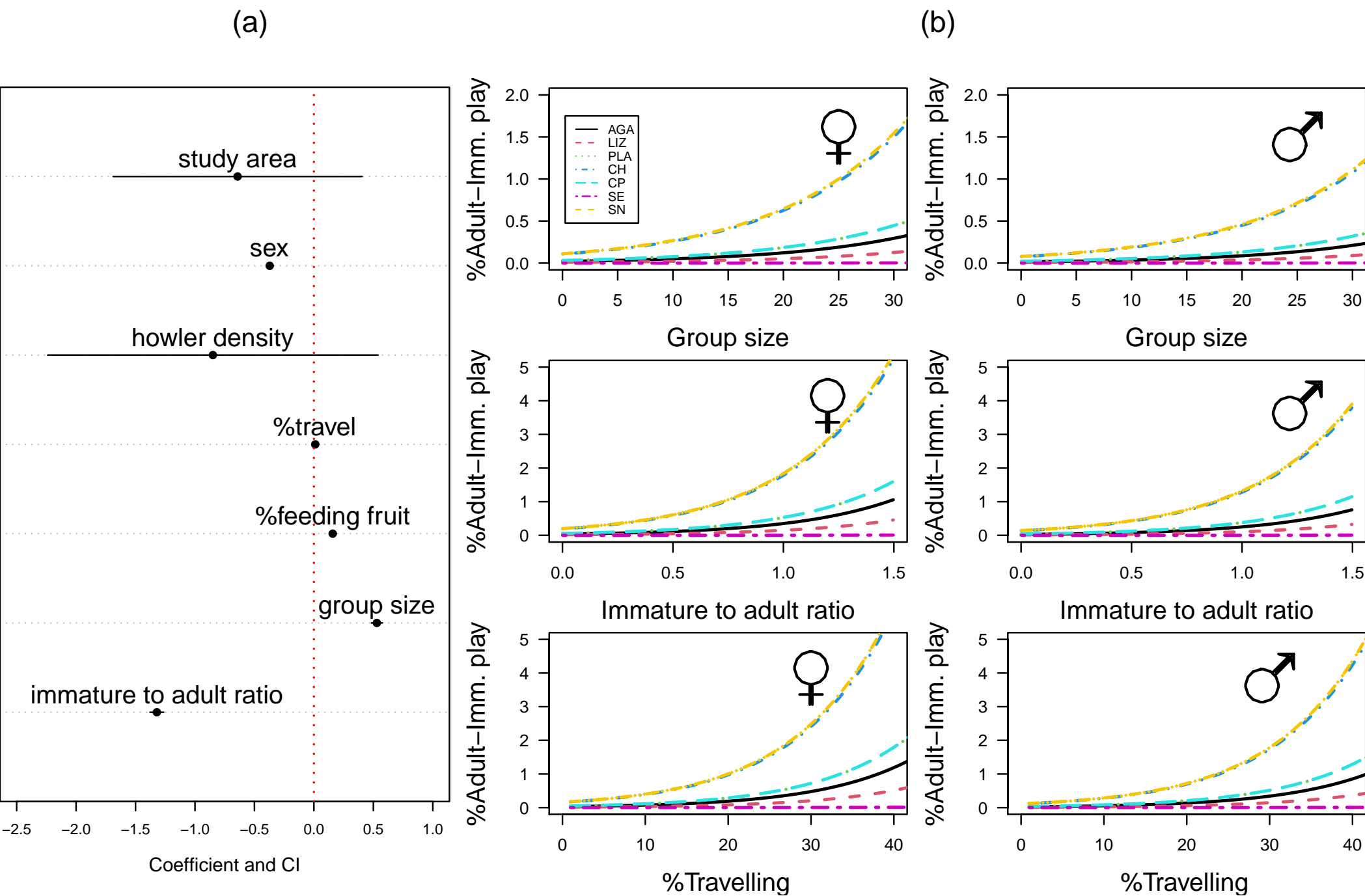
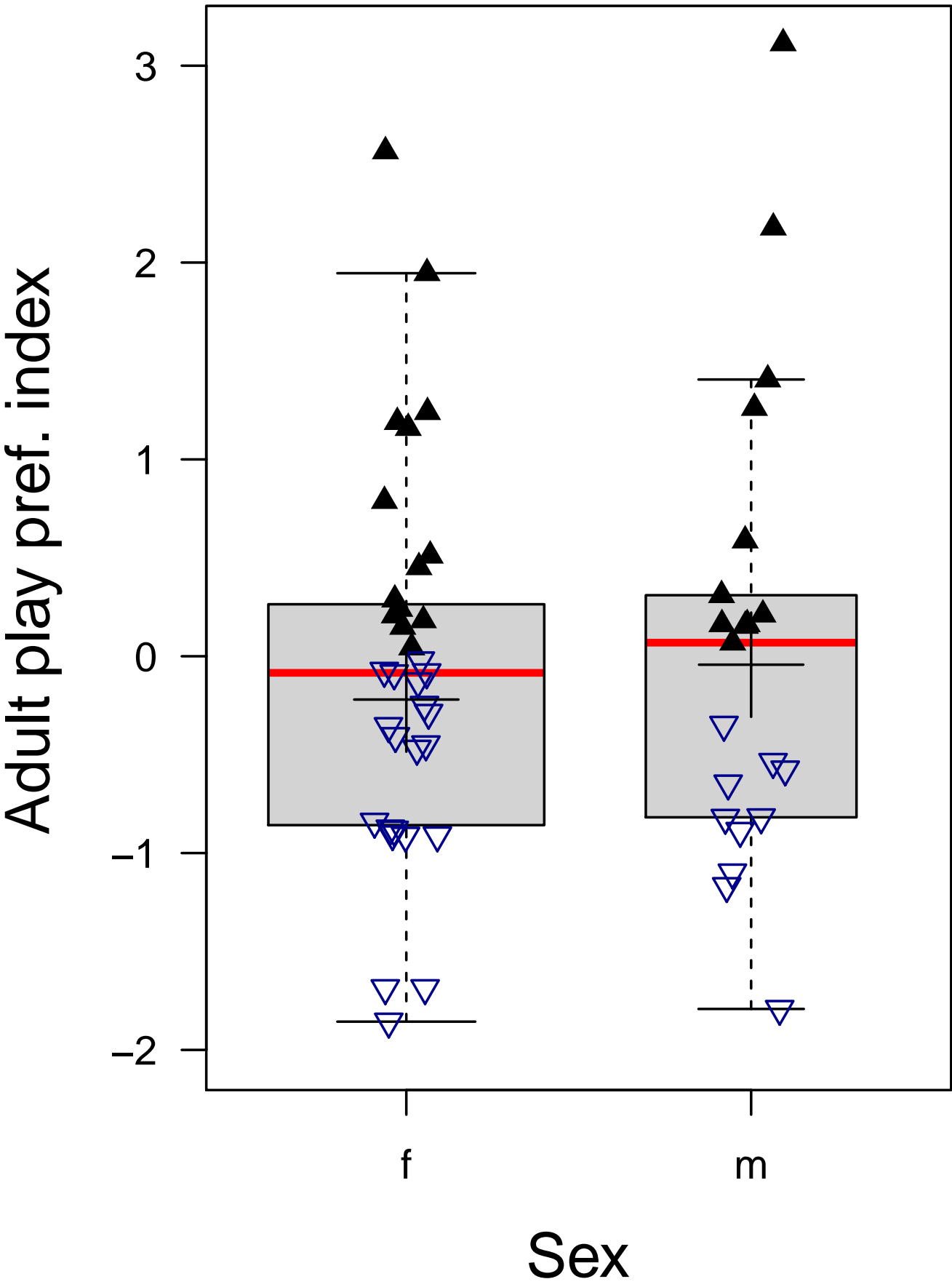


Figure 5

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## **Acknowledgements**

Funding by the Basque Government is gratefully acknowledged (BF198.16-AK) for the research conducted in Mexico, and also the sponsorship of ‘Fondazione Aldo Gini’ in Costa Rica. We wish to thank Pedro Dias and Filippo Aureli for advice on statistical modelling. We are also very grateful to the staff of the ‘Parque de la Flora y Fauna Silvestre Tropical’ in Catemaco, Mexico, and the staff of Guanacaste Conservation Area headquarters for their company and help during this work. We want to thank Anna Gemma Biasin, Federico Venturato, Riccardo De Conto, Chiara Miotto, Joaquin Vierna for their valuable assistance in the field in Costa Rica.

### **Animal welfare note**

Our study was non-invasive and exclusively observational, carried out with the permission of the corresponding authorities in Mexico and Costa Rica. The research adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates, and follows and the American Society of Mammologists' Guidelines on wild mammals in research.

### **Author Contribution Statement**

Norberto Asensio: Study design, data collection, data curation, data analyses and writing; Eugenia Zandona: Study design, data collection, data curation and writing; Jurgi Cristobal-Azkarate: Methodology, writing, review, editing; Jacob Dunn: Methodology, writing, review, editing.