1   **TITLE**

2   Socioecological factors affecting range defensibility among howler monkeys

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ABSTRACT

Range defensibility is defined as the ability of animals to efficiently move over an area to monitor and defend it. Therefore, range defensibility can help understand the spatial structure of animal territoriality. We used howler monkeys (*Alouatta* spp), a genus for which no agreement on the extent of their territoriality exists, to investigate the factors mediating range defensibility. We compared the defensibility index (D) across 63 groups of howler monkeys, representing 8 different species, based on a literature review. All species, except *Alouatta palliata*, were classified as potentially territorial according to D, although there was high variability within and among species. Group size had a positive effect on D, probably due to the greater ability of groups to defend a territory as they become larger. Study area had a negative effect on D, perhaps suggesting that unlike small areas, large areas allow groups to have territories that do not require significant defense from neighbours. However, population density was the factor with the strongest effect on D, with greater monitoring of home ranges under high levels of competition. Our results suggest that howler monkeys are theoretically capable of maintaining a territory and suggest that animals can show a gradient in territoriality, which can be mediated by the competitive context in which it occurs.

KEYWORDS: *Alouatta*; defensibility index; ranging costs; territoriality; socioecology

INTRODUCTION

Territoriality plays a key role in determining the structure, distribution, and behavior of individuals, groups and populations over available space, as it regulates how organisms share a particular area (Brown 1964; Maher and Lott 2000; Dugatkin 2009). However, we do not yet have a good understanding of the pressures leading to differences in territoriality within and among species (Packer *et al.* 2005; Shonfield *et al.* 2012; Sorato *et al.* 2015; Potts and Lewis 2016). Fundamentally, territoriality refers to the defense of an area against intruders through physical defense or tenure advertising displays (Noble 1939; Nice 1941; Burt 1943; Tinbergen 1957; Brown 1969; Carpenter and MacMillen 1967; Bates 1970; Wilson 1975; Maher and Lott 2000; Powel 2000; Mai et al 2005; Borger *et al.* 2008; Pott and Lewis 2014; Bartlett and Light 2017). Territorial displays consist of auditory, visual or olfactory signals that advertise area tenure to others, which act as a proxy of the riskier and more energy consuming overt defense (e.g. *Presbytis johnii*: Pourier 1968; *Hylobates agilis*: Mitani 1987; *Lemur catta*: Kappeler 1998). Consequently, territorial behavior is usually associated with a fixed and exclusive area called territory. However, there are a wide variety of conceptual definitions of territoriality, making it difficult to operationalize and compare between researchers (reviewed by Maher and Lott 1995). Furthermore, depending on the definition used in a given taxon, the study of territoriality may need quite detailed behavioral data (e.g., on ranging, home range overlap, intergroup behavior, critical resources, etc.), which can be difficult to acquire.

One related, but more accessible, parameter that studies have frequently used to understand territoriality among animals, and particularly primates, is range defensibility. Range defensibility refers to the capacity for an animal to move over a given area to monitor and defend it from intruders (Mitani and Rodman 1979, Lowen and Dunbar 1994). Mitani and Rodman (1979) operationalized range defensibility using the ratio of mean day journey

78   length to the diameter of the home range: the D index. Lowen and Dunbar (1994) further

79   developed the index by taking into account the detection distance of intruders, but this study

80   reached the same conclusions as Mitani and Rodman (1979): animals are more likely to be

81   territorial when the ratio of daily movement to home range is more than one.

82   Territoriality should occur when critical resources are sufficiently abundant and

83   predictable in space and time, i.e. when they are economically monopolizable, so that the

84   benefits from defending the area containing them outweigh the costs (Brown 1964; Carpenter

85   and MacMillen 1976; Schoener 1987, Pulliam and Caraco 1984, Grant *et al.* 1992). Similarly,

86   range defensibility should follow this economic notion of space; the benefits of being mobile

87   should be more rewarding than its costs (Schoener 1987; Kinnaird 1992; Maher and Lott

88   1995). Kinnaird and O'Brien (2007) found a clear relationship between hornbill body size

89   and D, supporting a classification of territorial and non-territorial hornbills by linking D to

90   fighting ability. In primates, Mitani and Rodman (1979) and Lowen and Dunbar (1994) both

91   found that that D positively discriminated territorial from non-territorial, with a tendency to

92   defend a range when it is more economically practicable to patrol it ($D > 1$). Several other

93   studies of primates have also associated D to territoriality (e.g. Chapman & Fedigan 1984;

94   Van Schaick *et al.* 1992; Peres 2000; Wich and Nunn 2002; Willems and van Schaick 2015).

95   However, none, to date, have examined the selection pressures driving it.

96   Howler monkeys (*Alouatta* spp.) may indicate territoriality in their eponymous roars

97   (e.g. Carpenter 1934; Bernstein 1964; Howich and Gebhard 1983; Da Cunha and Jalles-Filho

98   2007), scent marking (Braga Hirano 2008; Sekulic and Eisenberg 1983) and collective

99   defecation (Braza *et al.* 1981; Shoemaker 1982; Drubble and Gautier 1993). However, there

100   could be different interpretations of these behaviours. Rather than having a territorial

101   function, roaring could act as a mechanism for intergroup spacing and mutual avoidance

102   (Sekulic and Chivers 1986; Kitchen 2006; Da Cunha and Byrne 2006; Chiarello 1995). Scent

103   marking, defecation and intergroup encounters can occur anywhere in the home range, and

104   are not clustered at boundaries (Chivers 1969; Gittins 1980; Cornick and Markowitz 2002;

105   Gavazzi *et al.* 2008). Finally, the home ranges of neighboring groups often overlap

106   substantially (Klein 1974; Whitehead 1989; Gavazzi *et al.* 2008), which violates the essence

107   of a territory (Brown 1969).

108   Those who argue that howler monkeys are not territorial have suggested that their

109   highly folivorous diet and physiological inability to process cellulose do not allow them to

110   spend time in aggressive intergroup encounters or to patrol home ranges (Crocket and

111   Eisenberg 1987; Strier 1992). The traditional argument is that leaves are evenly distributed in

112   the landscape and do not to permit monopolization and food competition (Janson and van

113   Schaik 1986). However, howler monkeys are more correctly defined as folivorous-frugivores

114   and evidence exists for competition over limited fruit resources (Jones 1980; Chapman 1988;

115   Chaves and Bicca-Marques 2016). In addition, there is also support challenging the idea that

116   folivory does not create food competition (Snaith and Chapman 2005; Sayers 2013); howler

117   monkeys are highly selective in the leaves they consume (they forage from young leaves

118   from a wide range of species, to avoid intoxication from secondary compounds) and, thus,

119   competition for limited leaves can also arise (Milton 1979; Arroyo-Rodriguez and

120   Mandujano, 2006; Knopff and Pavelka, 2006). Moreover, there is evidence that howler

121   monkeys sometimes behave aggressively towards neighbors (Degusta and Milton 1998;

122   Cristobal-Azkarate *et al.* 2004).

123   Thus, there is no general agreement about the extent of territoriality among howler

124   monkeys, or the factors mediating range defensibility. Here we studied range defensibility

125   among howler monkeys using 63 groups, representing 8 species, and examined its socio-

126   ecological correlates using linear mixed models.

128 **METHODOLOGY**

129 *Study groups*

130 We used the database published by Fortes and colleagues (2015) on the movement ecology of

131 91 groups of howler monkeys, belonging to eight species. Only 64 groups, however, had

132 sufficient information on home range size and daily path length to allow us to calculate D

133 (online resource 1). For these 64 groups, we extracted the following socioecological

134 variables: study area (square km); group size; number of adult females; number of adult

135 males; number of immatures; howler monkey density (individuals per hectare); percentage of

136 fruit in the diet; forest type (araucaria forest, dry deciduous forest, rainforest, semideciduous

137 forest, seminatural forest, and subtropical forest) and home range overlap (online resource 1).

138 If the database provided a range of values instead of a single data point for any of the

139 variables, we used the median for posterior statistical analyses. To calculate D we used kernel

140 home range sizes when available, otherwise we used that estimated by other methods (i.e.

141 minimum convex polygon or grid cell).

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143 *Defensibility index*

144 We calculated the defensibility index (D) for each howler monkey group. This value

145 describes the likelihood that a group will encounter its own home range boundary as it moves

146 within it on an average day: $D = d/d'$, where d is equal to the average daily path length and d'

147 is equal to the diameter of a circle with the area equal to that of the observed home range

148 (Mitani & Rodman, 1979). A territorial species will theoretically have a D index > 1, which

149 represents the ability to cross the full width of the home range during a day of normal travel.

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151   *Statistical analyses*

152   We used analysis of variance (Kruskal-Wallis), followed by pairwise comparisons using

153   Tukey and Kramer (Nemenyi) posthoc tests, to examine differences in *D* across the eight

154   howler monkey species. We then ran linear mixed effect models (LMMs) to investigate how

155   the different independent variables (study area, group size, howler monkey density

156   percentage of fruit in the diet, and forest type) affected *D*, with species fitted as a random

157   factor. We eliminated an outlier point which was two standard deviations below the mean and

158   thus the database was finally equal to 63 groups. We also discarded home range overlap from

159   the LMMs due to the very low sample size (N = 20) to compare across different species and

160   predictors. Therefore, we compared the relationship between home range overlap and *D* using

161   a Spearman rank test. As we found high autocorrelation between group size, number of

162   females, number of males and number of immatures, we used only group size for analyses as

163   it had the greatest sample size. We applied natural logarithmic transformations to all

164   covariates, except proportion of fruit, which we arcsine square root transformed. Prior to

165   LMM analyses we also standardized all independent variables by first subtracting the mean

166   from each value, and then dividing by its standard deviation.

167   Because information-criteria based approaches require complete cases (i.e. no missing

168   data) in order to compare among different candidate models, we employed a multiple

169   imputation approach (online resource 2) to handle missing data while running LMMs

170   (Nakagawa and Freckleton 2001; van Buuren and Groothuis-Oudshoorn 2011). The multiple

171   imputation method fills in missing values ensuring that imputed data values are still plausible

172   as they are drawn from a distribution specifically designed for each missing value. When

173   used together with information criteria approaches, multiple imputation provides consistent

174   parameter estimation and confidence intervals that fully incorporate uncertainty due to

175   missing data in a lambda score (Rubin 1987). We used predictive mean matching (PMM) as

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176   the imputation method, which considers a scenario of data missing completely at random to

177   estimate 20 plausible imputed datasets (m = 20) based on 99 bootstrap replicates of the mean

178   (Morris et al. 2014). PMM fills in missing values randomly from the donors' closest matches,

179   then randomly samples one of the donors, and finally returns the observed value of the match

180   (Morris et al. 2014).

181   We fitted independent variables in all possible combinations to create a list of

182   explanatory models, with species fitted as a random factor to control for data dependency and

183   between-species variance. Then we ran each of the explanatory models with each of the 20

184   imputed databases and calculated the mean (SE) Akaike information criterion (AIC,

185   Tabachnick and Fidell 2007) for each model following Nakagawa and Freckleton (2001). We

186   considered the models within an AIC distance of ≤ 2 (ΔAIC ≤ 2) to indicate substantial

187   explanatory support and models with ΔAIC between 2 and 7 to indicate moderate support

188   (Burnham and Anderson 2002). Then, from this set of *a priori* models (ΔAIC< 7) we used

189   further AIC related statistics that consider model selection uncertainty (Snipes and Taylor,

190   2014):

191    $$Akaike\ Weight\ (w) = \frac{\exp(-\frac{1}{2}\Delta AIC_i)}{\sum_{r=1}^{R} \exp(\frac{1}{2}\Delta AIC_i)}$$

192    $$Evidence\ Ratio\ (ER) = \frac{w_{best}}{w_i}$$

193    $$Log_{10}(ER) : LER_i = log_{10}(ER_i)$$

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195   where AIC_i is the individual AIC score for each of the models, R is the total number of

196   models, r is the model being considered, w_{best} is the weight of the best model, and w is the

197   weight of the other individual models. Following Kass and Raftery (1995), we ranked models

198   as ''minimal'', "substantial", "strong", and "decisive" to correspond approximately to log

199   evidence ratios (LERs) of 0, 0.5, 1, and 2, respectively. We reported all factors included in the

200   best-supported models as applicable contributors to model outcome, including those that did

201   not give significant P values. We further investigated the factors in the models by assessing

202   their respective estimate coefficients, standard errors, and λ values (i.e. the proportion of total

203   variance that was attributable to the missing data). We visually inspected residual probability

204   plots for deviations from homoscedasticity and normality. We ran all statistical analyses in R

205   3.3.1 (R Development Core Team, 2016), using the libraries lme4 (Bates *et al.* 2012), MICE

206   (van Buuren and Groothuis-Oudshoorn 2011), and MuMIn (Barton 2016).

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208   **ETHICAL NOTE**

209   All the data we used are from published papers.

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211   **RESULTS**

212   All howler monkey species scored as territorial ($D \geq 1$) with the exception of *A. palliata* ($D =$

213   0.96, $\pm$SD = 0.49; Fig. 1). Nonetheless, there was considerable variation in the mean D values

214   across species (Fig. 1). We found significant differences in D across the eight howler monkey

215   species (Kruskal-Wallis χ^2 = 20.3, P = 0.005, df = 7). In particular, *A. caraya* (Kruskal-Wallis

216   poshoc-test, P = 0.007) and *A. guariba* (P = 0.006) had significantly higher D values than *A.*

217   *palliata*. Other pairwise posthoc comparisons were not significant.

218   Mean home range overlap ($\pm$SD) with neighboring groups was 30.2% ($\pm$ 5.5%) and

219   was highly variable (range 0% to 87%). We found no correlation between home range

220   overlap and D (rs = 0.17, P = 0.45, N = 20).

221   We first obtained 13 potential explanatory LMM models: three with strong support

222   (ΔAIC < 2) and 10 with moderate support (ΔAIC = 2-7, table 1). There was substantial

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223   evidence in favour of the model with the lowest AIC (i.e. the full model) relative to the other

224   models (LER > 0.5), with the exception of the next two best models (model 2 and model 3

225   hereafter) with delta AIC < 2. The best three models together received 69% of the weight of

226   all models considered, thus we selected these models as the final best explanatory models.

227   Visual inspection of residual plots of the best three models did not reveal deviations from

228   homoscedasticity or normality. In all models, group size had a positive effect on D, whereas

229   study area had a negative effect (Fig. 2; Table 2). Percentage of fruit in the diet had a weak

230   negative effect on D. The full model also included forest type among its explanatory

231   variables for D, but the standard errors of the effect of different forest types were too large to

232   conclude any clear pattern. Howler monkey density was the parameter with the strongest

233   effect on D in all the three models. Both model2 and model3 contained study area, group size

234   and howler monkey density with similar effects on D to the full model (table 2).

235

236   **DISCUSSION**

237   We found considerable variation in range defensibility both within and among howler

238   monkey species. This is, not all of the group home ranges were equally defendable from

239   potential intrusion. These results highlight the fact that range defensibility can be expressed

240   differently not only across closely related species, but among groups of the same species. In

241   addition, these results suggest that howler monkeys are theoretically able to move in a

242   manner that allows for the defense of a home range from rival neighbors.

243   *A. palliata* was the only species that could theoretically be non-territorial according

244   to D. Bergman *et al.* (2016) suggested that *A. palliata* is a species with high levels of

245   intragroup competition and low levels of intergroup competition, which could minimize their

246   interest in defending territories against neighbours. Mitani and Rodman (1979) also found a

247   similar pattern of D, with the variance spanning zero – from territorial to non-territorial – in

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248 black and white colobus monkeys (*Colobus guereza*) and gray langurs (*Presbytis entellus*). *A.*

249 *palliata* live in larger social groups than other howler monkey species, composed of several

250 males and females (Estrada *et al.* 2006; Asensio *et al.* 2007; Arroyo-Rodriguez *et al.* 2008;

251 Dunn *et al.* 2015). Large groups could deplete food sources faster than small groups (i.e.,

252 scramble competition, Dias and Rangel-Negrín 2015), which could lead to larger home

253 ranges (Isbell 1991) and in turn smaller D scores. However, indication of territoriality in *A.*

254 *palliata* was borderline, with a high within-species variability (mean $D = 0.96$, SD $= 0.49$) for

255 precluding any definitive territorial behavior in the species. Moreover, LMM analyses, taking

256 all the members of the genus together, found a positive relationship between D and group size

257 while controlling for the effect of "species". This general relationship supports the

258 resource holding potential hypothesis (Parker 1974) for *Alouatta*, which states that groups

259 with higher fighting ability (i.e. larger group sizes) will generally exhibit a higher ability to

260 defend a territory (e.g. Wilson and Wranghan 2003, Mosser and Packer 2008).

261   The percentage of fruit in the diet was negatively associated with range defensibility

262 in howler monkeys, although it had a weak effect and a relatively large part of its variance

263 was attributable to missing data, and thus interpretations should be taken with caution. The

264 contribution of fruit to the diet should theoretically have a positive impact on range

265 defensibility as fruit is a defendable resource (Brown 1964; Emlen and Oring 1977, Clutton-

266 Brock and Harvey 1977; Davies and Houston 1984). We should also expect a high D with a

267 frugivorous diet due to the relatively high energy provided by such a diet, which permits

268 more movement in comparison to that based on leaves (Milton 1980). The observed weak

269 effect of frugivory on range defensibility in howler monkeys could be related to the

270 relationship between resource value and fruit abundance not being necessarily strong and

271 linear (Grant 1993; Maher and Lot 2000). In addition, the stronger effect of howler monkey

272 density on D hindered a clear relationship between diet and range defensibility. It is also

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273   possible that there are effects of food abundance and distribution not accounted for in such a

274   relationship due to potential differences in seasonal territoriality not detected in the overall

275   large temporal scale of the studies (e.g. Marler and Moore 1989; Golabek *et al.,* 2012).

276   Study area had a negative effect on the defensibility index of howler monkeys. A large

277   area should provide more available territories compared to a small area (c.f. Fretwell 1972,

278   Pen and Wessing 2000). In turn, a scenario of groups with territories in a large area would

279   create little overlap between neighboring groups and thus, low need for territorial patrolling.

280   This is related to the ecological concept of the ideal free distribution (Fretwell 1972).

281   Interestingly, groups living in very small and isolated fragments (< 10 ha) in this study may

282   have not had neighbors close by, but still displayed a high *D*, which might give a false

283   impression of high territorial defense. Instead, high defensibility scores in these cases might

284   have been simply related to the necessity of moving constantly across a small area in search

285   of limited resources.

286   The density of howler monkeys was the parameter with the strongest effect on *D* in

287   the three supported models, with greater *D* at higher densities. Animals deplete food more

288   quickly when more individuals are in the landscape, and greater *D* values are probably the

289   result of a greater need to move in search of food. In addition, howler monkeys might display

290   territorial behavior in landscapes with high densities of individuals in response to the greater

291   intergroup competition, as occurs in ring tailed lemurs (Jolly *et al.* 1993). Kitchen *et al.*

292   (2015) reasoned that *A. palliata* may actively compete with neighboring groups when living

293   at high densities. Holzmann *et al.* (2012) suggested that *A. guariba* make lower frequency

294   calls at higher population densities than lower population densities. Similarly, Shonfield *et al.*

295   (2012) observed that red squirrels (*Tamiasciurus hudsonicus*) produced territorial

296   vocalizations more likely when surrounded by higher densities of conspecifics.

297   Range defensibility in howler monkeys varied among socioecological scenarios (i.e.

298   large group size, small area, frugivorous diet, high population density) that favored

299   competition. To better understand the territorial nature of howler monkeys detailed analyses

300   of whether different species and groups have site-specific aggression and range exclusion

301   assessed through direct behavioral observations are needed. Studies using D have not

302   typically addressed the limitations of associating D directly with territoriality, and a high D is

303   not necessarily an unconditional proxy of territoriality. For example, Mitani and Rodman

304   (1979) also found that some primate species presenting high D values were in fact not

305   territorial as they did not engage in aggressive encounters. Nonetheless, as the term "

306   defensibility" denotes, D has an inherent nexus to the spatial organization of territorial

307   maintenance as it indicates whether mobility permits area monitoring. Thus, our results on

308   howler monkeys' range defensibility still suggest a territorial gradient depending on the

309   competitive circumstances of each particular site and the cost-benefits of being territorial.

310   Animals recognized as territorial show high plasticity in their degree of territoriality

311   in response to variation in food abundance and distribution (e.g. *Motacilla alba*: Zahavi 1971;

312   *Turdoides bicolor*: Golabek *et al.* 2012), habitat quality (e.g. *Canis lupus*: Kittle *et al.* 2015;

313   *Cordylochernes scorpiodes*: Zeh *et al.* 1997), mates and breeding sites (several carnivore,

314   ungulate and primate species: Grant *et al.* 1992; *Passerella iliaca*: Alcock 2005), seasonality

315   (*Sceloporus jarrovi*: Marler and Moore 1989) or various mixed factors (*Pteronura*

316   *brasiliensis*: Leuchtenberger *et al.* 2015; *Pan troglodytes*: Moore *et al.* 2015; *Pomatostomus*

317   *ruficeps*: Sorato *et al.* 2015). Furthermore, a species generally assumed to be non-territorial

318   such as the pigtailed macaque (*Macaca leonina*) can show territorial patterns under particular

319   circumstances that force high levels of competition (Jose-Dominguez *et al.* 2015). There is

320   evidence that territoriality does not need to be a species-specific trait (Carpenter and

321   MacMillen 1976; Powel *et al.* 1997). Animals may present "facultative territoriality", which

322   means that they may exhibit territoriality only under particular social and environmental

323   circumstances such as high population density and small area available (Chapman and

324   Fedigan 1984; Kinnaird 1992). Therefore, a continuum that goes from defending to not

325   defending a territory might reasonably exist in howler monkeys, which would adjust to

326   particular socioecological factors that require or favour area defense.

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603

604　**FIGURE LEGENDS**

605

606　**Figure 1.** Mitani and Rodman defensibility index (*D*) across different *Alouatta* species based

607　on a review of 64 studies of eight howler monkey species. Open circles indicate data points.

608　The horizontal black lines and cross represent the mean and median values, respectively.

609　Boxes extend to data points that are less than 1.5 x IQR away from 1st/3rd quartile. Whiskers

610　extend to minimum and maximum values.

611　**Figure 2**. Effects of area, group size, howler monkey population density, percentage of fruit

612　in diet and forest type on the Mitani and Rodman defensibility index (*D*). The distributions of

613　the predictors (covariates) are displayed with vertical short lines on the horizontal axis and

614　95% confidence intervals are shown in grey around the regression line. For forest type (the

615　only categorical predictor) dots indicate the expected mean *D*.

Table 1 and 2

Table 1. Summary of Akaike information criterion (AIC) results for *a priori* models (ΔAIC < 7) explaining the defensibility index in howler monkeys for different models based on 20 imputed datasets (m = 20). The best three selected models are in bold (full model, model2, and model3). Data were based on a review of 64 studies of eight howler monkey species.

Model	Mean AIC	se	Δ	w	ER	LER
study area+group size+howler monkey density+percentage of fruit in diet+forest type (full model)	**131.66**	**2.10**	**0**	**0.32**	**1.00**	**0**
study area+group size+howler monkey density (model2)	**132.33**	**1.32**	**0.67**	**0.23**	**1.40**	**0.15**
study area+group size+howler monkey density+percentage of fruit in diet (model3)	**133.32**	**1.46**	**1.66**	**0.14**	**2.29**	**0.36**
study area+group size+howler monkey density+forest type	134.61	1.47	2.95	0.07	4.38	0.64
study area+howler monkey density	134.74	1.40	3.08	0.07	4.67	0.67
study area+howler monkey density+percentage of fruit in diet	135.91	1.46	4.25	0.04	8.38	0.92
group size+howler monkey density	136.58	1.26	4.92	0.03	11.71	1.07
howler monkey density	137.06	1.26	5.40	0.02	14.90	1.17
group size+howler monkey density+percentage of fruit in diet+forest type	137.36	1.58	5.70	0.02	17.27	1.24
group size+howler monkey density+percentage of fruit in diet	137.54	1.32	5.88	0.02	18.91	1.28
study area+howler monkey density+percentage of fruit in diet+forest type	137.56	1.90	5.90	0.02	19.13	1.28
howler monkey density+percentage of fruit in diet	138.17	1.32	6.50	0.01	25.85	1.41
study area+howler monkey density+forest type	138.42	1.49	6.76	0.01	29.41	1.47

Δ = Delta AIC, w = Akaike weight; ER = evidence ratio; LER = log evidence ratio

Table 2. Summary of estimates (β) and standard errors (*se*) of individual parameters explaining range defensibility index (*D*) in howler monkeys considering the 20 imputed dataset (m = 20). Data were based on a review of 64 studies of eight howler monkey species.

Model	β	**se**	*t*	*df*	*P*	λ*
Full model						
(Intercept)	1.750	0.372	4.700	34.491	0.000	0.226
study area	-0.239	0.135	-1.772	21.362	0.091	0.442
group size	0.203	0.094	2.150	36.336	0.038	0.199
howler monkey density	0.637	0.152	4.192	18.586	0.001	0.499
percent of fruit in diet	-0.143	0.136	-1.052	18.996	0.306	0.491
dry deciduous forest	0.535	0.588	0.910	25.389	0.371	0.368
rainforest	0.283	0.346	0.818	38.154	0.418	0.173
semideciduous forest	0.446	0.272	1.636	42.135	0.109	0.116
seminatural forest	-0.421	0.561	-0.750	27.026	0.460	0.341
subtropical forest	-0.162	0.343	-0.474	34.153	0.638	0.231
model2						
(Intercept)	1.907	0.232	8.210	40.769	0.000	0.195
study area	-0.207	0.117	-1.773	26.781	0.088	0.385
group size	0.166	0.095	1.745	46.023	0.088	0.129
howler monkey density	0.597	0.129	4.614	24.953	0.000	0.415
model3						
(Intercept)	1.924	0.242	7.963	38.441	0.000	0.216
study area	-0.204	0.117	-1.744	25.806	0.093	0.395
group size	0.169	0.097	1.750	43.599	0.087	0.150
howler monkey density	0.603	0.131	4.613	23.977	0.000	0.426
percent of fruit in diet	-0.047	0.117	-0.403	25.165	0.691	0.405

*****lambda values** explaining the proportion of total variance attributable to missing data
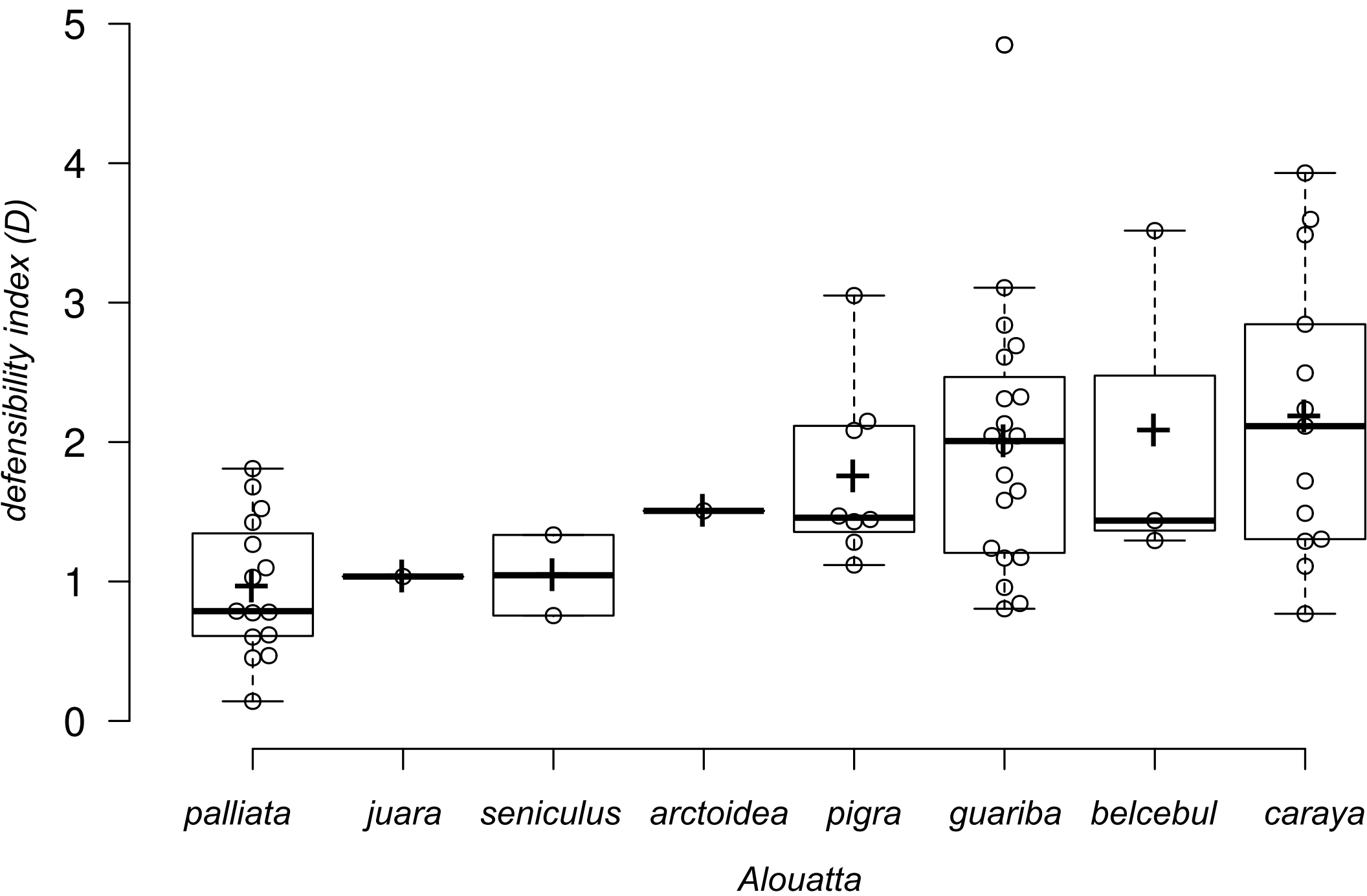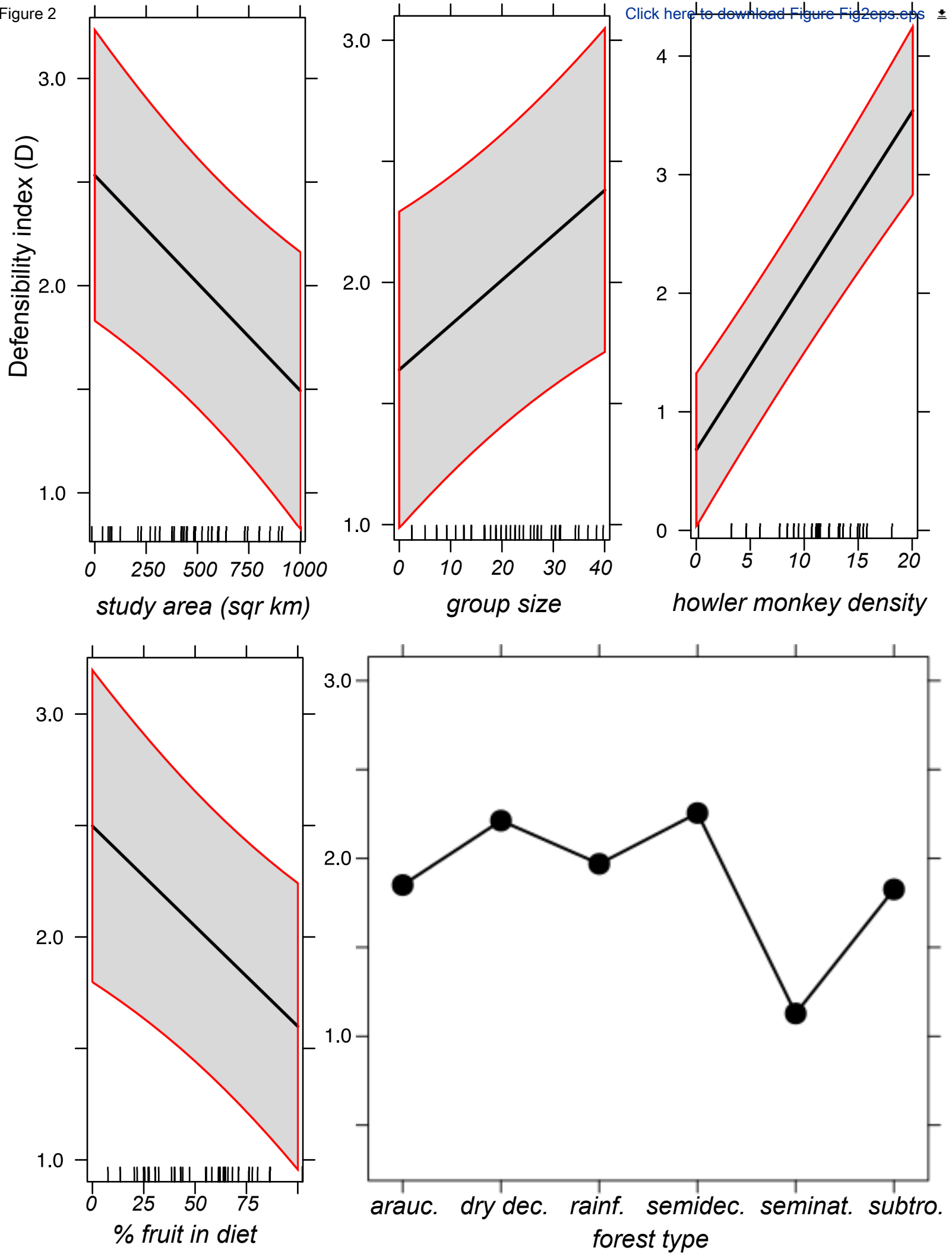
Figure 1

Figure 2

Click here to access/download
Supplemental File
IJP range defensibility howler raw data (2).xlsx

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Supplemental File
Sup Info 2 R code.txt