

Socioecological Factors Affecting Range Defensibility Among Howler Monkeys

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Received: 5 April 2017 / Accepted: 25 November 2017 / Published online: 27 January 2018
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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 us 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 owing 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 neighbors. 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

Handling Editor: Onja H. Razafindratsima

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10764-018-0016-z>) contains supplementary material, which is available to authorized users.

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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 · Socioecology · Territoriality

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; Dugatkin 2009; Maher and Lott 2000). 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; Potts and Lewis 2014; Shonfield *et al.* 2012; Sorato *et al.* 2015). Fundamentally, territoriality refers to the defense of an area against intruders through physical defense or tenure advertising displays (Bartlett and Light 2017; Bates 1970; Börger *et al.* 2008; Brown 1969; Burt 1943; Carpenter and MacMillen 1976; Maher and Lott 2000; Mai *et al.* 2005; Nice 1941; Noble 1939; Potts and Lewis 2014; Powell 2000; Tinbergen 1957; Wilson 1975). 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 a 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 (Lowen and Dunbar 1994; Mitani and Rodman 1979). Mitani and Rodman (1979) operationalized range defensibility using the ratio of mean day journey length to the diameter of the home range: the D index. Lowen and Dunbar (1994) further developed the index by taking into account the detection distance of intruders, but this study reached the same conclusions as Mitani and Rodman (1979): animals are more likely to be territorial when the ratio of daily movement to home range is >1 .

Territoriality should occur when critical resources are sufficiently abundant and predictable in space and time (i.e., when they are economically monopolizable), so that the benefits from defending the area containing them outweigh the costs (Brown 1964; Carpenter and MacMillen 1976; Grant *et al.* 1992; Pulliam and Caraco 1984; Schoener 1987). Similarly, range defensibility should follow this economic notion of space; the benefits of being mobile should be more rewarding than its costs (Kinnaird 1992; Maher and Lott 1995; Schoener 1987). Kinnaird and O'Brien (2007) found a clear relationship between hornbill body size and D , supporting a classification of territorial and nonterritorial hornbills by linking D to fighting ability. In primates,

Mitani and Rodman (1979) and Lowen and Dunbar (1994) both found that that D positively discriminated territorial from nonterritorial, with a tendency to defend a range when it is more economically practicable to patrol it ($D > 1$). Several other studies of primates have also associated D to territoriality (e.g., Chapman and Fedigan 1984; Peres 2000; Van Schaik 1992; Wich and Nunn 2002; Willems and van Schaik 2015). However, none, to date, have examined the selection pressures driving it.

Howler monkeys (*Alouatta* spp.) may indicate territoriality in their eponymous roars (e.g., Bernstein 1964; Carpenter 1934; Da Cunha and Jalles-Filho 2007; Horwich and Gebhard 1983), scent marking (Braga Hirano *et al.* 2008; Sekulic and Eisenberg 1983), and collective defecation (Braza *et al.* 1981; Drubbe and Gautier 1993; Shoemaker 1982). However, there could be different interpretations of these behaviors. Rather than having a territorial function, roaring could act as a mechanism for intergroup spacing and mutual avoidance (Chiarello 1995; Da Cunha and Byrne 2006; Kitchen 2006; Sekulic and Chivers 1986). Scent marking, defecation, and intergroup encounters can occur anywhere in the home range, and are not clustered at boundaries (Chivers 1969; Cornick and Markowitz 2002; Gavazzi *et al.* 2008; Gittins 1980). Finally, the home ranges of neighboring groups often overlap substantially (Gavazzi *et al.* 2008; Klein 1974; Whitehead 1989), which violates the essence of a territory (Brown 1969).

Those who argue that howler monkeys are not territorial have suggested that their highly folivorous diet and physiological inability to process cellulose do not allow them to spend time in aggressive intergroup encounters or to patrol home ranges (Crockett and Eisenberg 1987; Strier 1992). The traditional argument is that leaves are evenly distributed in the landscape and do not to permit monopolization and food competition (Janson and van Schaik 1988). However, howler monkeys are more correctly defined as folivore-frugivores and evidence exists for competition over limited fruit resources (Chapman 1988; Chaves and Bicca-Marques 2016; Jones 1980). In addition, there is also support challenging the idea that folivory does not create food competition (Sayers 2013; Snaith and Chapman 2005); howler monkeys are highly selective in the leaves they consume (they forage from young leaves from a wide range of species, to avoid intoxication from secondary compounds) and, thus, competition for limited leaves can also arise (Arroyo-Rodriguez and Mandujano 2006; Knopff and Pavelka 2006; Milton 1979). Moreover, there is evidence that howler monkeys sometimes behave aggressively towards neighbors (Cristóbal-Azkarate *et al.* 2004; Degusta and Milton 1998).

Thus, there is no general agreement about the extent of territoriality among howler monkeys, or the factors mediating range defensibility. Here we studied range defensibility among howler monkeys using 63 groups, representing 8 species, and examined its socioecological correlates using linear mixed models.

Methods

Study Groups

We used the database published by Fortes *et al.* (2015) on the movement ecology of 91 groups of howler monkeys, belonging to 8 species. Only 64 groups, however, had sufficient information on home range size and daily path length to allow us to calculate D (Electronic Supplementary Material [ESM] 1). For these 64 groups, we extracted the

following socioecological variables: study area (km²), group size, number of adult females, number of adult males, number of immatures, howler monkey density (individuals per hectare), percentage of fruit in the diet, forest type (araucaria forest, dry deciduous forest, rainforest, semideciduous forest, seminatural forest, and subtropical forest), and home range overlap (ESM 1). If the database provided a range of values instead of a single data point for any of the variables, we used the median for posterior statistical analyses. To calculate D we used kernel home range sizes when available; otherwise we used that estimated by other methods (i.e., minimum convex polygon or grid cell).

Defensibility Index

We calculated the defensibility index (D) for each howler monkey group. This value describes the likelihood that a group will encounter its own home range boundary as it moves within it on an average day: $D = d/d'$, where d is equal to the average daily path length and d' is equal to the diameter of a circle with the area equal to that of the observed home range (Mitani and Rodman 1979). A territorial species will theoretically have a D index >1 , which represents the ability to cross the full width of the home range during a day of normal travel.

Statistical Analyses

We used analysis of variance (Kruskal–Wallis), followed by pairwise comparisons using Tukey and Kramer (Nemenyi) *post hoc* tests, to examine differences in D across the eight howler monkey species. We then ran linear mixed effect models (LMMs) to investigate how the different independent variables (study area, group size, howler monkey density, percentage of fruit in the diet, and forest type) affected D , with species fitted as a random factor. We eliminated an outlier point that was two standard deviations below the mean and thus the database was finally equal to 63 groups. We also discarded home range overlap from the LMMs because of the very low sample size ($N = 20$) to compare across different species and predictors. Therefore, we compared the relationship between home range overlap and D using a Spearman rank test. As we found high autocorrelation between group size, number of females, number of males, and number of immatures, we used only group size for analyses, as it had the greatest sample size. We applied natural logarithmic transformations to all covariates, except proportion of fruit, which we arcsine square root transformed. Prior to LMM analyses we also standardized all independent variables by first subtracting the mean from each value and then dividing by its standard deviation.

Because information criteria-based approaches require complete cases (i.e., no missing data) in order to compare among different candidate models, we employed a multiple imputation approach (ESM 2) to handle missing data while running LMMs (Nakagawa and Freckleton 2011; van Buuren and Groothuis-Oudshoorn 2011). The multiple imputation method fills in missing values ensuring that imputed data values are still plausible, as they are drawn from a distribution specifically designed for each missing value. When used together with information criteria approaches, multiple imputation provides consistent parameter estimation and confidence intervals that fully incorporate uncertainty due to missing data in a lambda score (Rubin 1987). We used predictive mean matching

(PMM) as the imputation method, which considers a scenario of data missing completely at random to estimate 20 plausible imputed datasets ($m = 20$) based on 99 bootstrap replicates of the mean (Morris *et al.* 2014). PMM fills in missing values randomly from the donors' closest matches, then randomly samples one of the donors, and finally returns the observed value of the match (Morris *et al.* 2014).

We fitted independent variables in all possible combinations to create a list of explanatory models, with species fitted as a random factor to control for data dependency and interspecific variance. Then we ran each of the explanatory models with each of the 20 imputed databases and calculated the mean (SE) Akaike information criterion (AIC, Tabachnick and Fidell 2007) for each model following Nakagawa and Freckleton (2011). We considered the models within an AIC distance of ≤ 2 ($\Delta AIC \leq 2$) to indicate substantial explanatory support and models with ΔAIC between 2 and 7 to indicate moderate support (Burnham and Anderson 2002). Then, from this set of *a priori* models ($\Delta AIC < 7$) we used further AIC related statistics that consider model selection uncertainty (Snipes and Taylor 2014):

$$\text{Akaike weight } (w) = \frac{\exp\left(-\frac{1}{2} \Delta AIC_i\right)}{\sum_{r=1}^R \exp\left(\frac{1}{2} \Delta AIC_i\right)}$$

$$\text{Evidence ratio } (ER) = \frac{w_{best}}{w_i}$$

$$\text{Log}_{10}(ER) : LER_i = \log_{10}(ER_i)$$

where AIC_i is the individual AIC score for each of the models, R is the total number of models, r is the model being considered, w_{best} is the weight of the best model, and w is the weight of the other individual models. Following Kass and Raftery (1995), we ranked models as minimal, substantial, strong, and decisive to correspond approximately to log evidence ratios (LERs) of 0, 0.5, 1, and 2, respectively. We reported all factors included in the best-supported models as applicable contributors to model outcome, including those that did not give significant P values. We further investigated the factors in the models by assessing their respective estimate coefficients, standard errors, and λ values (i.e., the proportion of total variance that was attributable to the missing data). We visually inspected residual probability plots for deviations from homoscedasticity and normality. We ran all statistical analyses in R 3.3.1 (R Development Core Team 2008), using the libraries lme4 (Bates *et al.* 2012), MICE (van Buuren and Groothuis-Oudshoorn 2011), and MuMIn (Bartoń 2016).

Ethical Note

All the data we used are from published papers. The authors declare they have no conflicts of interest.

Results

All howler monkey species scored as territorial ($D \geq 1$) with the exception of *Alouatta palliata* ($D = 0.96$, \pm SD = 0.49; Fig. 1). Nonetheless, there was considerable variation in the mean D values across species (Fig. 1). We found significant differences in D across the eight howler monkey species (Kruskal–Wallis $\chi^2 = 20.3$, $P = 0.005$, $df = 7$). In particular, *A. caraya* (Kruskal–Wallis *post hoc* test, $P = 0.007$) and *A. guariba* ($P = 0.006$) had significantly higher D values than *A. palliata*. Other pairwise *post hoc* comparisons were not significant.

Mean home range overlap (\pm SD) with neighboring groups was 30.2% (\pm 5.5%) and was highly variable (range 0% to 87%). We found no correlation between home range overlap and D ($r_s = 0.17$, $P = 0.45$, $N = 20$).

We first obtained 13 potential explanatory LMM models: three with strong support (Δ AIC < 2) and 10 with moderate support (Δ AIC = 2–7, Table I). There was substantial evidence in favor of the model with the lowest AIC (i.e., the full model) relative to the other models (LER > 0.5), with the exception of the next two best models (model 2 and model 3 hereafter) with delta AIC < 2. The best three models together received 69% of the weight of all models considered; thus we selected these models as the final best explanatory models. Visual inspection of residual plots of the best three models did not reveal deviations from homoscedasticity or normality. In all models, group size had a positive effect on D , whereas study area had a negative effect (Fig. 2; Table II). Percentage of fruit in the diet had a weak negative effect on D . The full model also included forest type among its explanatory variables for D , but the standard errors of the effect of different forest types were too large to conclude any clear pattern. Howler monkey density was the parameter with the strongest effect on D in all the three models. Both model 2 and model 3 contained study area, group size, and howler monkey density with effects on D similar to those of the full model (Table II).

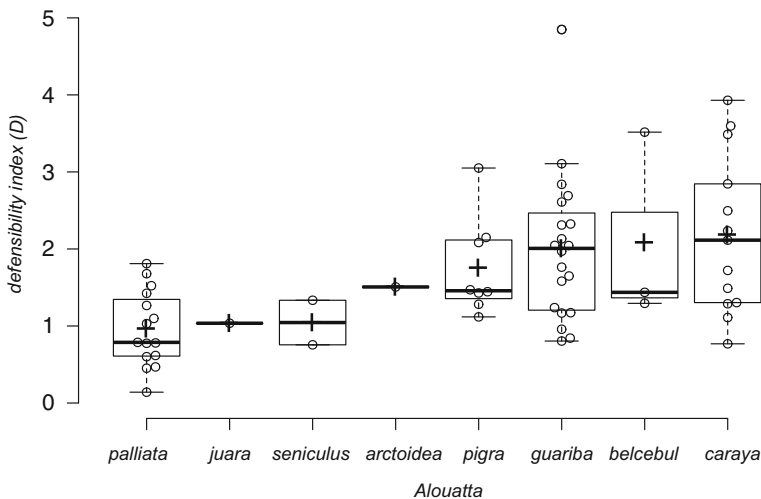


Fig. 1 Mitani and Rodman defensibility index (D) across different *Alouatta* species based on a review of 64 studies of 8 howler monkey species. Open circles indicate data points. The horizontal black lines and cross represent the mean and median values, respectively. Boxes extend to data points that are less than $1.5 \times$ IQR away from 1st/3rd quartile. Whiskers extend to minimum and maximum values.

Table 1 Summary of Akaike information criterion (AIC) results for *a priori* models ($\Delta\text{AIC} < 7$) explaining the defensibility index in howler monkeys for different models based on 20 imputed datasets ($m = 20$)

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 (model 2)	132.33	1.32	0.67	0.23	1.40	0.15
Study area + group size + howler monkey density + percentage of fruit in diet (model 3)	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

The best three selected models are in bold (full model, model 2, and model 3). Data were based on a review of 64 studies of eight howler species

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

Discussion

We found considerable variation in range defensibility both within and among howler monkey species. This is, not all of the group home ranges were equally defensible from potential intrusion. These results highlight the fact that range defensibility can be expressed differently not only across closely related species, but among groups of the same species. In addition, these results suggest that howler monkeys are theoretically able to move in a manner that allows for the defense of a home range from rival neighbors.

Alouatta palliata was the only species that could theoretically be nonterritorial according to *D. Bergman et al.* (2016) suggested that *A. palliata* is a species with high levels of intragroup competition and low levels of intergroup competition, which could minimize their interest in defending territories against neighbors. Mitani and Rodman (1979) also found a similar pattern of *D*, with the variance spanning zero—from territorial to nonterritorial—in black-and-white colobus monkeys (*Colobus guereza*) and gray langurs (*Presbytis entellus*). *A. palliata* live in larger social groups than other howler monkey species, composed of several males and females (Arroyo-Rodríguez *et al.* 2008; Asensio *et al.* 2007; Dunn *et al.* 2015; Estrada *et al.* 2006). Large groups could deplete food sources faster than small groups (i.e., scramble competition, Dias

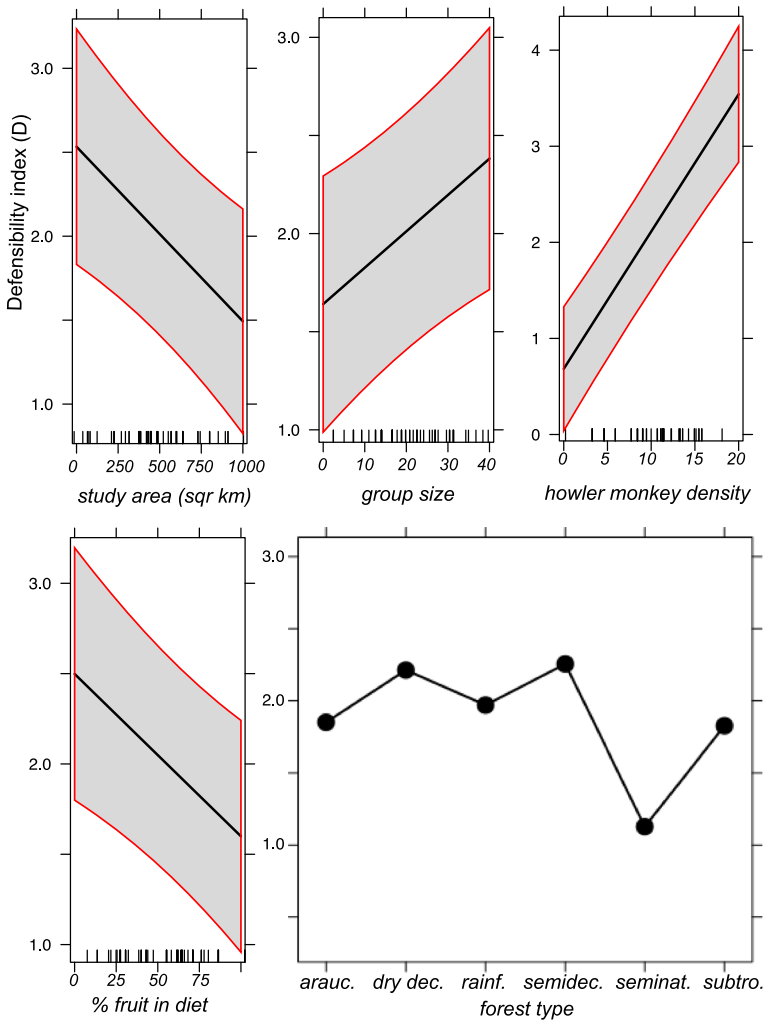


Fig. 2 Effects of area, group size, howler monkey population density, percentage of fruit in diet, and forest type on the Mitani and Rodman defensibility index (D). The distributions of the predictors (covariates) are displayed with vertical short lines on the horizontal axis and 95% confidence intervals are shown in gray around the regression line. For forest type (the only categorical predictor) dots indicate the expected mean D .

and Rangel-Negrín 2015), which could lead to larger home ranges (Isbell 1991) and in turn smaller D scores. However, indication of territoriality in *A. palliata* was borderline, with a high intraspecific variability (mean $D = 0.96$, $SD = 0.49$) for precluding any definitive territorial behavior in the species. Moreover, LMM analyses, taking all the members of the genus together, found a positive relationship between D and group size while controlling for the effect of species. This general relationship supports the resource holding potential hypothesis (Parker 1974) for *Alouatta*, which states that groups with higher fighting ability (i.e., larger group sizes) will generally exhibit a higher ability to defend a territory (e.g., Mosser and Packer 2008; Wilson and Wrangham 2003).

Table II Summary of estimates (β) and standard errors (SE) of individual parameters explaining range defensibility index (D) in howler monkeys considering the 20 imputed dataset ($m = 20$)

Model	β	SE	t	df	P	λ^a
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
Model 2						
(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
Model 3						
(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

Data were based on a review of 64 studies of eight howler monkey species

^a λ values explaining the proportion of total variance attributable to missing data

The percentage of fruit in the diet was negatively associated with range defensibility in howler monkeys, although it had a weak effect and a relatively large part of its variance was attributable to missing data, and thus interpretations should be taken with caution. The contribution of fruit to the diet should theoretically have a positive impact on range defensibility as fruit is a defendable resource (Brown 1964; Clutton-Brock and Harvey 1977; Davies and Houston 1984; Emlen and Oring 1977). We should also expect a high D with a frugivorous diet owing to the relatively high energy provided by such a diet, which permits more movement in comparison to that based on leaves (Milton 1980). The observed weak effect of frugivory on range defensibility in howler monkeys could be related to the relationship between resource value and fruit abundance not being necessarily strong and linear (Grant *et al.* 1992; Maher and Lott 2000). In addition, the stronger effect of howler monkey density on D hindered a clear relationship between diet and range defensibility. It is also possible that there are effects of food abundance and distribution not accounted for in such a relationship owing to potential differences in seasonal territoriality not detected in the overall large temporal scale of the studies (e.g., Golabek *et al.* 2012; Marler and Moore 1989).

Study area had a negative effect on the defensibility index of howler monkeys. A large area should provide more available territories compared to a small area (*cf.* Fretwell 1972; Pen and Weissing 2000). In turn, a scenario of groups with territories in a large area would create little overlap between neighboring groups, and thus low need for territorial patrolling. This is related to the ecological concept of the ideal free distribution (Fretwell 1972). Interestingly, groups living in very small and isolated fragments (< 10 ha) in this study may have not had neighbors close by, but still displayed a high D , which might give a false impression of high territorial defense. Instead, high defensibility scores in these cases might have been simply related to the necessity of moving constantly across a small area in search of limited resources.

The density of howler monkeys was the parameter with the strongest effect on D in the three supported models, with greater D at higher densities. Animals deplete food more quickly when more individuals are in the landscape, and greater D values are probably the result of a greater need to move in search of food. In addition, howler monkeys might display territorial behavior in landscapes with high densities of individuals in response to the greater intergroup competition, as occurs in ring-tailed lemurs (Jolly *et al.* 1993). Kitchen *et al.* (2015) reasoned that *Alouatta palliata* may actively compete with neighboring groups when living at high densities. Holzmann *et al.* (2012) suggested that *A. guariba* make lower frequency calls at higher population densities than lower population densities. Similarly, Shonfield *et al.* (2012) observed that red squirrels (*Tamiasciurus hudsonicus*) were more likely to produce territorial vocalizations when surrounded by higher densities of conspecifics.

Range defensibility in howler monkeys varied among socioecological scenarios (i.e., large group size, small area, frugivorous diet, high population density) that favored competition. To better understand the territorial nature of howler monkeys, detailed analyses of whether different species and groups have site-specific aggression and range exclusion assessed through direct behavioral observations are needed. Studies using D have not typically addressed the limitations of associating D directly with territoriality, and a high D is not necessarily an unconditional proxy of territoriality. For example, Mitani and Rodman (1979) also found that some primate species presenting high D values were in fact not territorial, as they did not engage in aggressive encounters. Nonetheless, as the term defensibility denotes, D has an inherent nexus to the spatial organization of territorial maintenance, as it indicates whether mobility permits area monitoring. Thus, our results on howler monkeys' range defensibility still suggest a territorial gradient depending on the competitive circumstances of each particular site and the cost–benefits of being territorial.

Animals recognized as territorial show high plasticity in their degree of territoriality in response to variation in food abundance and distribution (e.g., *Motacilla alba*: Zahavi 1971; *Turdoides bicolor*: Golabek *et al.* 2012), habitat quality (e.g., *Canis lupus*: Kittle *et al.* 2015; *Cordylochernes scorpiodes*: Zeh *et al.* 1997), mates and breeding sites (several carnivore, ungulate, and primate species: Grant *et al.* 1992; *Passerella iliaca*: Alcock 2005), seasonality (*Sceloporus jarrovi*: Marler and Moore 1989), or various mixed factors (*Pteronura brasiliensis*: Leuchtenberger *et al.* 2015; *Pan troglodytes*: Moore *et al.* 2015; *Pomatostomus ruficeps*: Sorato *et al.* 2015). Further, a species generally assumed to be nonterritorial such as the pigtailed macaque (*Macaca leonina*) can show territorial patterns under particular circumstances that force high levels of competition (José-Domínguez *et al.* 2015). There is evidence that

territoriality does not need to be a species-specific trait (Carpenter and MacMillen 1976; Powell *et al.* 1997). Animals may present “facultative territoriality,” which means that they may exhibit territoriality only under particular social and environmental circumstances such as high population density and small area available (Chapman and Fedigan 1984; Kinnaird 1992). Therefore, a continuum that goes from defending to not defending a territory might reasonably exist in howler monkeys, which would adjust to particular socioecological factors that require or favor area defense.

Acknowledgments We thank T. Savini and W. Y. Brockelman for their insightful discussions on this study. We are also grateful to D. Lukas, M. Grainger, D. Ngoprasert, V. Arroyo-Rodríguez, and N. Juat for their patient assistance with the statistical modeling and to S. Nakagawa for providing hints for running the imputation analyses. We thank associate editor O. H. Razafindratsima and two anonymous referees who kindly gave constructive editions, suggestions, and comments.

References

- Alcock, J. (2005). *Animal behaviour: an evolutionary approach* (8th ed.). Sunderland: Sinauer Associates.
- Arroyo-Rodríguez, V., & Mandujano, S. (2006). Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology*, *27*, 1079–1096.
- Arroyo-Rodríguez, V., Asensio, N., & Cristobal-Azkarate, J. (2008). Long-term study on the evolution of a Mexican mantled howler group in a rainforest fragment: demography, life history and migrations. *American Journal of Primatology*, *70*, 114–118.
- Asensio, N., Cristobal-Azkarate, J., Dias, P. A. D., Veá, J., & Rodríguez-Luna, E. (2007). Foraging habits of Mexican howler monkeys (*Alouatta palliata mexicana*) inhabiting three different forest fragments. *Folia Primatologica*, *78*, 141–153.
- Bartlett, T. Q., & Light, L. E. O. (2017). Territory. *The International Encyclopedia of Primatology*, 1–3. <https://doi.org/10.1002/9781119179313.wbprim0420/abstract;jsessionid=B7B8F066341EE3DD1AE5CA330FDC57C2.f03t01>.
- Bartoń, K. (2016). MuMin: multi-model inference. R package version 1.15.6. Available at <https://CRAN.R-project.org/package=MuMin>.
- Bates, B. C. (1970). Territorial behavior in primates: a review of recent field studies. *Primates*, *11*, 271–284.
- Bates, D. M., Maechler, M., & Bolker, B. (2012). Lme4: linear mixed-effects models using S4 classes. R package version 0.999999–0.
- Bergman, T. J., Cortes-Ortiz, L., Dias, P. A. D., Ho, L., Adams, A., Canales-Espinosa, D., & Kitchen, M. (2016). Striking differences in the loud calls of howler monkey sister species (*Alouatta pigra* and *A. palliata*). *American Journal of Primatology*, *78*(7), 755–766.
- Bernstein, I. S. (1964). A field study of the activities of howler monkeys. *Animal Behaviour*, *12*, 92–97.
- Börger, L., Dalziel, B. D., & Fryxel, J. M. (2008). Are there general mechanisms of animal home range behavior? A review and prospects for future research. *Ecology Letters*, *11*, 637–650.
- Braga Hirano, Z. M., Coelho Correa, I., & Gonçalves de Oliveira, D. A. (2008). Contexts of rubbing behavior in *Alouatta guariba clamitans*: a scent-marking role? *American Journal of Primatology*, *70*, 575–583.
- Braza, F., Alvarez, F., & Azcarate, T. (1981). Behaviour of the red howler monkey (*Alouatta seniculus*) in the Llanos of Venezuela. *Primates*, *22*, 459–473.
- Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bulletin*, *76*, 160–169.
- Brown, J. L. (1969). Territorial behavior and population regulation in birds: a review and re-evaluation. *Wilson Bulletin*, *81*, 293–329.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach* (2nd ed.). New York: Springer Science+Business Media.
- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *24*, 346–352.
- Carpenter, C. R. (1958). Territoriality: a review of concepts and problems. In A. Roe & G. G. Simpson (Eds.), *Behavior and evolution* (pp. 224–250). New Haven: Yale University Press.
- Carpenter, F. L., & MacMillen, R. E. (1976). Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science*, *194*, 634–642.

- Chapman, C. A. (1988). Patterns of foraging and range use by three species of neotropical primates. *Primates*, 29, 177–194.
- Chapman, C. A., & Fedigan, L. M. (1984). Territoriality in the St. Kitts vervet monkey. *Journal of Human Evolution*, 13, 677–686.
- Chaves, Ó. M., & Bicca-Marques, J. C. (2016). Feeding strategies of brown howler monkeys in response to variations in food availability. *PLoS One*, 11(2), e0145819.
- Chiarello, A. G. (1995). Role of loud calls in brown howler monkeys, *Alouatta fusca*. *American Journal of Primatology*, 36, 213–222.
- Chivers, D.J. (1969). On the daily behaviour and spacing of howling monkey groups. *Folia Primatologica*, 10, 48–102.
- Clutton-Brock, T. H., & Harvey, P. H. (1977). Species differences in feeding and ranging behavior in primates. In T. H. Clutton-Brock (Ed.), *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys and apes* (pp. 557–584). London: Academic Press.
- Cornick, L. A., & Markowitz, H. (2002). Diurnal vocal patterns of the black howler monkey (*Alouatta pigra*) at Lamanai, Belize. *Journal of Mammalogy*, 83, 159–166.
- Cristóbal-Azkarate, J., Dias, P. A., & Veà, J. (2004). Causes of intraspecific aggression in the mantled howler monkey (*Alouatta palliata mexicana*): evidence from injuries, demography, and habitat. *International Journal of Primatology*, 25, 939–953.
- Crockett, C. M., & Eisenberg, J. F. (1987). Howlers: variation in group size and demography. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 54–68). Chicago: University of Chicago Press.
- da Cunha, R. G. T., & Byrne, R. W. (2006). Roars of black howler monkeys: evidence for a function in intergroup spacing. *Behaviour*, 143, 1169–1199.
- da Cunha, R. G. T., & Jalles-Filho, E. (2007). The roaring of Southern brown howler monkeys (*Alouatta guariba clamitans*) as a mechanism of active defence of borders. *Folia Primatologica*, 78, 259–271.
- Davies, N. B., & Houston, A. I. (1984). Territory economics. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology an evolutionary approach* (2nd ed., pp. 148–169). Sunderland: Sinauer Associates.
- DeGusta, D., & Milton, K. (1998). Skeletal pathologies in a population of *Alouatta mexicana*: behavioral, ecological, and evolutionary implications. *International Journal of Primatology*, 19, 615–650.
- Dias, P. A. D., & Rangel-Negrín, A. (2015). Diets of howler monkeys. In M. M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation. Developments in primatology: progress and prospects* (pp. 21–56). New York: Springer Science+Business Media.
- Drubble, R. V. & Gautier, J. P. (1993). On the occurrence of nocturnal and diurnal loud calls, differing in structure and duration, in red howlers (*Alouatta seniculus*) of French Guyana. *Folia Primatologica*, 60, 195–209.
- Dugatkin, L. A. (2009). Habitat selection, territoriality and migration. In L. A. Dugatkin (Ed.), *Principles of animal behavior* (pp. 431–451). New York: W. W. Norton & Company.
- Dunn, J. C., Halenar, L. B., Davies, T. G., Cristóbal-Azkarate, J., Reby, D., et al (2015). Evolutionary trade-off between vocal tract and testes dimensions in howler monkeys. *Current Biology*, 25, 2839–2844.
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197, 215–223.
- Emmons, L., & Feer, F. (1990). *Neotropical rainforest mammals*. Chicago: University of Chicago Press.
- Estrada, A., Garber, P., Pavelka, M., & Luecke, L. (2006). Overview of the Mesoamerican primate fauna, primate studies, and conservation concerns. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates distribution, ecology, behavior, and conservation. Developments in primatology: progress and prospects* (pp. 1–22). New York: Springer Science+Business Media.
- Fortes, V. B., Bicca-Marques, J. C., Urbani, B., & da Silva Pereira, T. (2015). Ranging behavior and spatial cognition of howler monkeys. In M. M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation. Developments in primatology: progress and prospects* (pp. 219–255). New York: Springer Science+Business Media.
- Fretwell, S. D. (1972). *Populations in seasonal environments*. Princeton: Princeton University Press.
- Gavazzi, A. J., Cornick, L. A., Markowitz, T. M., Green, D., & Markowitz, H. (2008). Density, distribution, and home range of the black howler monkey (*Alouatta pigra*) at Lamanai, Belize. *Journal of Mammalogy*, 89, 1105–1112.
- Gittins, S. P. (1980). Territorial behavior in the agile gibbons. *International Journal of Primatology*, 1, 39–71.
- Golabek, K. A., Ridley, A. R., & Radford, A. N. (2012). Food availability affects strength of seasonal territorial behavior in a cooperatively breeding bird. *Animal Behaviour*, 83, 613–619.

- Grant, J. W. A., Chapman, C. A., & Richardson, K. S. (1992). Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology*, *31*, 149–161.
- Holzmann, I., Agostini, I., & Di Bitetti, M. (2012). Roaring behavior of two syntopic howler species (*Alouatta caraya* and *A. guariba clamitans*): evidence supports the mate defense hypothesis. *International Journal of Primatology*, *33*, 338–355.
- Horwich, R. H., & Gebhard, K. (1983). Roaring rhythms in black howler monkeys (*Alouatta pigra*) of Belize. *Primates*, *24*, 290–296.
- Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior. *Behavioral Ecology*, *2*, 143–155.
- Janson, C. H., & van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: methods. *Behaviour*, *105*, 165–186.
- Jolly, A., Rasamimanana, H. R., Kinnaird, F., O'Brien, T. G., Crowley, H. M., et al (1993). Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. In P. M. Kappeler & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 85–109). New York: Plenum Press.
- Jones, C. B. (1980). The functions of status in the mantled howler monkey (*Alouatta palliata* Gray): intraspecific competition for group membership in a folivorous primate. *Primates*, *21*, 389–405.
- José-Domínguez, J. M., Huynen, M. C., Garcia, C. J., Albert, A., Savini, T., & Asensio, N. (2015). Nonterritorial macaques can range like territorial gibbons when partially provisioned with food. *Biotropica*, *47*, 733–744.
- Kappeler, P. M. (1998). To whom it may concern: the transmission and function of chemical signals in *Lemur catta*. *Behavioral Ecology and Sociobiology*, *42*, 411–421.
- Kass, R., & Raftery, A. (1995). Bayes factors. *Journal of the American Statistical Association*, *90*, 773–795.
- Kinnaird, M. F. (1992). Variable resource defense by the Tana River crested mangabey. *Behavioral Ecology and Sociobiology*, *31*, 115–122.
- Kinnaird, M. F., & O'Brien, T. G. (2007). *The ecology and conservation of Asian hornbills: farmers of the forest*. Chicago: University of Chicago Press.
- Kitchen, D. M. (2006). Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: effects of numeric odds, vulnerable offspring, and companion behavior. *American Journal of Physical Anthropology*, *131*, 73–83.
- Kitchen, D. M., da Cunha, R. G. T., Holzmann, I., & Oliveira, D. A. G. (2015). Function of loud calls in howler monkeys. In M. M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation. Developments in primatology: progress and prospects* (pp. 369–399). New York: Springer Science+Business Media.
- Kittle, A. M., Anderson, M., Avgar, T., Baker, J. A., & Brown, G. S. (2015). Wolves adapt territory size, not pack size to local habitat quality. *Journal of Animal Ecology*, *84*, 1177–1186.
- Klein, L. L. (1974). Agonistic behavior in Neotropical primates. In R. L. Hooloway (Ed.), *Primate aggression, territoriality, and xenophobia* (pp. 77–122). New York: Academic Press.
- Knopff, K. H., & Pavelka, M. S. M. (2006). Feeding competition and group size in *Alouatta pigra*. *International Journal of Primatology*, *27*, 1059–1078.
- Leuchtenberger, C., Magnusson, W. E., & Mourão, G. (2015). Territoriality of giant otter groups in an area with seasonal flooding. *PLoS One*, *10*, e0126073.
- Lowen, C., & Dunbar, R. I. M. (1994). Territory size and defendability in primates. *Behavioral Ecology and Sociobiology*, *35*, 347–354.
- Maher, C. R., & Lott, D. F. (1995). Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour*, *49*, 1581–1597.
- Maher, C. R., & Lott, D. F. (2000). A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist*, *143*, 1–29.
- Mai, L. L., Owl, M. Y., & Kersting, M. P. (2005). *The Cambridge dictionary of human biology and evolution*. Cambridge: Cambridge University Press.
- Marler, C. A., & Moore, M. C. (1989). Time and energy cost of aggression in testosterone-implanted free-living male mountain spiny lizards (*Sceloporus jarrovi*). *Animal Behaviour*, *42*, 209–219.
- Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, *114*, 362–378.
- Milton, K. (1980). *The foraging strategies of howler monkeys*. New York: Columbia University Press.
- Mitani, J. C. (1987). Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behavioral Ecology and Sociobiology*, *20*, 265–269.
- Mitani, J. C., & Rodman, P. (1979). Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology*, *5*, 241–251.

- Moore, D. L., Langergraber, K. E., & Vigilant, L. (2015). Genetic analyses suggest male philopatry and territoriality in savanna-woodland chimpanzees (*Pan troglodytes schweinfurthii*) of Ugalla, Tanzania. *International Journal of Primatology*, *36*, 377–397.
- Morris, T., White, I. R., & Royston, P. (2014). Tuning multiple imputation by predictive mean matching and local residual draws. *BMC Medical Research Methodology*, *14*, 75.
- Mosser, A., & Packer, C. (2008). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, *78*, 359–370.
- Nakagawa, S., & Freckleton, R. P. (2011). Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behavioral Ecology and Sociobiology*, *65*, 103–116.
- Nice, M. M. (1941). The role of territory in bird life. *American Midland Naturalist*, *26*, 441–487.
- Noble, G. K. (1939). The role of dominance in the social life of birds. *The Auk*, *56*(3), 263–273.
- Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., et al (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*, *307*, 390–393.
- Parker, G. A. (1974). Assessment strategy and evolution of fighting behavior. *Journal of Theoretical Biology*, *47*, 223–243.
- Pen, I., & Weissing, F. (2000). Optimal floating and queuing strategies: the logic of territory choice. *American Naturalist*, *155*, 512–526.
- Peres, C. A. (2000). Territorial defense and the ecology of group movements in small-bodied neotropical primates. In S. Boinski & P. Garber (Eds.), *On the move: how and why animals travel in groups* (pp. 100–123). Chicago: University of Chicago Press.
- Potts, J., & Lewis, M. (2014). How do animal territories form and change? Lessons from 20 years of mechanistic modelling. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20140231.
- Pourier, F. E. (1968). Nilgiri langur (*Presbytis johnii*) territorial behavior. *Primates*, *9*, 351–364.
- Powell, R. (2000). Animal home ranges and territories and home range estimators. In L. Boitani & T. K. Fuller (Eds.), *Research techniques in animal ecology: controversies and consequences* (pp. 65–103). New York: Columbia University Press.
- Powell, R. A., Zimmerman, J. W. & Seaman, D. E. (1997). *Ecology and Behaviour of North American Black Bears: Home Ranges, Habitat and Social Organization*. London: Chapman & Hall.
- Pulliam, H.R. & Caraco, T. (1984). Living in groups: is there an optimal group size? In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: an evolutionary approach, 2nd edition* (pp. 122–147). Oxford: Blackwell Scientific.
- R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Rubin, D. B. (1987). *Multiple imputation for nonresponse in surveys*. New York: John Wiley & Sons.
- Sayers, K. (2013). On folivory, competition, and intelligence: generalism, overgeneralizations, and models of primate evolution. *Primates*, *54*, 111–124.
- Schoener, T. W. (1987). Time budgets and territory size: some simultaneous optimization models for energy maximizers. *American Zoologist*, *27*, 259–291.
- Sekulic, R., & Chivers, D. J. (1986). The significance of call duration in howler monkeys. *International Journal of Primatology*, *7*, 183–190.
- Sekulic, R., & Eisenberg, J. F. (1983). Throat-rubbing in red howler monkeys (*Alouatta seniculus*). In D. Müller-Schwarze & R. M. Silverstein (Eds.), *Chemical signals in vertebrates* (pp. 347–350). New York: Plenum Press.
- Shoemaker, A. H. (1982). Fecundity in the captive howler monkey, *Alouatta caraya*. *Zoo Biology*, *1*, 149–156.
- Shonfield, J., Taylor, R. W., Boutin, S., Humphries, M. M., & McAdam, A. G. (2012). Territorial defence behavior in red squirrels is influenced by local density. *Behaviour*, *149*, 369–390.
- Snaith, T. V., & Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Ptilocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, *59*, 185–190.
- Snipes, M. & Taylor, D. C. (2014). Model selection and Akaike Information Criteria: An example from wine ratings and prices. *Wine Economics and Policy*, *3*(1), 3–9.
- Sorato, E., Gullett, P. R., Creasey, M. J. S., Griffith, S. C., & Russell, A. F. (2015). Plastic territoriality in group-living chestnut-crowned babbler: roles of resource value, holding potential and predation risk. *Animal Behaviour*, *101*, 155–168.
- Strier, K. B. (1992). Atelinae adaptations: behavioral strategies and ecological constraints. *The American Journal of Physical Anthropology*, *88*, 515–524.
- Tabachnick, B. G., & Fidell, L. S. (2007). *Using multivariate statistics* (5th ed.). New York: Allyn and Bacon.
- Tinbergen, N. (1957). The functions of territory. *Bird Study*, *4*, 14–27.

- van Buuren, S., & Groothuis-Oudshoorn, C. G. M. (2011). Mice: multivariate imputation by chained equations in R. *Journal of Statistical Software*, 45, 1–67.
- Van Schaik, C. P. (1992). Territorial behavior in Southeast Asian langurs: resource defense or mate defense? *American Journal of Primatology*, 26, 233–242.
- Whitehead, J. M. (1989). The effect of the location of a simulated intruder on responses to long-distance vocalizations of mantled howling monkeys, *Alouatta Palliata Palliata*. *Behaviour*, 108, 73–103.
- Wich, S. A., & Nunn, C. L. (2002). Do male “long-distance calls” function in mate defense? A comparative study of long-distance calls in primates. *Behavioral Ecology and Sociobiology*, 52, 474–484.
- Willems, E. P., & van Schaik, C. P. (2015). Collective action and the intensity of between-group competition in nonhuman primates. *Behavioral Ecology*, 26, 625–631.
- Wilson, E. O. (1975). *Sociobiology*. Cambridge: Harvard University Press.
- Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology*, 32, 363–392.
- Zahavi, A. (1971). The social behavior of the white wagtail wintering in Israel. *Ibis*, 113, 203–211.
- Zeh, D. W., Zeh, J. A., & Bermingham, E. (1997). Polyandrous, sperm-storing females: carriers of male genotypes through episodes of adverse selection. *Proceedings of the Royal Society of London B: Biological Sciences*, 264, 119–125.