






Effects of camera trap placement on photo rates of jaguars, their prey, and competitors in northwestern Costa Rica

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Abstract

The use of camera-trap methods, though important, has pitfalls and inconsistencies such as factors and interactions that may influence species photo rates. Jaguar (*Panthera onca*) camera-trap studies place cameras at sites where jaguar detections are likely greater (e.g., sites with previous evidence such tracks, feces, and other presence signs), but do not account for potential placement biases. Our study evaluated methodological implications of a paired camera-trap design at trail and off-trail locations, and climate seasonality, on photo rates of jaguars, their prey, and competitors. From June 2016 to June 2017, camera traps were deployed at 58 different sites in a hexagon grid array of 3 km² each in the Sector Santa Rosa (SSR) of Área de Conservación Guanacaste in Costa Rica. Half of the cameras were located at a trail location that jaguars were likely to use, and the other half at an off-trail location closest to each hexagon centroid. We estimated a photographic relative abundance index (RAI; no. of independent photos/100 trap nights) and used Generalized Linear Models (GLMs) to assess statistical evidence of trail location and climate seasonality. With a total effort of 19,408 trap nights, we recorded 12,678 independent photo events of 64 species of amphibians, reptiles, birds, and mammals. For the 3 bird species and 14 mammal species we focused on, most

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species-specific RAIs were greater at trail locations ($n = 8$ species, including jaguars and pumas [*Puma concolor*]), some were greater at off-trail locations ($n = 2$ species, including collared peccaries [*Pecari tajacu*]), and there was no discernable location effect for others ($n = 7$ species, including tapirs [*Tapirus bairdii*] and white-tailed deer [*Odocoileus virginianus*]). For jaguars, sex ratio data showed a smaller proportion of males at off-trail locations. Analysis of competitor and prey interaction data indicated temporal segregation at trail locations. Further jaguar camera-trap studies should highlight camera placement as important source of bias that might influence results; hence, conservationists must be aware of this to avoid erroneous decisions.

KEYWORDS

birds, Costa Rica, dry forest, location, mammals, Neotropics, *Panthera onca*, random

Camera trapping is a popular, noninvasive method to assess wildlife over long periods of time (Rovero and Zimmermann 2016) due to low maintenance and the high volume of information collected. Thus, large-scale wildlife ecological studies have implemented camera trapping using different variations (O'Connor et al. 2017) and analytical applications (e.g., capture-recapture, occupancy, photo indexes). The extensive use of camera traps has various pitfalls and inconsistencies (Cusack et al. 2015) that might influence interpretations of how particular species' distributions and interactions may influence other species' photo rates. Species interaction mechanisms of avoidance often are assessed by comparing occupied vs. unoccupied site differences (Gause 1932) through camera-trap metrics (Harmsen et al. 2010, Sollmann et al. 2012, Booker 2016), and biases in site selection might have important consequences on species photo rates.

For jaguars (*Panthera onca*) and other wildlife, most habitat studies show a variety of ecological responses depending on local environmental factors (Carrillo et al. 2009, Morato et al. 2016, Rovero and Zimmermann 2016, Rabelo et al. 2019). These studies used different assessment techniques (Novack et al. 2005, Morato et al. 2016, De la Torre et al. 2017, Gutiérrez-González and López-González 2017), but camera trapping is primarily used for jaguar and medium-sized sympatric species (O'Connell et al. 2011). Most jaguar camera-trap studies place cameras in sites where jaguar detection probability is expected to be higher, hence maximizing the number of photos based on previous signs of jaguar presence (Cusack et al. 2015, O'Connor et al. 2017); however, biased jaguar location placements (e.g., trails and unpaved roads) might lead to incorrect inferences (O'Connor et al. 2017). While it is common practice to use the same design to associate other wildlife species with jaguars at the same camera sampling site (Blake and Mosquera 2014), it may be that prey avoid places frequented by predators (Valeix 2011), and therefore ignoring interactions on photo rates could lead to spurious results. Several studies have argued for the use of nonrandom camera trap placement (Cusack et al. 2015, O'Connor et al. 2017), but this can limit the proportion of environmental variation and cause a sampling bias resulting from differences in the presence or relative abundance of multiple species at other kinds of sites (Kolowski and Forrester 2017).

Given the potential sources of bias that camera trap placement could impact, photo rate results of target and associated wildlife may lead to incorrect inferences. We evaluated methodological implications of camera trap placement using a paired camera trap design at trail and off-trail locations, while considering the effect of climate seasonality on photo rates of jaguars and associated wildlife. Previous studies have recommended camera placement at trail locations

(Silver et al. 2004), ignoring whether off-trail locations are also used by jaguar or potential prey and competitors. Thus, we also evaluated whether interpretation of jaguar-specific ecological study data (sex ratio, competitor relationships, activity patterns, abundance, and prey interactions) collected with camera traps are influenced by camera placement.

STUDY AREA

Our study was conducted in Sector Santa Rosa (SSR), within the Área de Conservación Guacaste (ACG) located in northwest Costa Rica ($10^{\circ}53'01''\text{N}$ $85^{\circ}46'30''\text{W}$; Figure 1). The SSR encompasses 387 km² and is dominated by one of the few remaining tropical dry forests in Central America (Janzen 1988, Boza 1992, Gillespie et al. 2000). Average annual rainfall of 1,600 mm is highly seasonal (monthly averages from 0 mm to 1,040 mm) and the wet season usually spans from May to November with the dry season (with almost no rain and temperatures over 37°C) from December to April (Figure 2). Additionally, due to the rarity of dry forest ecosystems, a large-scale restoration effort was initiated in the 1980s involving protected area status, the recovery of abandoned pastures by active fire suppression (Klemens et al. 2011), protection from human activities, and the recovery of populations of large vertebrates.

METHODS

Data collection

From June 2016 to June 2017, automatic trail cameras (Bushnell®, Trophy Cam models 119436, 119446, 119456; Overland Park, KS, USA) were deployed at 58 different sites in a hexagonal grid array of 3 km² each at SSR (Figure 1).

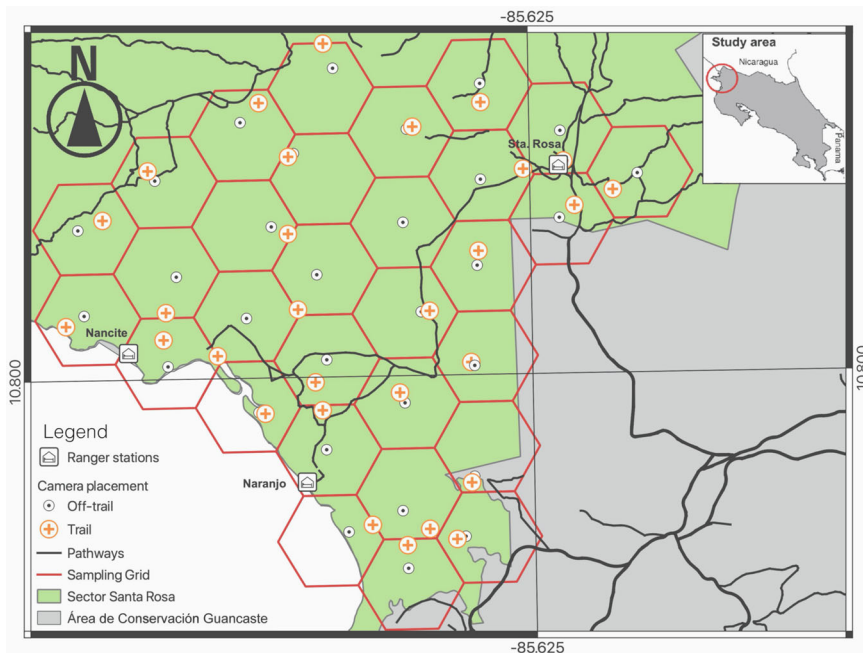


FIGURE 1 Camera trap deployment array at off-trail ($n = 29$) and trail ($n = 29$) locations in Sector Santa Rosa, Área de Conservación Guacaste, northwestern Costa Rica, during 2016–2017.

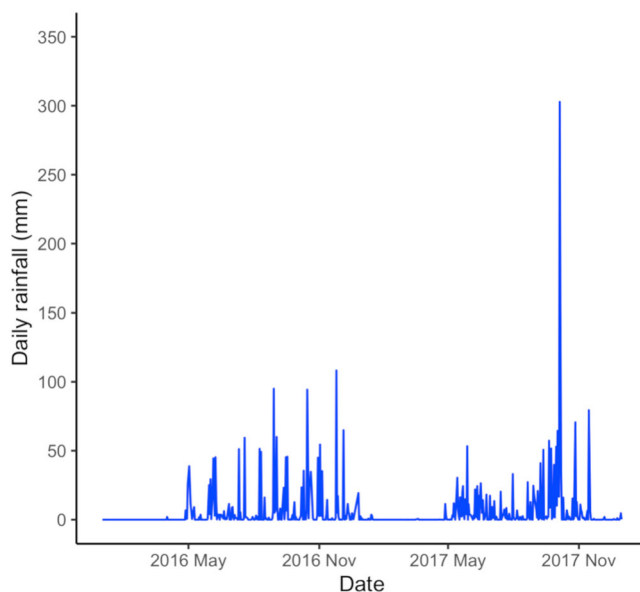


FIGURE 2 Daily rainfall during 2016–2017 in the Sector Santa Rosa, Área de Conservación Guancaste, northwestern Costa Rica.

Half of the cameras were located at a trail location that a jaguar was likely to use, and the other half at an off-trail location closest to each hexagon centroid; on average each off-trail camera location was $0.59 \text{ km} \pm 0.25 \text{ SD}$ away from available trails inside the study area within a range of 0.2 km of each hexagon centroid. Additionally, due to the high climate variation over the last several decades (Campos 2018), seasonality was defined from SSR historic precipitation records (Figure 2) and included as a covariate in the analyses. We aggregated the weekly accumulated precipitation to identify whether the week's precipitation sum was greater or lesser in comparison with the average annual weekly precipitation ($\mu = 10 \text{ mm}$). Thus, a week with $\geq 10 \text{ mm}$ was classified as wet, whereas a week with $\leq 10 \text{ mm}$ was dry.

Each camera was affixed to a tree at a height of approximately 40 cm and set to be active for 24 hours per day in photo mode with the minimum delay (1 second) between consecutive triggers. We recognize that whether the target area of a camera is in direct sunlight or shade may affect photo rates, but we have no reason to believe that, in our forested study area and given the types of trails we monitored, the distribution of cameras relative to target areas was different between trail and off-trail cameras. Once deployed, cameras were checked on average every month to replace batteries and change memory cards, if necessary. For each camera deployment, we recorded the location, camera operation dates (and therefore, number of trap nights), and the number of independent photo events for each species. As Montalvo et al. (2019) recommended, photos were considered independent if (1) they were taken at least 30 minutes apart (e.g., a series of 3 photos of the same species taken in consecutive seconds = 1 photo event), (2) consecutive photos of the same species could be identified as different individuals (spots, scars, horns or antlers, sex) and not part of the same group (e.g., 15 minutes apart, going in opposite directions = 2 photo events), or (3) photos of the same species separated by photos of a different species (e.g., species 1, followed 2 minutes later by a species 2, followed 5 minutes later by species 1 = one species with 2 photo events and one species with 1 photo event).

Statistical analyses

To examine and identify potential data issues (e.g., normality, overdispersion, outliers) and fulfill model assumptions, we followed the data exploration protocol suggested by Zuur et al. (2010). The number of independent photos of

TABLE 1 Description of 5 *a priori* candidate models describing the effect of location (Loc: Trail or Off-trail) and seasonality (Seas: Dry or Wet) on Relative Abundance Index (RAI: no. independent photos per 100 trap nights) in Sector Santa Rosa, Área de Conservación Guanacaste, northwestern Costa Rica.

Model	Description
1) RAI = log (Trap nights)	Intercept only
2) RAI = log (Trap nights) + Seas	RAI vary by Seas
3) RAI = log (Trap nights) + Loc	RAI vary by Loc
4) RAI = log (Trap nights) + Seas + Loc	RAI vary by Seas and Loc in an additive way
5) RAI = log (Trap nights) + Seas * Loc	RAI vary differently by Seas and Loc

species at a site were analyzed using generalized linear models (GLM; Zuur et al. 2009) with a log link function implemented using program R (v. 4.0.0; R Core Team 2020) with the package lme4 1.1 (Bates et al. 2015). Due to overdispersion in the counts, we assumed a negative binomial error distribution (Zuur et al. 2009), and to account for variation in effort, we used the log of the number of trap nights as an offset to standardize the counts. To assess the effects of location (Loc) and seasonality (Seas; Montalvo et al. 2019) on photographic relative abundance index (RAI: no. of independent photos/100 trap nights), 5 *a priori* models were developed for each species. One model included the intercept, 2 included each singular predictor, one included the additive effect of the 2 predictors, and one included the first order interactions for the 2 predictors (Table 1). The empirical support of the 5 candidate models were evaluated using the Akaike Information Criterion (AIC; Burnham and Anderson 2002), and throughout the model comparison for each species we determined the most plausible models using the highest Akaike weight (W ; range = 0 to 1; Anderson 2007). Based on the W we assessed the evidence from one model over another (Burnham and Anderson 2002). Because we were particularly interested in those models showing interactions and the additive effects of Seas and Loc on photo rates, we included in the confidence set of models, based on the Akaike weight value, those for species where the interaction and the additive effect of Seas and Loc differed by <10% from the top model (Thompson and Lee 2000). Specifically, for jaguar photo rates at trail and off-trail locations, we contrasted additional ecological information gathered from camera traps. We assessed sex ratio differences at off-trail and trail locations with Welch t-tests (Shahbaba 2011). Competitor relationships with pumas (*Puma concolor*) and prey interactions (jaguar with white-tailed deer [*Odocoileus virginianus*] and collared peccary [*Pecari tajacu*]) at off-trail and trail locations were contrasted with linear regression analysis using RAI of each species (Zuur et al. 2007). To quantify activity patterns we used Ridout and Linkie's (2009) approach with the package Activity 1.3 (Rowcliffe 2019), using Wald test to contrast temporal distribution aggregation differences for circular data, smoothed with 10,000 bootstrap resamples to calculate confidence intervals (Rovero and Zimmermann 2016).

RESULTS

We had a total effort of 19,408 trap nights and recorded 12,678 independent photo events of 64 species of amphibians or reptiles ($n = 2$), birds ($n = 37$) and mammals ($n = 25$). Three bird species and 14 mammal species, all with >10 independent photo records, were included in our analysis (Table 2) and included jaguars, their competitors (pumas, coyotes [*Canis latrans*], ocelots [*Leopardus pardalis*]), and likely prey species (as documented in the region; Chinchilla 1997, Novack et al. 2005, Weckel et al. 2006).

Model selection based on W (Table 3) showed the location parameter (Loc) best fit the data for crested guans (*Penelope purpurascens*; 0.36), nine-banded armadillos (*Dasyus novemcinctus*; 0.43), white-faced capuchin

TABLE 2 Relative Abundance Index (RAI: no. independent photos per 100 trap nights; no. of trap nights in parentheses) for 3 bird species and 14 mammal species, seasonally during 2016–2017 at trail and off-trail locations in Sector Santa Rosa, Área de Conservación Guancaste, northwestern Costa Rica.

Species	Common name	Dry season		Wet season	
		Trail (3,291)	Off-trail (3,056)	Trail (7,337)	Off-trail (5,724)
Birds					
<i>Crax rubra</i>	Great curassow	8.51	2.72	11.70	6.71
<i>Penelope purpurascens</i>	Crested guan	0.71	0.50	0.76	0.25
<i>Crypturellus cinnamomeus</i>	Thicket tinamou	0.06	0.10	0.57	0.56
Mammals					
<i>Didelphis marsupialis</i>	Common opossum	0.43	0.12	0.12	0.05
<i>Dasypus novemcinctus</i>	Nine-banded armadillo	0.00	0.13	0.06	0.18
<i>Cebus imitator</i>	White-faced capuchin monkey	2.28	0.03	2.28	0.03
<i>Dasyprocta punctata</i>	Agouti	3.96	5.45	4.46	9.06
<i>Canis latrans</i>	Coyote	0.20	0.00	0.09	0.02
<i>Procyon lotor</i>	Raccoon	0.26	0.07	0.18	0.02
<i>Nasua narica</i>	Coati	0.11	0.43	0.23	0.25
<i>Conepatus semistriatus</i>	Striped hog-nosed skunk	0.23	0.10	0.11	0.06
<i>Leopardus pardalis</i>	Ocelot	0.90	0.47	0.69	0.62
<i>Puma concolor</i>	Puma	1.33	0.33	0.96	0.79
<i>Panthera onca</i>	Jaguar	2.24	0.37	3.15	0.34
<i>Tapirus bairdii</i>	Tapir	1.76	1.63	1.48	1.08
<i>Pecari tajacu</i>	Collared peccary	0.51	2.42	0.41	1.07
<i>Odocoileus virginianus</i>	White-tailed deer	25.13	25.28	23.38	25.76

monkeys (*Cebus imitator*; 0.37), coyotes (0.36), coatis (*Nasua narica*; 0.31), raccoons (*Procyon lotor*; 0.42), jaguars (0.67), and collared peccaries (0.38). Seasonality (Seas) was the most plausible model for thicket tinamous (*Crypturellus cinnamomeus*; 0.60), additive effect of Loc and Seas was the top model for great curassows (*Crax rubra*; 0.46) and common opossums (*Didelphis marsupialis*; 0.44), and the interaction of Loc and Seas was the most plausible for pumas (0.39). The intercept model best fit the data for agoutis (*Dasyprocta punctata*; 0.46), striped hog-nosed skunks (*Conepatus semistriatus*; 0.32), ocelots (0.43), tapirs (*Tapirus bairdii*; 0.45), and white-tailed deer (0.54).

Based on our modeling results, average RAIs appeared greater at trail locations for jaguars ($n = 222$ independent photo events), pumas, coyotes, common opossums, white-faced capuchin monkeys, raccoons, great curassows, and crested guans, whereas those for nine-banded armadillos, and collared peccaries seemed greater at off-trail locations (Table 2). For thicket tinamous, agoutis, coatis, striped hog-nosed skunks, ocelots, tapirs, and white-tailed deer, photo rates were not influenced by location of cameras.

Overall, the most empirical support for jaguar RAI effect was Loc ($W = 0.67$). Further sex ratio analysis at off-trail and trail locations showed a lower proportion of males at off-trail ($\bar{x} = 0.25$; 16 female records and 4 male records) than trail locations ($\bar{x} = 0.62$; $t_{(14)} = -2.27$, $P = 0.039$; 123 female records and 79 male records), with no

TABLE 3 Model importance weights for 3 bird species and 14 mammal species, describing the effect of seasonality (Seas) and Location (Loc: Trail or Off-trail) on Relative Abundance Indices (RAI) in Sector Santa Rosa, Área de Conservación Guancaste, northwestern Costa Rica, 2016–2017. Category with the highest importance weight for each species in bold.

Species	Common name	Model description and AIC weights (W)				
		Intercept	Loc	Seas	Loc + Seas	Loc x Seas
Birds						
<i>Crax rubra</i>	Great curassow	0.04	0.20	0.04	0.46	0.26
<i>Penelope purpurascens</i>	Crested guan	0.32	0.36	0.12	0.14	0.06
<i>Crypturellus cinnamomeus</i>	Thicket tinamou	0.02	0.00	0.60	0.28	0.10
Mammals						
<i>Didelphis marsupialis</i>	Common opossum	0.06	0.18	0.16	0.44	0.16
<i>Dasyopus novemcinctus</i>	Nine-banded armadillo	0.08	0.43	0.04	0.25	0.20
<i>Cebus imitator</i>	White-faced capuchin monkey	0.15	0.37	0.14	0.24	0.10
<i>Dasyprocta punctata</i>	Agouti	0.46	0.24	0.18	0.09	0.03
<i>Canis latrans</i>	Coyote	0.01	0.36	0.01	0.35	0.27
<i>Procyon lotor</i>	Raccoon	0.23	0.42	0.09	0.19	0.07
<i>Nasua narica</i>	Coati	0.31	0.31	0.12	0.11	0.15
<i>Conepatus semistriatus</i>	Striped hog-nosed skunk	0.32	0.27	0.20	0.16	0.05
<i>Leopardus pardalis</i>	Ocelot	0.43	0.28	0.15	0.09	0.05
<i>Puma concolor</i>	Puma	0.10	0.34	0.04	0.13	0.39
<i>Panthera onca</i>	Jaguar	0.00	0.67	0.00	0.24	0.09
<i>Tapirus bairdii</i>	Tapir	0.45	0.19	0.23	0.10	0.03
<i>Pecari tajacu</i>	Collared peccary	0.26	0.38	0.13	0.17	0.06
<i>Odocoileus virginianus</i>	White-tailed deer	0.54	0.19	0.19	0.06	0.02

records of females with cubs at any location. There was temporal segregation of male and female jaguars at off-trail locations (Figure 3A; Wald value = 10.01, $P = 0.001$), but not at trail locations (Figure 3B; Wald value = 0.375, $P = 0.541$).

Jaguar and puma RAI regression coefficients at off-trail and trail locations showed poor correlation, and no differences between species (Figure 4; $R^2 = 0.034$, $P = 0.125$); nevertheless, temporal aggregation analysis indicated avoidance between jaguars and pumas at trail (Figure 5A; Wald value = 6.92, $P = 0.01$), but not off-trail, locations (Figure 5B; Wald value = 1.828, $P = 0.17$), though temporal patterns at both locations were the same. For jaguars and white-tailed deer, RAI regression coefficients showed no pattern (Figure 6; $R^2 = 0.04$, $P = 0.058$) between species, but temporal activity suggested at both trail and off-trail sites jaguars were more nocturnal and white-tailed deer were more diurnal (Figure 7). Statistical evidence of temporal partition between jaguars and white-tailed deer were not found at off-trail locations (Figure 7A; Wald value = 0.001, $P = 0.97$) but was evident at trail locations (Figure 7B; Wald value = 4.27, $P = 0.038$); though both locations evinced the same pattern, our data suggested jaguars and white-tailed deer temporally increase overlap at off-trail locations. Collared peccary and jaguar RAI regression coefficients indicated no pattern (Figure 8; $R_2 = 0.003$, $P = 0.125$); nevertheless, temporal activity suggested avoidance patterns

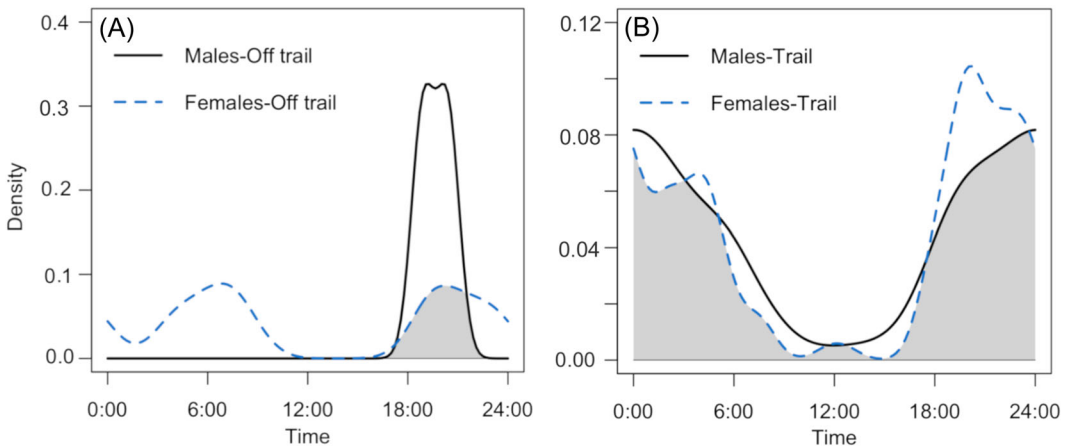


FIGURE 3 Jaguar male and female activity overlap (gray shaded area) at A) off-trail camera locations (overlap = 28%), and B) trail camera locations (overlap = 87%) in Sector Santa Rosa, Área de Conservación Guacaste, northwestern Costa Rica, during 2016–2017.

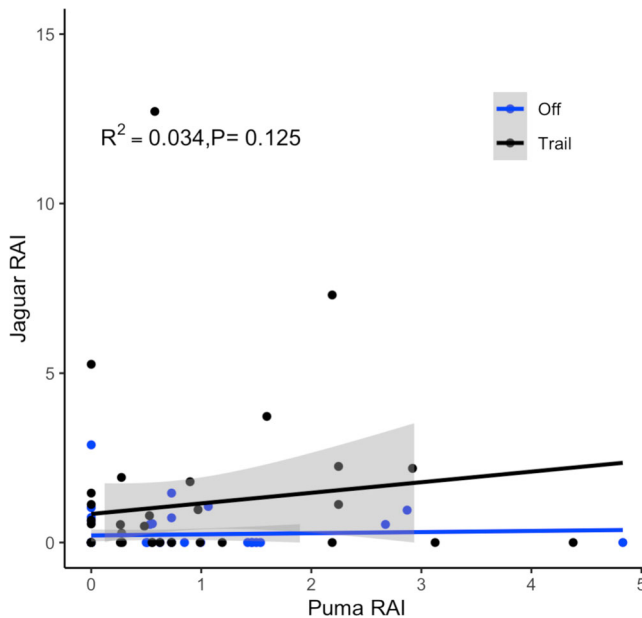


FIGURE 4 Jaguar and puma relative abundance index (RAI) correlation at off-trail or trail camera trap locations in Sector Santa Rosa, Área de Conservación Guacaste, Costa Rica, during 2016–2017; solid blue line represents off-trail trend and solid black line trail trend, and the gray shadow represents confidence intervals for both off-trail and trail trends.

(where peccaries tend to increase diurnal activity during jaguars' lowest activity peak). Statistical evidence of partition was not found at off-trail locations (Figure 9A; Wald value = 0.375, $P = 0.541$), and at trail locations the activity pattern followed the same trend but with statistical significance (Figure 9B; Wald value = 6.41, $P = 0.011$); both peccaries and white-tailed deer displayed the greatest temporal segregation with jaguar at trail locations.

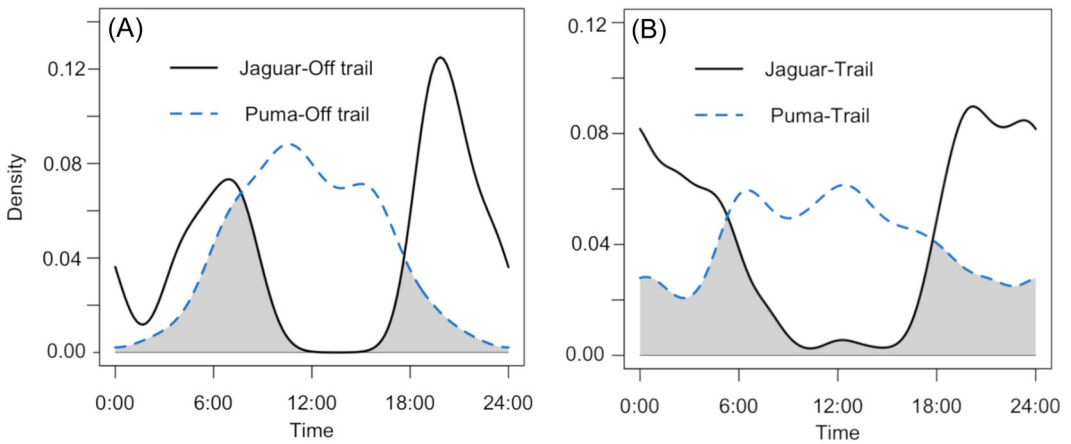


FIGURE 5 Jaguar and puma activity overlap (gray shaded area) at A) off-trail camera locations (overlap = 37%), and B) trail camera locations (overlap = 49%), in Sector Santa Rosa, Área de Conservación Guancaste, northwestern Costa Rica, during 2016–2017.

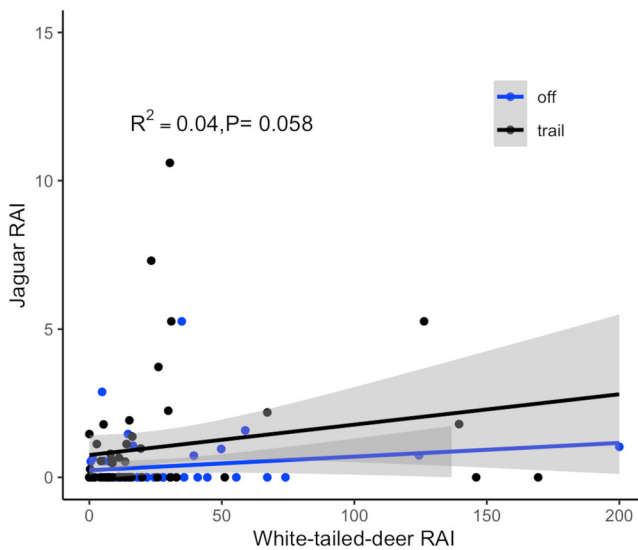


FIGURE 6 Jaguar and white-tailed deer relative abundance index (RAI) correlation at off-trail or trail camera trap locations in Sector Santa Rosa, Área de Conservación Guancaste, Costa Rica, during 2016–2017; solid blue line represents off-trail trend and solid black line trail trend, and the gray shadow represents confidence intervals for both off-trail and trail trends.

DISCUSSION

An entirely randomized design is a common requirement for biological field studies (Quinn and Keough 2002), but few field-based, camera-trap studies fulfill this assumption due to logistical or budgetary constraints (Cusack et al. 2015). Though our study did not completely achieve 100% randomness, our off-trail camera trap placement attempted to reach the closest random placement to compare photo rates with trail locations. The RAIs of 3 bird

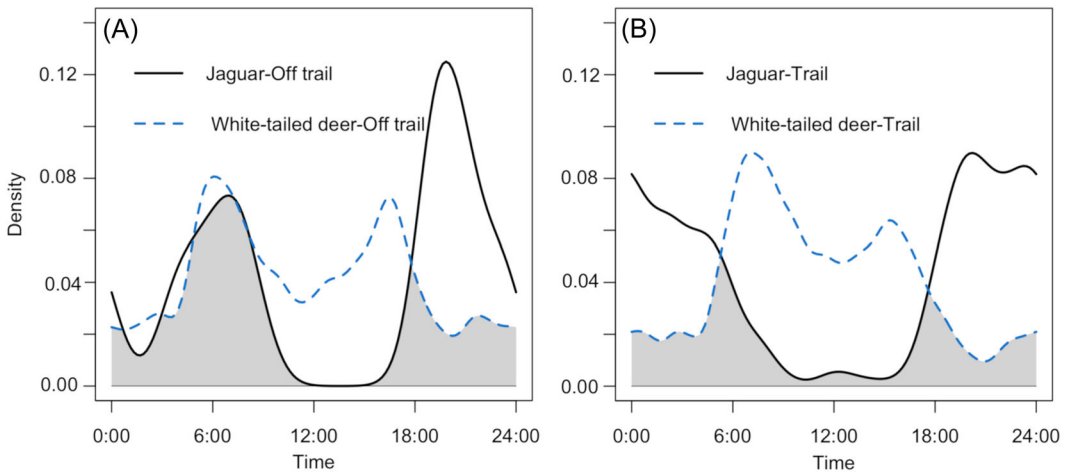


FIGURE 7 Jaguar and white-tailed deer activity overlap (gray shaded area) at A) off-trail camera locations (overlap = 56%), and B) trail camera locations (overlap = 38%), in Sector Santa Rosa, Área de Conservación Guancaste, northwestern Costa Rica, during 2016–2017.

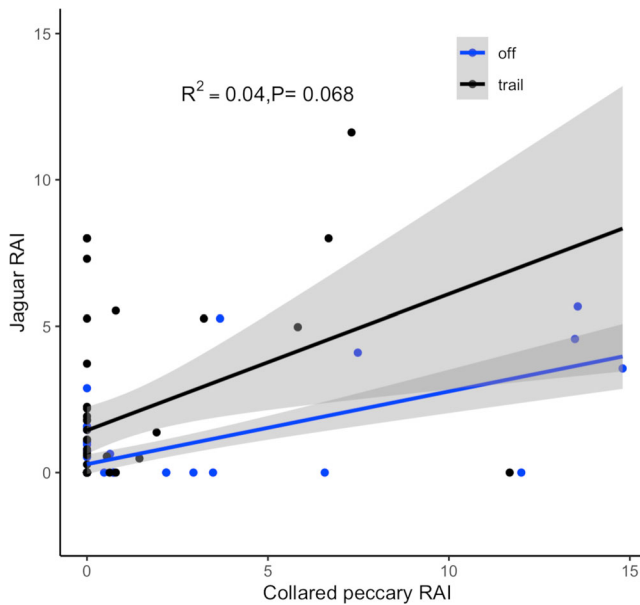


FIGURE 8 Jaguar and collared peccary relative abundance index (RAI) correlation at off-trail or trail camera trap locations in Sector Santa Rosa, Área de Conservación Guancaste, Costa Rica, during 2016–2017; solid blue line represents off-trail trend and solid black line trail trend, and the gray shadow represents confidence intervals for both off-trail and trail trends.

species and 14 mammals at trail and off-trail camera locations indicated that placement and seasonality are important and that camera trap placement strategies might lead to different results regarding species abundances and interactions. Our observations suggested that trail, in comparison to off-trail, locations provide ease of access for foraging and movement for generalists and large, ground-dwelling bird species (Stiles et al. 2007).

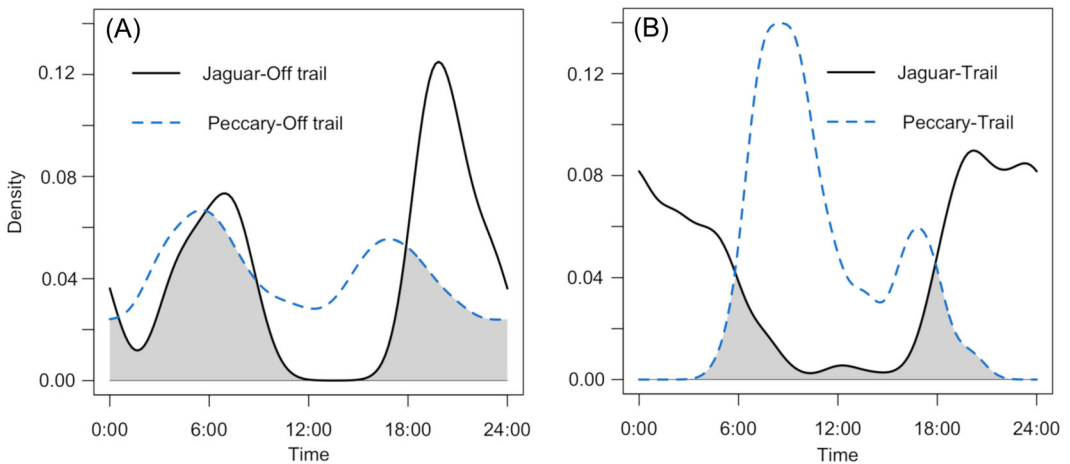


FIGURE 9 Jaguar and collared peccary activity overlap (gray shaded area) at A) off-trail camera locations (overlap = 62%), and B) trail camera locations (overlap = 21%) in Sector Santa Rosa, Área de Conservación Guancaste, northwestern Costa Rica, during 2016–2017.

Mammal species that showed a location effect on RAI were mostly generalists and included jaguars (Carrillo et al. 2000). Trail use preference could be for ease of travel or a foraging strategy (Pianka 1966) to increase detectability and thus increase resource allocation. Weckel et al. (2006) and Harmsen et al. (2009) reported similar findings in the tropical rainforest where some species had high photographic rates at human-made trails instead of other type of pathways, suggesting trail photo rates are biased toward large carnivores such as pumas and jaguars. Additive effect of location and seasonality on mammal RAI was only registered for the common opossum, a generalist species with a weak sense of smell (Carrillo et al. 2000), which may use trails due to their openness, which may allow odors to carry farther, thus allowing them to more easily identify potential resource items during scarcity periods (Morgan et al. 1995). Pumas were recorded more frequently at trail cameras, but the interaction of location and seasonality affected places puma use the most frequently. Perhaps factors such as competition with jaguars and prey availability would affect puma behavior and the places they visit (Gutiérrez-González and López-González 2017) as we documented that both jaguars and pumas are likely to use the same places but with temporal segregation.

Ecological studies using camera traps mostly described 5 uses of the method, including sex interactions, competition, prey-predator relationships, abundance, and temporal interactions (O'Connell et al. 2011, Trolliet et al. 2014, Rovero and Zimmermann 2016). Our results indicated that females temporally and spatially used more off-trail locations compared to males, a behavior reported in other studies (Sunquist and Sunquist 2002, Silver et al. 2004, Salom et al. 2007, Astete et al. 2017). We did not identify spatial differences between jaguar and pumas, which are competitors, related to camera placement but did find temporal segregation where both species frequented the same places. The spatiotemporal pattern has been previously described in rainforest ecosystems where, due to prey overlap, both species frequent the same places (Emmons 1987, Foster et al. 2010, Gutiérrez-González and López-González 2017), but are temporally segregated with pumas becoming more diurnal during nocturnal activity peaks of jaguars (Harmsen et al. 2009, Herrera et al. 2018). We found no evidence for differences in jaguar-prey interactions (white-tailed deer, collared peccary) due to site placement, though we hypothesized that predator-prey camera trap studies may be biased since places frequented by predators would repel prey due to the high-risk foraging activity involved (Valeix 2011). However, our hypothesis may be partially supported by the observation that white-tailed deer and collared peccaries were active the most during the lowest peaks of jaguar activity, and that collared peccaries were more frequent at off-trail locations less frequented by jaguar.

RESEARCH IMPLICATIONS

Our study suggests camera location placement and seasonality are methodological variables likely to influence inferences, depending on target animal species, in the dry forest of northwestern Costa Rica. Detailed jaguar analyses show that females used the off-trail locations more often than males, and jaguar conspecific and prey interaction analyses indicated temporal segregation, mostly at trail locations. Further jaguar camera trap ecological studies could consider camera placement as an important source of bias that might influence inferences about species distribution, abundance, or multiple-species interactions. We suggest that conservation decision makers should also carefully consider camera placement design to help avoid making erroneous decisions.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study fulfilled all the permissions required by the ministry of environment of Costa Rica, and the ethics of animal welfare, under the permission R-SINAC-ACG-PI-008-2021.

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REFERENCES

- Anderson, D. R. 2007. Model Based Inference in the Life Sciences: A Primer on Evidence. Second edition Springer Science & Business Media, New York, New York, USA.
- Astete, S., J. Marinho-Filho, G. Kain, B. Penido, R. Zimbres, R. Sollmann, A. Jácomo, N. M. Tórres, and L. Silveira. 2017. Forced neighbours: coexistence between jaguars and pumas in a harsh environment. *Journal of Arid Environments* 146:27–34.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Blake, J., and D. Mosquera. 2014. Camera trapping on and off trails in lowland forest of Eastern Ecuador: does location matter? *Mastozoología Neotropical* 21:17–26.
- Booker, H. 2016. The application of occupancy modeling to evaluate the determinants of distribution of jaguars *Panthera onca*, pumas *Puma concolor*, and valued prey species in a protected area. Dissertation, Waterloo University, Ontario, Canada.
- Boza, M. 1992. National Parks of Costa Rica. Second edition, Northwestern University Press, Evanston, Illinois, USA.
- Burnham, K., and D. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second edition, Springer, New York, New York, USA.
- Campos, F. 2018. A synthesis of long-term environmental change in Santa Rosa, Costa Rica. Pages 331–358 in U. Kalbitzer and K. Jack, editors. Primate life histories, sex roles, and adaptability, Essays in honour of Linda M. Fedigan. Springer, New York, USA.

- Carrillo, E., T. K. Fuller, and J. C. Saenz. 2009. Jaguar (*Panthera onca*) hunting activity: effects of prey distribution and availability. *Journal of Tropical Ecology* 25:563–567.
- Carrillo, E., J. Sáenz, and G. Wong. 2000. Guía mamíferos de Costa Rica. Second edition, Instituto Nacional de Biodiversidad (INBIO), Heredia, Costa Rica.
- Chinchilla, F. A. 1997. La dieta del jaguar (*Panthera onca*), el puma (*Felis concolor*) y el manigordo (*Felis pardalis*) (Carnivora: Felidae) en el Parque Nacional Corcovado, Costa Rica. *Revista de Biología Tropical* 45:1223–1229.
- Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson. 2015. Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS ONE* 10(5):e0126373.
- De la Torre, J. A., J. M. Núñez, and R. Medellín. 2017. Spatial requirements of jaguars and pumas in Southern Mexico. *Mammalian Biology* 84:52–60.
- Emmons, L. H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology* 20:271–283.
- Foster, R. J., B. J. Harmsen, and C. P. Doncaster. 2010. Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica* 42:724–731.
- Gause, M. 1932. Experimental studies on the struggle for existence. *Journal of Experimental Biology* 9:389–402.
- Gillespie, T. W., A. Grijalva, and C. N. Farris. 2000. Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology* 147:37–47.
- Gutiérrez-González, C. E., and C. A. López-González. 2017. Jaguar interactions with pumas and prey at the northern edge of jaguars' range. *Peer J* 5:e2886.
- Harmsen, B. J., R. Foster, S. Silver, L. Ostro, and C. P. Doncaster. 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. *Biotropica* 1:126–133.
- Harmsen, B. J., R. J. Foster, S. C. Silver, L. Ostro, and C. P. Doncaster. 2009. Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and Pumas (*Puma concolor*) in a neotropical forest. *Journal of Mammalogy* 90:612–620.
- Herrera, H., E. Chávez, L. Alfaro, T. K. Fuller, V. H. Montalvo, F. Rodrigues, and E. Carrillo. 2018. Time partitioning among jaguar *Panthera onca*, puma *concolor*, and ocelot *Leopardus pardalis* (Carnivora:Felidae) in Costa Rica's dry and rainforest. *Revista Biología Tropical* 66:1559–1568.
- Janzen, D. H. 1988. Guanacaste National Park: tropical ecological and biocultural restoration. Pages 143–192 in J. Cairns, editor, *Rehabilitating Damaged Ecosystems*, CRC Press, Florida, USA.
- Klemens, J. A., N. Deacon, and J. Cavender-Bares. 2011. Pasture recolonization by a tropical oak and the regeneration ecology of seasonally dry tropical forests. Pages 221–238 in R. Dirzo, H. Young, H. Mooney, and G. Ceballos, editors, *Seasonally dry tropical forests*. Island Press, Washington, USA.
- Kolowski, J., and T. Forrester. 2017. Camera trap placement and the potential for bias due to trails and other features. *PLoS ONE* 12(10):e0186679.
- Montalvo, V., C. Sáenz-Bolaños, L. Alfaro, J. C. Cruz, F. Guimaraes-Rodrigues, E. Carrillo, C. Sutherland, and T. K. Fuller. 2019. Seasonal use of waterholes and pathways by macrofauna in the dry forest of Costa Rica. *Journal of Tropical Ecology* 35:68–73.
- Morato, R., A. Stabach, H. Fleming, J. M. Calabrese, R. C. De Paula, K. Ferraz, D. Kantek, S. Miyazaki, T. Pereira, G. Araujo, et al. 2016. Space use and movement of a Neotropical top predator: the endangered jaguar. *PLoS ONE* 11(12): e0168176.
- Morgan, D. R., J. Innes, C. M. Frampton, and A. D. Woodhouse. 1995. Responses of captive and wild possums to lures used in poison baiting. *New Zealand Journal of Zoology* 22:123–129.
- Novack, J., M. Main, M. Sunquist, and R. Labisky. 2005. Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. *Journal of Zoology* 267: 167–178.
- O'Connell, A., J. Nichols, and U. Karanth. 2011. *Camera Traps in Animal Ecology. Methods and Analyses*. Springer, New York, USA.
- O'Connor, K., L. Nathan, M. Liberati, M. Tingley, J. Vokoun, and T. Rittenhouse. 2017. Camera trap arrays improve detection probability of wildlife: investigating study design considerations using an empirical dataset. *PLoS ONE* 12(4): e0175684.
- Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47:1055–1059.
- Quinn, G., and M. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge, University Press, New York, USA.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabelo, R., S. Aragón, and J. Bicca-Marques. 2019. Prey abundance drives habitat occupancy by jaguars in Amazonian floodplain fluvial islands. *Acta Oecologica* 97:28–33.

- Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural Biological and Environmental Statistics* 14:322–337.
- Rovero, F., and F. Zimmermann. 2016. *Camera trapping for wildlife research*. Pelagic Press, city, UK.
- Rowcliffe, M. 2019. *Activity: animal activity statistics*. Version 1.3. <<https://cran.r-project.org/web/packages/activity/index.html>>. Access Ed (date).
- Salom, R., E. Carrillo, J. Sáenz, and J. Mora. 2007. Critical condition of the jaguar (*Panthera onca*) population in Corcovado National Park, Costa Rica. *Oryx* 41:51–56.
- Shahbaba, B. 2011. *Biostatistics with R, an introduction to statistics through biological data*. Springer, New York, USA.
- Silver, S., L. Ostro, L. Marsh, L. Maffei, A. Noss, M. Kelly, and G. Ayala. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* 38:148–154.
- Sollmann, R., B. Gardner, and J. Belant. 2012. How does spatial study design influence density estimates from spatial capture-recapture models? *PLoS ONE* 7(4):e34575.
- Stiles, G., A. Skutch, and D. Gardner. 2007. *Guía de aves de Costa Rica*. Fourth edition, Instituto Nacional de Biodiversidad (INBIO), Heredia, Costa Rica.
- Sunquist, M., and F. Sunquist. 2002. *Wild cats of the world*. The University of Chicago Press, Chicago, USA.
- Thompson, W. L., and D. C. Lee. 2000. Modeling relationships between landscape-level attributes and snorkel counts of Chinook salmon and steelhead parr in Idaho. *Canadian Journal of Fish and Aquatic Sciences* 57:1834–1842.
- Trolliet, F., M.-C. Huynen, C. Vermeulen, and A. Hambuckers. 2014. Use of camera traps for wildlife studies. A review. *Biotechnologie, Agronomie, Société et Environnement* 18:446–454.
- Valeix, M. 2011. Temporal dynamics of dry-season water-hole use by large African herbivores in 2 years of contrasting rainfall in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology* 27:163–170.
- Weckel, M., W. Giuliano, and S. Silver. 2006. Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *Journal of Zoology* 270:25–30.
- Zuur, A. F., E. N. Ieno, and M. Smith. 2007. *Analyzing ecological data*. Springer, New York, USA.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, NY, USA.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

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