

Landscape of human fear in Neotropical rainforest mammals

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ARTICLE INFO

Keywords:

Atlantic forest
Avoidance
Brazil
Human activity
Night-time light
Nocturnality
Poaching

ABSTRACT

The landscape of fear has profound effects on the species behavior, with most organisms engaging in risk avoidance behaviors in areas perceived as riskier. Most risk avoidance behaviors, such as temporal avoidance, have severe trade-offs between foraging efficiency and risk reduction. Human activities are able to affect the species landscape of fear, by increasing mortality of individuals (i.e. hunting, roadkill) and by disruption of the clues used by the species to estimate predation risk (e.g. light pollution). In this study, we used an extensive camera-trapping and night-time light satellite imagery to evaluate whether human activities affect the diel activity patterns of 17 species of rainforest dwelling mammals. We found evidence of diel activity shifts in eight of 17 analyzed species, in which five species become 21.6 % more nocturnal and three species become 11.7% more diurnal in high disturbed areas. This activity shifts were observed for both diurnal and nocturnal species. Persecuted species (game and predators) were more susceptible to present activity shifts. Since changes in foraging activity may affect species fitness, the behavior of humans' avoidance may be another driver of the Anthropocene defauna.

1. Introduction

The biosphere is becoming increasingly modified by human activities, where 75% of the world area experiences measurable amounts human pressure (Venter et al., 2016). Activities such as the direct removal of natural forests and grasslands to allocate croplands, livestock pastures, urban development and expansion of road networks are the main drivers of the reduction of the natural biomes (Mittermeier et al., 2004). As a consequence, the populations of innumerable species have been also severely impacted by direct and indirect human driven habitat modification and harvesting, with 25 % of mammals, 13 % of birds and 41 % of amphibian species being considered threatened to some degree (IUCN, 2018). Moreover, beyond the direct habitat destruction and species overharvesting, the effects of human activities have also discreet but equally pervasive consequences on population dynamics, caused by changes in the species perception of an area as safe or dangerous (Frid and Dill, 2002).

All species on Earth evolved strategies to avoid predation and are

capable of modulate their behavior to achieve the energetic daily demands while avoiding being killed. The oldfield mice (*Peromyscus polionotus*), for instance, reduces predation risk by foraging on safer areas, under vegetation shelter and during darker nights, while avoiding open areas especially under the moonlight (Orrock et al., 2004). In a similar way, the paca (*Cuniculus paca*) and nine-banded armadillo (*Dasypus novemcinctus*), also avoid foraging under the bright full moon, when the perceived predation risk is higher, but concentrate the foraging on new moon nights, when the perceived risk is lower (Harmsen et al., 2011).

The spatial and temporal variation in risk perception by the species is called the “landscape of fear”, and have profound effect on the species ecological interactions along both space and time (Laundre et al., 2010). The landscape of fear perceived by elks in response to re-introduced wolves, is directly related with the herbivory levels along the Yosemite National Park, with higher herbivory levels occurring on areas perceived as safer (Laundre et al., 2010). The landscape of fear perceived by a predator species also affects the distribution of its preys, with higher prey density on areas perceived as risky by the predator

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<https://doi.org/10.1016/j.biocon.2019.108257>

Received 2 March 2019; Received in revised form 13 June 2019; Accepted 18 September 2019

Available online 12 November 2019

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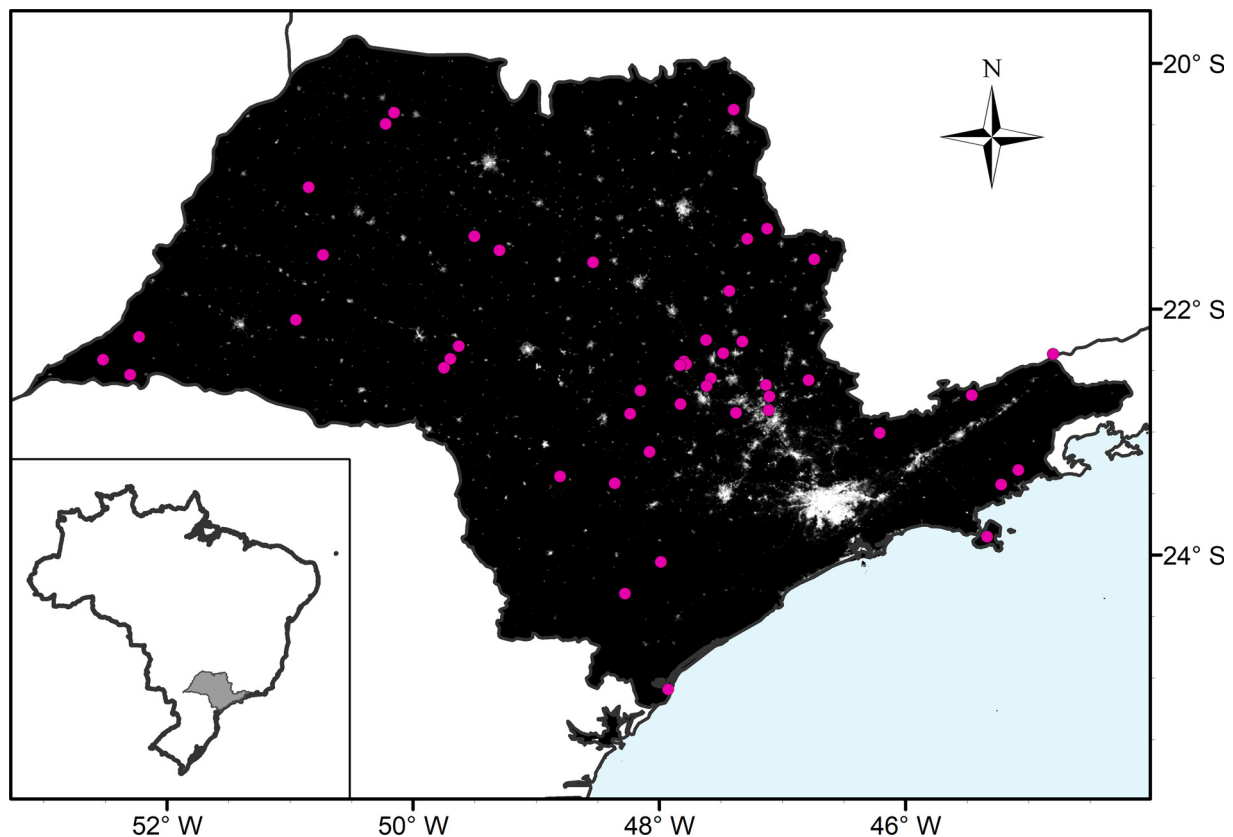


Fig. 1. The night-time light emissivity in the state of São Paulo and the location of the 47 study sites (points).

(Muhly et al., 2011). Fear have strong effects in foraging efficiency (Verdolin, 2006), and the species' choice about how much risk is acceptable depends on the cost-benefit ratio of forage in dangerous areas and on the amount of information available to estimate the risk (Bouskila and Blumstein, 2002).

It is important to highlight that the landscape of fear is not based on the real predation risk, but in the individuals' perceived predation risk. Foraging individuals rarely have complete knowledge about the real predation risk they are exposed, and therefore, they usually estimate the risk based on environmental clues, such as light intensity, canopy density, and noise (Orrock et al., 2004; Verdolin, 2006). This happens because it is safer to estimate the risk by indirect methods than rely on direct detection of a predator nearby, when it may be too late. It is also less harmful to overestimate the predation risk and lose some foraging efficiency, than to underestimate the risk, which can lead to death by predation (Bouskila and Blumstein, 2002; Frid and Dill, 2002). These non-lethal interactions between prey-predator can have even bigger effects on ecosystems dynamics than direct prey-predator interactions (Preisner et al., 2015).

Since the wildlife estimate the predation risk mostly based on clues, human activities can easily confound these clues and lead to false risk estimations, causing entire populations to live and behave under a level of risk perception which is disconnected with the reality, creating landscapes of fear that did not correspond to the real distribution of risks (Frid and Dill, 2002). Wildlife can perceive the noise of vehicles, agriculture machinery, airplanes, electric illumination and even the simple presence of humans as predation risk (Frid and Dill, 2002). As consequence, the high risk perception is known to increase stress hormones (Zbyryt et al., 2018), reduce feeding efficiency (Orrock et al., 2004) and reproductive success (Sheriff et al., 2009). In addition, it can also trigger risk avoidance behaviors, such as the spatial and temporal avoidance.

Temporal avoidance between the predator and prey is the risk

avoidance behaviors in which the prey shift its normal diel activity period to become active on a safer period, thus, reducing the chances of encounter a predator or any other threat (Saleni et al., 2007). It is also an alternative and/or complement for spatial avoidance (i.e. avoid risky areas) when the latter is not possible due to low habitat availability, or not enough to avoid conflicts (Martin et al., 2010; Saleni et al., 2007). However, since most species are not cathemeral (i.e. adapted to be equally active at any period of the day), shifts in diel activity period can negatively impact the species capability to locomote in the environment, find food, detect mates and predators (Bennie et al., 2014; Gaston et al., 2014). Despite its drawbacks, temporal avoidance has been showed as a common strategy used by mammals under human disturbed areas (Gaynor et al., 2018).

Since camera-trap data is widely used in research and conservation efforts, but human-driven disturbances not always produce detectable changes in the frequency of species records, we used camera-trap data to test for evidences of temporal avoidance behavior of forest-dwelling mammals in response to human-driven disturbances. We expected to: 1) observe temporal shifts on poached or persecuted species, such as ungulates, armadillos and wild felids (Bitetti et al., 2008; Cullen et al., 2000; Espinosa and Salvador, 2017; Gaynor et al., 2018); 2) confirm temporal shifts to occur mainly towards nocturnality, with species becoming relatively more nocturnal in more disturbed areas (Gaynor et al., 2018); 3) confirm no temporal avoidance in response to human disturbance by small body sized non-poached species, such as opossums (*Didelphis* spp.) small rodents, species that increase density in fragmented landscapes, such as squirrels (Koprowski, 2005; Mendes et al., 2016), and synanthropes (i.e. which benefit from association with humans), such as dogs (Paschoal et al., 2012).

2. Methods

2.1. Survey

To detect possible shifts in activity period, we used a large dataset from camera-traps (Bushnell HD Nature View and Reconyx RC55) to record the activity period of mammalian species along a gradient of habitat disturbance and degradation in continuous and fragmented areas of Atlantic Forest in Brazil. The sampling occurred from August 2012 to December 2018 along 47 Atlantic Forest sites (Fig. 1 and Fig S1), with sizes ranging from 16 ha to continuous (here defined as forest patches with more than 1 million ha). The region is highly biodiverse (Gonçalves et al., 2018; Lima et al., 2017) and the sampled forest sites are immersed in a very diversified landscape, ranging from monoculture (sugar cane), peri-urban areas to some of the most preserved Atlantic Forest reserves in the Serra do Mar massif (Ribeiro et al., 2009).

We sampled 47 forest sites with 697 camera stations, where each station received one camera for a period between eight and 278 days (45 ± 29.2). The camera-traps were placed around 30 cm above the ground, recording video or a rapid 5 pictures sequence in response to the activation of a passive infrared sensor. We used 60 min as a minimum time allowed between two records for the same species at the same camera, as a safety measure to avoid extreme variation in sample sizes, since due to the temporal nature of the study question, each record is treated as a day/night Bernoulli trial (i.e. binomial trial). This effort resulted on a total of 31,491 camera/days, and 54 mammal species recorded (Beca et al., 2017; Brocardo et al., 2018; L. Lautenschlager and P. Akkawi unpub. data).

With the data obtained from camera-trapping, we classified the records in two groups based on the time of sunset and sunrise. Records taken when the sun was up in the sky (i.e. after sunrise and before sunset) were considered “day” records, while records taken after the sunset or before the sunrise were considered “night” records. Since the exact timing of sunrise and sunset vary up to 30 min along the entire study area according with latitude and season, we delimited five “time zones” (longitudes: 51.75 W, 50.20 W, 48.65 W, 47.09 W, 45.53 W), for which the exact timing of sunrise and sunset was obtained from a solar calendar (U.S. Naval Observatory, 2019). The records of each sampling station were classified in day/night based on the solar time of the nearest time zone, to guarantee a day/night classification with less than 3 min of error along the entire study area and along the sampling years. Using the day/night records for each one of the 47 forest sites as a binomial variable, we evaluated the effect of the human disturbance on

17 mammalian species (Table 1), including two exotic species, the domestic dog (*Canis lupus familiaris*) and the wild pig (*Sus scrofa*). Since small sized terrestrial rodents cannot be reliably identified by camera-trap records, we grouped all the records and analyzed it as a single group, here called “small rodents”. Other 37 mammal species could not be evaluated due to the reduced number of records or because the number of forest sites where these species were recorded was not enough to allow statistical comparisons. Sites where a given species was recorded less than five times were also not include in the analysis of the species.

2.2. Human disturbance proxy

Since human disturbance is a multiform phenomenon with a diverse array of pathways in which it can affect the local fauna, we decided to use the anthropogenic night-time light radiance, measured from satellite imagery, in a buffer around the sample forest patches as a proxy of human disturbance. Considering that mammals can be affected by human infrastructure more than 5 km away and that different mammal taxa present responses in different spatial scales (Benítez-López et al., 2010), we decided to test the effects of anthropogenic night-time light radiance in three different spatial scales, using concentric buffers of three, five and 10 km around the sampling sites.

Anthropogenic night-time light can be described as the light radiated by a region during the night period, whereas the light is created by human devices, such as the lightbulbs used for house and streets illumination. This light radiance is measured by satellites, such as the Suomi-NPP satellite, and filtered to remove natural atmospheric and surface light reflections (mainly moonlight and starlight reflections, see Lee et al., 2006). Ephemeral light producing events, such as fires, can also be identified and removed by comparing sequences of images or by light spectrum analysis. The spectral radiance unite used in the resulting raster is the microflick, measured in watt/cm²/sr/μm, where “sr” is a square radian, and the “μm” is a micrometer of span in wavelength. More technical information is available on Elvidge et al. (1997) and Lee et al. (2006). However, for reference, in a 10 km buffer in an isolated area of the Amazon Forest (7°48′06″S, 59°03′38″W) the measured mean of spectral radiance is -0.068 microflicks, while in a similar area in the São Paulo metropolitan area (23°33′01″S, 46°38′29″W) the measured mean radiance is 73 microflicks. The night-time light imagery used in this study is available freely by the Earth Observation Group (EOG, 2018), as a raster file, already filtered to remove natural reflections and ephemeral light producing events. We used ArcGIS (ESRI, 2016) to calculate and extract the radiance values

Table 1

Main results of the regression analysis, testing the effect of human disturbance on the nocturnality of each species and groups of species. Significant results are in bold. The group small rodents contain several unidentified species of rodents.

Species *Groups	Popular name	Spatial scale	Estimate	z value or *χ Square	P value
<i>Puma concolor</i>	Puma	5 km	0.3985	1.305	0.192
<i>Leopardus pardalis</i>	Ocelot	3 km	-0.6527	0.3073	0.034
<i>Canis lupus familiaris</i>	Domestic dog	5 km	0.2307	0.455	0.649
<i>Sus scrofa</i>	Wild pig	10 km	0.442	4.129	< < 0.01
<i>Cuniculus paca</i>	Paca	3 km	0.629	1.931	0.053
<i>Dasyprocta azarae</i>	Agouti	5 km	-0.247	-5.048	< < 0.01
<i>Dasyprocta novemcinctus</i>	Nine-banded armadillo	5 km	-0.284	-2.709	0.007
<i>Mazama gouazoubira</i>	Gray-brocket deer	3 km	-0.164	-1.599	0.110
<i>Pecari tajacu</i>	Collared peccary	3 km	-0.713	-3.125	0.002
<i>Tayassu pecari</i>	White-lipped peccary	5 km	-0.837	-5.119	< < 0.01
<i>Tapirus terrestris</i>	Tapir	10 km	-0.060	-0.629	0.530
<i>Didelphis albiventris</i>	White-eared opossum	5 km	-0.089	-1.059	0.289
<i>Didelphis aurita</i>	Black-eared opossum	5 km	-0.104	-0.751	0.453
<i>Eira barbara</i>	Tayra	5 km	-0.644	-1.082	0.279
<i>Nasua nasua</i>	South-American coati	10 km	0.164	0.758	0.449
<i>Guerlinguetus brasiliensis</i>	Atlantic-forest squirrel	10 km	0.215	1.181	0.238
<i>Sylvilagus brasiliensis</i>	Brazilian cottontail	10 km	0.370	1.982	0.047
small rodents*	Rat	5 km	-0.176	-1.522	0.128

from the raster.

The decision of use night-time lights as a human disturbance proxy was made based in several factors, including: A) Night-time light is commonly used as a proxy of human density, infrastructure density and intensity of light pollution (Elvidge et al., 1997); B) For nocturnal species, light pollution is, per se, a human caused disturbance which can be malefic or beneficial according to the species traits (Gaston et al., 2013), although, for diurnal species, it may facilitate the displacement and habitat use during night time (Gaston et al., 2013); C) In our study area, night-time light is negatively correlated with forest cover percentage (Pearson's product-moment correlation, $\text{cor} = -0.68$, $\text{df} = 34$, $p\text{-value} < 0.01$), whereas the matrix on these landscapes (mostly crops and pastures) were also created and maintained by human activities; D) Night-time light is also negatively correlated with the log of the sampled forest size in the study sites (Pearson's product-moment correlation, $\text{cor} = -0.65$, $\text{df} = 34$, $p\text{-value} < 0.01$), an important information since temporal avoidance behaviors are frequently used in conjunction with spatial avoidance (Martin et al., 2010). Thus, at least in our study areas, night-time light could be safely used not only as a proxy of light pollution and human infrastructure density, but also as a general human disturbance proxy. This approach is also similar to the technique that uses of cellphone coverage area as a proxy of human presence (Macedo et al., 2018). Other possible predictor variables, such as forest size and landscape forest cover were tested during preliminary analysis but were excluded from the study due to high collinearity and poor model performance when compared to the night-light variable.

2.3. Data analysis

We used logistic regressions to evaluate the effect of human disturbance on forest-dwelling mammal temporal avoidance behavior, with the day/night records for each species within each forest site, as a binomial response variable and the human disturbance proxy (i.e. night-time light, in logarithm with base 10) as explanatory variable. To determine the best spatial scale, for each species, three logistic models were created using the night-time lights from buffers with radius of three, five and 10 km, which were compared by the Akaike Information Criterion corrected for small sample sizes - AICc - (Burnham and Anderson, 2010). For each species, the model with smallest AICc value was used for the logistic regression, while the others were excluded. Since the model selection was used only to select the best spatial scale for each species, a null model was not required. For the species which presented responses to human disturbance, we also calculated its activity shift, here described as the difference in the model predicted diurnality between the most preserved and most disturbed areas in which the species was recorded. Finally, the activity period of all species was also plotted for visual inspection (Fig. 2), and circular metrics of diel activity, such as mean direction and Rho (i.e. a measurement of circular mean and dispersion, respectively) were calculated and reported in the supplementary material (Table S1). The species were also classified as diurnal, nocturnal or cathemeral based on these circular metrics, and classified as game species or non-game species based on both local expert experience and literature information (de Souza and Alves, 2014; Hanazaki et al., 2009; Instituto Chico Mendes de Conservação da Biodiversidade, 2018). All analysis were performed in R (R Core Team, 2016), using the packages “circular” (Agostinelli and Lund, 2011), “GAM” (Hastie, 2017) and ggplot2 (Wickham, 2016).

3. Results

We found evidence of activity shifts in response to human disturbance for eight of the 17 evaluated species, where five became more nocturnal in more disturbed areas and three become more diurnal in more disturbed areas (Fig. 3, Table 1). The average increase in nocturnality was 216% from the less disturbed areas to the more disturbed

ones, whereas the average increase in diurnality was 11.7% from the less disturbed areas to the more disturbed ones (Fig. 4). However, we must clarify that by “becoming more nocturnal” or “becoming more diurnal”, we did not mean that a species shifted its peak of activity from a period to another. Instead, it means that although the species main activity still occulting during its natural activity period (i.e. night for nocturnal species and day for diurnal species), the proportions of the day/night records have changed.

The species which responded to human disturbance by becoming more nocturnal are the azara's agouti (*Dasyprocta azarae*), nine-banded armadillo (*Dasybus novemcinctus*), ocelots (*Leopardus pardalis*), collared peccary (*Pecari tajacu*), white-lipped peccary (*Tayassu pecari*). The species which responded to human disturbance by becoming more diurnal are the paca (*Cuniculus paca*), wild pig (*Sus scrofa*) and Brazilian cottontail (*Sylvilagus brasiliensis*). These species, with the only exception of the Brazilian cottontail, are all considered game species, being hunted for its meat (peccaries) or persecuted (ocelots) as threats to livestock and domestic animals.

Other nine species did not present detectable activity shifts in response to human disturbance. The white-eared opossum (*Didelphis albiventris*), black-eared opossum (*Didelphis aurita*), tayra (*Eira barbara*), Atlantic Forest squirrel (*Guerlinguetus brasiliensis*), coati (*Nasua nasua*), domestic dog (*Canis lupus familiaris*), gray brocket deer (*Mazama gouazoubira*), puma (*Puma concolor*) and tapir (*Tapirus terrestris*). From these nine species, only tree (gray brocket deer, tapir and puma) are hunted or persecuted. Small rodents, which are not hunted, also did not respond for human disturbance).

4. Discussion

We found that 47% of tested forest-dwelling mammals changed their activity period in response to human disturbance. This result agrees with other studies that reported diel activity changes in wildlife as a consequence of human disturbances, including activity shifts toward diurnality, which is less common in the literature reports (Bennie et al., 2014; Gaynor et al., 2018; but also see: Hirakawa, 2006; Ross et al., 2013). Both diurnal and nocturnal species responded to human disturbance, with half of the eight diurnal species and four of the seven nocturnal species presenting shifts in diel activity. The two species which presented a cathemeral activity period (i.e. puma and gray brocket deer), did not responded to human disturbance, despite being a valued game species and a highly persecuted species, respectively (Hanazaki et al., 2009; Instituto Chico Mendes de Conservação da Biodiversidade, 2018).

The observed results support the first prediction, that poached or persecuted species, such as ungulates, armadillos and wild felids would respond to human disturbance by temporal shifts on its diel activity. We found that seven of the eight species (*Cuniculus paca*, *Dasyprocta azarae*, *Dasybus novemcinctus*, *Leopardus pardalis*, *Pecari tajacu*, *Sus scrofa*, *Tayassu pecari*) for which we observed temporal shifts, are game or persecuted species. On the other hand, from the 10 species for which no activity shifts were observed (including here the small rodents), only three species, the gray brocket deer, the tapir and the puma, are game or persecuted species. Moreover, the observed differences in the response of mammals to human disturbance are probably related to how the species perceive the human presence and activities as a threat, varying also in spatial scale according to the species. Although perceived predation risk is mostly estimated and susceptible to disruption (Frid and Dill, 2002), the species are also able to perform accurate estimates, such as demonstrated by the Japanese sika deer (*Cervus nippon*), which is capable of differentiate the threat represented by humans during and out of hunting season, increasing its avoidance behavior in the prior (van Doormaal et al., 2015). In this context, the absence of nocturnality shift in the gray brocket deer and tapir is particularly surprising since temporal avoidance is a strategy commonly reported for cervids, including close related species such as the red

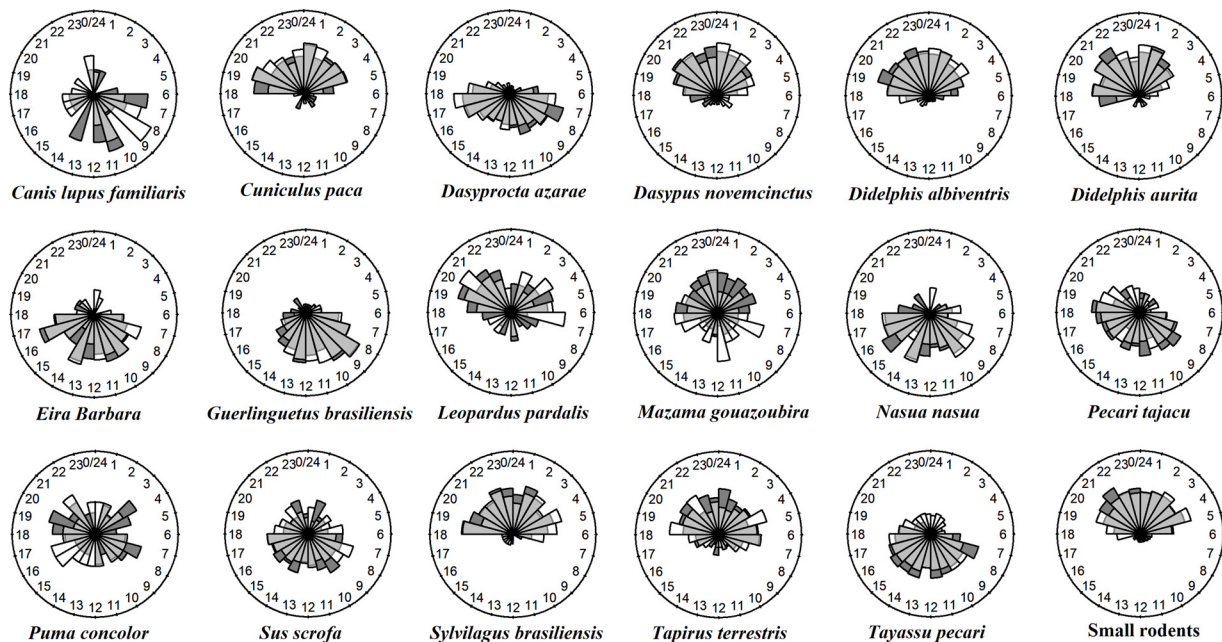


Fig. 2. Circadian activity of the 17 mammalian species, plus the group small rodents in 47 sites in the Brazilian Atlantic forest. Dark gray bars represent sites more preserved, and white bars more disturbed sites. For this figure, a site was considered disturbed when presented a night-light emissivity above the mean, considering only the sites where each species was recorded.

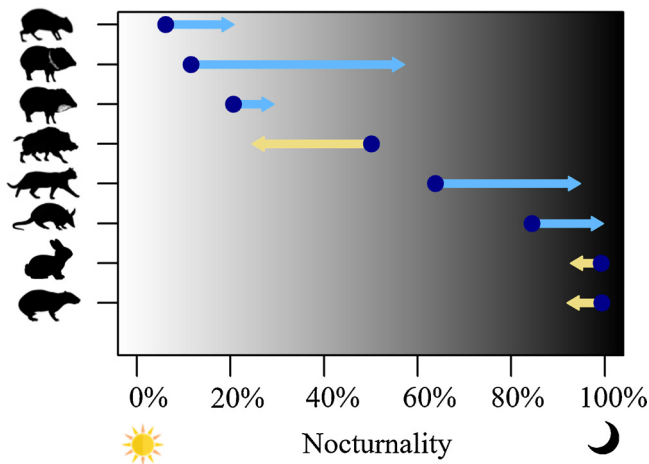


Fig. 3. Shifts in nocturnality of forest-dwelling mammals in response to human disturbance in the Brazilian Atlantic forest, from the most preserved site (blue points) to the most disturbed site (arrow point) in which each species was recorded. Arrows to the right represent shifts toward nocturnality, while arrows to the left represent shifts toward diurnality. From top to bottom, the species are: *Dasyprocta azarae*, *Pecari tajacu*, *Tayassu pecari*, *Sus scrofa*, *Leopardus pardalis*, *Dasyprocta novemcinctus*, *Sylvilagus brasiliensis* and *Cuniculus paca*.

brocket deer (*Mazama americana*, see Bitetti et al., 2008), and for tapirs (Gaynor et al., 2018).

The second prediction, that activity shifts would occur mainly towards nocturnality, is generally supported, but with exceptions. Five of the 8 species which presented activity shifts becoming more nocturnal, whereas the other 3 did the opposite. Although this proportion by itself is not enough to support the prediction, the shifts toward nocturnality were generally more pronounced than the shifts toward diurnality. It is also important to highlight two important points about the species which become more diurnal: First, the wild pig is an invasive species, with a recent domestication historic, hybridization events with domestic lineages and have a diet that include agricultural crops (Barrios-Garcia and Ballari, 2012). Considering the wild pig's large body mass

and the absence of top predators, such as jaguars, in most of the Atlantic Forest (Paviolo et al., 2016), humans have become their main "predator", with the species being target of both illegal poaching and being legally controlled by hunting, which are activities performed mainly at night time (Rosa et al., 2018). In this context, the species' activity shifts toward diurnality may be very similar response to the observed for the bearded pig (*Sus barbatus*) avoiding a nocturnal predator, the Sunda clouded leopard (*Neofelis diardi*, see Ross et al., 2013); Second, the other two species which become more diurnal, the Brazilian cottontail and the paca, are the two most nocturnal of the studied species, with only 2.5 % and 2.8 % of the total records occurring during the day, respectively. Although they did become more diurnal in response to human disturbance, the shifts were the smallest detected in the study, with only 5.95 % and 6.67 % of the records being diurnal in the most disturbed areas, respectively. This way, it is possible to argue that the main activity shifts observed indeed occurred toward nocturnality, as stated in the second, although exceptions (i.e. wild pigs) do exist.

The third prediction, that no temporal shifts would be expected for small body sized non-poached species, for species that increase density in fragmented landscapes and for synanthropic species, also received a mixed support. The prediction was contradicted by the observed activity shifts to the Brazilian cottontail, which is a small body sized non-poached species, and for the wild pig, which is a synanthropic species. Nevertheless, despite these two exceptions, other seven species which are either small body sized non-poached, increase density in fragmented landscapes or synanthropes did not presented activity shifts, as stated by the prediction. This way, most species fitted in the prediction, but exceptions were also reported.

Although we have evidences pointing to the effects of hunting as a mechanism driving activity shifts in forest-dwelling mammals, since we used a proxy of human disturbance instead of a direct hunting measurement, we cannot exclude other human-driven mechanisms which can potentially affect the observed activity changes on the local fauna, such as changes in food availability, habitat reduction and light pollution. Food availability, for instance, can be greatly increased by human activities if a species is able of consume crops or garbage (Weiser and Powell, 2010), but it can also be decreased if the food sources are destroyed (Galetti and Aleixo, 1998). As consequence,

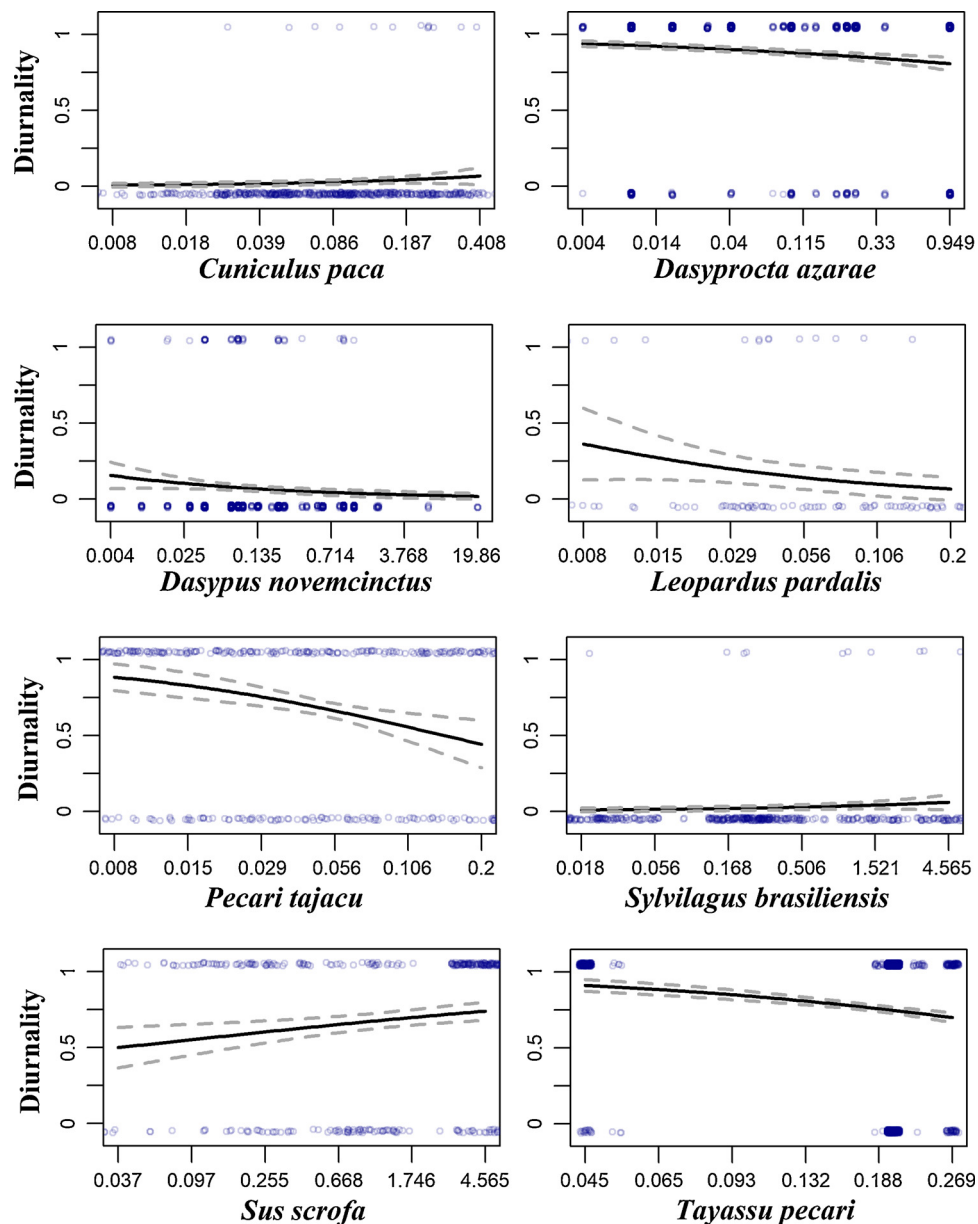


Fig. 4. Changes in diel activity of the species which were affected by human disturbance. The human disturbance (x-axis) was measured using the night-time light radiance of each site as a proxy and is recorded in microflashes.

changes on food availability affect the time required to an individual fulfill its daily diet requirements, sometimes forcing individuals to forage on less optimal time periods (Hirakawa, 2006; van Schaik and Griffiths, 1996). Nevertheless, although some of the evaluated species are known to consume crops (Barrios-Garcia and Ballari, 2012) and to increase population density in fragmented areas, changes on food availability should not be the main driver of the observed results since it would affect both game species and non-game species, whereas we observed game species to respond more often than non-game species.

The reduction of habitat availability is another mechanism with possible effects on the observed activity shifts. Since temporal avoidance is a complement for spatial avoidance strategies (Kronfeld-Schor and Dayan, 2003), it is expected that disturbed populations on small forest patches rely more on temporal avoidance than equally disturbed population on large patches, which have more space available to benefit from spatial avoidance. Considering that, in the study region, night-time light was correlated with forest size and landscape forest cover, the differential reliance on temporal avoidance of the wildlife populations

along the disturbance gradient may partially explain the observed results. However, although habitat availability may affect the observed results, it cannot be the main drive of the observed activity shifts for two reasons: 1) Forest size and landscape forest cover per se were such a poor predictors of the species activity period that we decided to remove the variables from the final analysis, preferring to use only the night-time lights, which have an intrinsic human density factor (Elvidge et al., 1997) lacking on the pure habitat availability variables; 2) Even if habitat availability indeed changes the populations reliance on temporal avoidance, the population still needs a cause for engage in avoidance behavior, such as high perceived risk or competition for resources.

Light pollution is another mechanism with strong potential as a driver to the observed activity shifts, and since our human disturbance proxy (i.e. night-time lights) is based on the amount of light emitted to the night sky, it is also a direct measurement of light pollution. Light is the most obvious environmental variable that changes along the diel cycle, ranging from 103000 lx under full sunlight to 0.001 lx in a clear

starry night (Gaston et al., 2013). These cycles of light and darkness remained constant along the entire evolutionary history, and most species have evolved sensorial systems optimized to operate during a specific period of the diel cycle (Bennie et al., 2014; Gaston et al., 2013). However, today, more than 80 % of earth's surface is under some degree of light pollution (Falchi et al., 2016), and in intensely light polluted regions, the illuminance provided by the urban skyglow can be brighter than in a clear full moon night (Gaston et al., 2013). In this way, since several nocturnal species shift their activities in response to the moon cycles (Harmsen et al., 2011), the light pollution have illuminance more than enough to cause changes in species activity period (Gaston et al., 2013).

Moreover, light pollution drive the species activities mostly towards nocturnality, by increasing the amount of light available at night time for the navigation of diurnal and cathemeral species, while reducing the activity of species that naturally avoid illuminated nights (Gaston et al., 2013). Changes on activity due to the moonlight cycles were reported for some of the evaluated species, including the nine-banded armadillo, paca (Harmsen et al., 2011) and ocelot (Pratas-Santiago et al., 2016), but not for tapirs (Oliveira-santos et al., 2010). Thus, light pollution added to hunting, are probably an important driver behind the observed activity shifts in disturbed areas, although other drivers probably exist. It is also possible that the observed results are affected by the interactions between species and ecological chain effects. For example, the increase in diurnality of the highly nocturnal paca and Brazilian cottontail may be a response to the increase in nocturnality of the ocelot in disturbed areas, added to the enhanced detectability by predators due to the light-pollution. More detailed studies would be required to test the existence of such a complex type of interactions.

4.1. Conclusions

In summary, human disturbance was observed to cause activity shifts in eight of the 17 evaluated forest-dwelling mammal species, with five of these becoming more nocturnal and three more diurnal. Nocturnality was increased 21.6% in average, while diurnality was increased 11.7% in average. Among other factors, hunting and light pollution are the most plausible drivers of the observed activity changes. Consequently, human disturbed areas are probably perceived as higher risk areas by the wildlife, or at least by the species observed to change their activity patterns. Beyond the usually reported effects of human disturbance on species community composition and population densities, our results highlight how human presence and activities also affect the species behavior in a landscape scale. The ecological consequences of these behavioral changes are particularly difficult to predict due to the myriad of possible scenarios and possible causal pathways (see Gaston et al., 2013, 2014; Gaynor et al., 2018). Thus, a careful evaluation of how the proximal drivers affect the diel activity of each species is highly recommended, as well as the consequences of these diel shifts in the individual's survival, stress level and fitness. Finally, since several human settlements are located inside protection parks, we advise the use of night-time light imagery, in a finer resolution, to map the distribution of these settlements and to select areas for conservation action.

Acknowledgements

The resources required to the development of this study were provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (processes: 168080/2014-1 and 300970/2015-3) and by the Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP (processes: 2014/01986-0, 2014/09300-0, 2014/23095-0, 2015/22844-1 and 2015/18381-6).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.biocon.2019.108257>.

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