

## DOES MOONLIGHT SUPPRESS OR STIMULATE ACTIVITY OF A TROPICAL FOREST SMALL MAMMAL

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**Abstract:** Small nocturnal mammals must balance their activity to maximize foraging efficiency while reducing vulnerability to predators, and moonlight has been widely investigated as a predation risk cue. *Didelphis aurita*, a nocturnal marsupial, can act as both a competitor and an intraguild predator, and as a prey, increasing or reducing activity under this condition, respectively. We evaluated the effect of moonlight, temperature, and age on the bimodal activity pattern of *D. aurita* in an Atlantic Forest area, southeastern Brazil. Opossums were more active at low light conditions and in colder nights in the second activity peak. Adults were more active in the second peak, when compared to juveniles and subadults. We suggest that the observed behavior can be a consequence of a preference to periods of low light conditions, to increase foraging efficiency, since *D. aurita* display features that reflect specialization to scotopic vision such as the *tapetum lucidum*.

Keywords: activity pattern; behavior; lunarphobia; marsupial; predation risk.

Moonlight can have profound influence on the activity patterns of nocturnal species (Prugh & Golden 2014). Species may respond to variation in moon phases by increasing (lunarphilia) or decreasing (lunarphobia) activity (Prugh & Golden 2014, Ferreira 2022). The lunarphobic behaviour is usually associated to a suppression in activity in bright moon nights to avoid predators, since predators would become more efficient under these conditions, while the lunarphilic behavior is associated with an increase in activity to improve foraging efficiency of both predators and preys (Prugh & Golden 2014). Some bats, for example, have their activity inhibited both under natural

(Crespo 1972) and laboratory conditions (Haeussler & Erkert 1978), while other nocturnal mammals that detect prey visually will find prey more frequently as luminosity increases (Prugh & Golden 2014). In addition to bats, moonlight also influences the activity pattern of other nocturnal mammals, such as marsupials, rodents, and lagomorphs (Prugh & Golden 2014, Ferreira 2022)

Three potential hypotheses were proposed by Prugh & Golden (2014) underlying the effects of moonlight on the activity patterns of nocturnal mammals. The predation risk hypothesis states that if predators are more effective in capturing preys in bright moon nights, preys would respond by shifting their activity to evade predation. The visual-acuity hypothesis states that if preys rely on vision as their primary sensory system, activity will equally increase, and not be affected by predators. The habitat-mediated predation risk hypothesis states that if moonlight increases predation risk, the suppressive effect of moonlight on prey activity should decrease as habitat cover increases.

Neotropical marsupials can act as both predators and prey (Lessa & Geise 2010, Huck *et al.* 2016, Pratas-Santiago *et al.* 2016) and, therefore, show different responses to bright moon nights (Ferreira 2022). While the white-eared opossum *Didelphis albiventris* decreased activity in periods of low luminosity in the piedmont forest of the Yungas, northwestern Argentina (Albanesi *et al.* 2016), another population of *D. albiventris* behaved in the opposite direction, increasing activity in a Humid Chaco region, in the north part of the country (Huck *et al.* 2016). Moonlight, therefore, can act in different ways on Neotropical marsupials, and responses may be related to differences in community composition and habitat structure.

This study aimed to evaluate the effect of moonlight on the activity pattern of the black-eared opossum Didelphis aurita (Wied-Neuwied 1826) in the Serra dos Órgãos National Park, southeastern Brazil. The black-eared opossum weighs 1034 ± 273 g (mean ± SD) and is omnivorous (Astúa de Moraes et al. 2003) and scansorial, occasionally using the understorey and the canopy (Cunha & Vieira 2002). Didelphis aurita can likely increase or decrease activity under bright moon nights since the study area lacks most of the visually oriented predators found in less disturbed tropical forests (Macedo et al. 2007, Cecília Cronemberger, pers. commun.), it behaves as an intraguild predator and potential competitor of other small mammals (Fonseca & Robinson 1990, Moura et al. 2009), and has features that reflect specialization to improve vision in low light conditions (Hokoç et al. 2012).

From June 2009 to December 2010, we recorded 37 individuals of *D. aurita* 51 times (nine juveniles, 19 subadults, and 23 adults) in three trapping grids, in 10 bimonthly sessions of five nights each. Overall, one session occurred during summer (austral), four in spring, three in autumn, and two in winter. The study was carried out in the locality of Garrafão (22°28'28" S, 42°59'86" W), at the municipality of Guapimirim in the Serra dos Órgãos National

Park (PARNASO), which is part of the largest continuous Atlantic Forest remnant in the state of Rio de Janeiro, southeastern Brazil. This locality is situated in a montane rainforest complex, in an old-growth successional stage (see Macedo et al. 2007). The area is cut by dirt roads and streams that are affluent of the Iconha River. The topography is irregular, and the vegetation is typical of Hillside forests with a high closed canopy and presence of devastated midstory. For details of the grid design and capture-recapture methods see Ferreira et al. (2016). Tomahawk live traps were equipped with digital timing devices that indicated the exact time the animal was captured (Ferreira & Vieira 2014a,b). Time of capture was converted to minutes after sunset (min as), and subsequent captures of the same individual during the same trapping session were ignored because of potential stress-related changes in activity. Due to the bimodal distribution of activity observed in this dataset by Ferreira & Vieira (2014a), the first (117  $\pm$  90.0 min as) and in second (560 ± 137 min as) peaks of activity were analyzed separately. We formulated nine linear models to determine the effects of the fraction of the moon illuminated (hereafter, moonlight), nightly minimum temperature, and age on the time of capture in each peak of activity. Data on nightly minimum temperature per hour were obtained from the climatic station located in the PARNASO (22°25' S, 42°58' W), and data on the moonlight were obtained at the Astronomical Applications Department of the U.S. Naval Observatory (USNO 2021). Moonlight was estimated as the fraction of the visible lunar disk illuminated at the hour of capture and is a quantitative measure of the lunar phase. Moonlight at new moon is 0.00, at first and last quarter is 0.50, and at full moon is 1.00. Individuals were classified in three age classes based on the pattern of tooth eruption sequence (Macedo et al. 2006).

Dependent variables were normally distributed according to the Shapiro-Wilk test (first peak: W = 0.95482, p = 0.3671; second peak: W = 0.95786, p = 0.2398), and a visual inspection of the diagnostic plot (plot function in R) confirmed the homoscedasticity of residuals (i.e., equal variance of residuals). Our study follows Ferreira & Vieira (2014) that found a negative effect of minimum temperature on opossum's activity, and differences in activity among age classes mainly at the second peak of activity. Here, we tested the influence of moonlight with these influential variables and modeled each variable separately and as both additive and interactive models (Table 1). We used Akaike's Information Criterion corrected for small sample size (AICc) to compare models (Burnham & Anderson 2002). We also included an interceptonly model to compare the explanatory power of predictor variables relative to other unaccounted sources of variation. Model selection was performed with the package MuMIn (version 1.9.11). All analyses were performed in R environment (version 2.13.0, R Development Core Team).

*Didelphis aurita* was more active in low light conditions; activity increased as the fraction of the moon illuminated decreased, but only in the second peak of activity (Figure 1a; Table 1). The top-ranked model had an additive combination of moonlight, minimum temperature, and age (Table 1 and 2). Minimum temperature had a similar effect on opossum's activity, with increase in activity in colder nights (Figure 1b). Adults were also more active in the second peak ( $N_{1st peak} = 8 \text{ vs. } N_{2nd peak} = 15$ ), and differed significantly from subadults (Figure 1c; Table 2). The top-ranked model of the first peak of activity included only the negative influence of minimum temperature, but was followed by the intercept-only model, suggesting a weak explanatory power of minimum temperature (Table 1 and 2).

Of the three hypotheses proposed by Prugh & Golden (2014) to explain the effect of moonlight on activity patterns, the predation risk hypothesis would be supported if *D. aurita* behaved as a prey. Two potential predators are recorded in the study area, the domestic dog, *Canis lupus* 

**Table 1.** Comparison of models predicting activity patterns of the marsupial *Didelphis aurita* in the Serra dos Órgãos National Park, southeastern Brazil. Time of capture was converted to minutes after the sunset. Explanatory variables were age class (juvenile, subadult, and adult), the fraction of the moon illuminated (Moon; 0 - 1), and minimum temperature (Tmin; °C). K = number of parameters of the model, AICc = Akaike Information Criteria corrected for small ratio sample size/number of parameters, DAICc = AICci – minimum AICc, wi = Akaike weight.

Model	К	AICc	∆AICc	w <sub>i</sub>
First peak of activity				
Tmin	3	285.6	0	0.38
Constant	2	286	0.48	0.30
Tmin + Moon	4	287.6	2.04	0.14
Moon	3	288.5	2.98	0.09
Tmin * Moon	5	289.8	4.25	0.05
Tmin + Age	5	290.3	4.77	0.04
Tmin + Age + Moon	6	291.9	6.31	0.02
Tmin * Age	7	297.5	11.98	0.00
Tmin * Age * Moon	13	334.9	49.32	0
Second peak of activity				
Tmin + Age + Moon	6	414.8	0	0.87
Tmin + Age	5	419.2	4.43	0.10
Moon	3	422.3	7.58	0.02
Tmin + Moon	4	424.4	9.68	0.01
Tmin * Age	7	425.0	10.19	0.01
Tmin * Moon	5	427.3	12.5	0.00
Constant	2	430.6	15.88	0
Tmin	3	430.8	15.99	0
Tmin * Age * Moon	13	438.5	23.72	0

**Table 2.** Standardized parameters of the top-ranked models predicting the first and the second peak of activity of the marsupial *Didelphis aurita* in the Serra dos Órgãos National Park, southeastern Brazil. Time of capture was converted to minutes after the sunset. Explanatory variables were age class (juvenile, subadult, and adult), the fraction of the moon illuminated (Moon; 0 - 1), and minimum temperature (Tmin; °C). Significant codes: \* 0.05, \*\* 0.01, \*\*\* 0.001.

Variable	Estimate	Standard Deviation
First peak of activity		
Intercept	316.772**	102.823
Tmin	-9.647*	5.501
Second peak of activity		
Intercept	1170.3***	178.77
Moon	-341.63*	128.09
Tmin	-29.65**	10.21
Age		
juvenile	-127.13	81.72
subadult	-250.41***	61.01

*familiaris*, and the margay, *Leopardus wiedii* (Cecília Cronemberger, pers. commun.). If these predators were more successful under bright moon nights, *D. aurita* would become lunarphobic by reducing full moon activity. However, domestic dogs are more frequently recorded during the day in the Atlantic Forest (*e.g.*, Silva *et al.* 2018, Srbek-Araujo & Chiarello 2008), and the margay, despite being nocturnal, usually prey mammals (rodents and marsupials) with less than 1 kg (Bianchi *et al.* 2011). To corroborate or dismiss the predation risk hypothesis, data of both predator and prey activity on the same study area is needed.

With predominantly nocturnal habits (Ferreira & Vieira 2014a), opossums present well-developed eyes, displaying features that reflect specialization to scotopic vision such as the *tapetum lucidum*, a membrane positioned in the back of the eye capable of reflecting the light, thus accentuating the contrast of objects, and improving vision in low light conditions (Hokoç et al. 2012). Although its poor visual acuity compared with other nocturnal mammals (e.g., primates and carnivores; Veilleux & Kirk 2014), opossums can be very accurate in catching small vertebrates or preying on small arthropods from the leaflitter (e.g., orders Diplopoda, Chilopoda, Blattodea, Formicidae e Orthoptera; Ceotto et al. 2009; Santori et al. 2012). The black-eared opossum can easily discriminate small invertebrates at a considerable distance (Volchan *et al.* 2004). In the study area, *Didelphis aurita* indeed prefers microclimates with lower luminosity (Aprigliano 2003). Thus, *D. aurita* may increase activity during low-light conditions to increase capture efficiency, a hypothesis not predicted by Prugh & Golden (2014).

Opossums exhibit behavioral plasticity in activity in response to moonlight, as detected in many populations and species of *Didelphis*. While some species increase activity (*D. marsupialis* -Harmsen *et al.* 2011, *D. albiventris* - Huck *et al.* 2016), others decrease (*D. pernigra* - Barrera-Niño & Sánchez 2014, *D. albiventris* - Albanesi *et al.* 2016), have no response (*D. marsupialis* - Botts *et al.* 2021), or even show mixed results (*D. marsupialis* - Pratas-Santiago *et al.* 2016). In our study, this is made clear when we evaluate the activity of adults, subadults, and juveniles; opossums of different age classes were found active at different times, as also observed in *D. virginiana* (Ladine 1997).

Analyses evaluating the effect of moonlight on activity can be affected by confounding factors such as cloud cover and precipitation (Karger *et al.* 2021, Krieg *et al.* 2021). The effect of cloud cover on nighttime illumination can be complex, with both positive and negative effects (Krieg *et al.* 2021). No data on cloud cover was available, but precipitation, which is positively related to cloud cover (Karger *et al.* 2021), was obtained from the climatic station. During 10 trapping sessions opossums were



**Figure 1.** Relationship between activity patterns (Minutes after the sunset) of the second peak of activity of the marsupial *Didelphis aurita* and (a) the fraction of the moon illuminated (0.0 - new moon to 1.0 – full moon), (b) nightly minimum temperature (°C), and (c) age class (juvenile, subadult, and adult) at the Serra dos Órgãos National Park, southeastern Brazil. Time of capture was converted to minutes after the sunset. The plots were built with the package visreg in R, and graphs show how the expected value of the outcome (Minutes after the sunset) changes as a function of each explanatory variable and age class, with all others in the model held fixed.

mostly captured at times with no (83.6%) or very little rain (from 0.2 to 0.8 mm; 14.5%). In just one night (December 2010) an opossum was captured under intensive rain (4.4 mm/1 hour). We therefore concluded that cloud cover and precipitation would only have weaken the existing relationships between moonlight and activity.

Overall, the opossum was less active in bright moon nights, which could result from top-down or bottom-up factors: top-down if opossums are reducing predation risk by mesopredators or domestic dogs; bottom-up if individuals are tracking the activity of invertebrates and vertebrate preys, as a way to increase foraging efficiency. Based on the current evidence, we suggest that *D. aurita* maximize their foraging efficiency by being active in periods of low light conditions, and that predation risk is not the main determinant of the moonlight avoidance in the study area.

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