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Relationship between moonlight and nightly activity patterns of the ocelot (*Leopardus pardalis*) and some of its prey species in Formosa, Northern Argentina

Running title: Relationship of moonlight and activity patterns of ocelots and prey

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Abstract:

The moon can profoundly influence the activity patterns of animals. If predators are more successful under bright moonlight, prey species are likely to respond by shifting their own activity patterns (predator-avoidance hypothesis). However, the assumption that prey will necessarily avoid full-moon nights does not take into account that moonlight also allows

prey to more easily detect predators, and to forage more efficiently. Thus, nightly activity patterns could depend on night vision capabilities (visual-acuity hypothesis). To consider the possible influences of moonlight and to distinguish between these hypotheses, we used camera-trapping records of a predator, the ocelot (*Leopardus pardalis*), and several of its night-active prey to compare activity patterns under different moonlight conditions. The ocelots' activity patterns were not strongly related to moonlight, but showed a slight tendency for higher activity during brighter nights. Tapeti rabbits (*Sylvilagus brasiliensis*) and brocket deer (*Mazama americana*) showed a clear preference for brighter nights. White-eared opossums (*Didelphis albiventris*) also showed a trend to be less active in new moon light. In contrast, smaller grey four-eyed opossums (*Philander opossum*) and the poor eyesight nine-banded armadillo (*Dasyus novemcinctus*) showed similar activity patterns across all moon phases. Since activity patterns of most prey species were not shifted away from the activity of the ocelot, the differences between species are probably linked to their night vision capabilities, and emphasise the need for more information on the visual system of these taxa. Their activity patterns seem to be less strongly linked to avoidance of predation than previously thought, suggesting that foraging and predator detection benefits may play a more important role than usually acknowledged.

Key-words: Camera-traps; Lunar activity; Moon phase; Night vision; Predator-prey interaction

Introduction

Moonlight can have a profound influence on the activity patterns of nocturnal vertebrate species (Di Bitetti et al., 2006; Fernandez-Duque et al., 2010; Starr et al., 2012). Some nocturnal predators hunt more successfully on bright moon nights, and this can lead to a change in their activity patterns (Clarke, 1983). Not surprisingly, many prey species respond to their predators' activity patterns with corresponding changes in their own patterns. For example, in a lab experiment mimicking new moon, full moon and intermediate light conditions, deermice (*Peromyscus maniculatus*) reduced their activity under the brightest light, whereas hunting by their predator, the short-eared owls (*Asio flammeus*), was more efficient under full moon illumination (Clarke, 1983). Likewise, pygmy loris (*Nycticebus pygmaeus*) are more active in dark than in bright nights, and this has been attributed to predator avoidance (Starr et al., 2012). This potential shift of the activity patterns of prey species to avoid the periods of activity of their predator is known as the 'predator-avoidance hypothesis'.

However, there may also be potential benefits to the prey of remaining active with higher light levels: it is then easier to detect predators, and to forage more efficiently (Bearder et al., 2006; Bouskila, 1995; Prugh and Golden, 2013). Spectral tarsiers (*Tarsius spectrum*), for example, significantly increase foraging time and insect capture rates in full moon nights (Gursky, 2003). Similarly, Southern African lesser galagos (*Galago moholi*) seem to get more frequently captured by Cape genets (*Genetta tigrina*) during new moon than during full moon nights, and male galagos move farther on moon nights than during periods without moon light (Bearder et al., 2002). Under the 'visual-acuity hypothesis' it is therefore possible that the adaptations involved in a prey-predator relationship may not result in a

change of activity patterns, but in changes of micro-habitat use related to foraging. For example, both spiny rats (*Proechimys* spp.) and ocelots (*Leopardus pardalis*), their predators, did not change their activity patterns following changes in moonlight, but changed instead the locations of their activities (Emmons et al., 1989).

In our study, we used camera-trapping records of a Neotropical predator, the ocelot, and several of its prey species (nine-banded armadillos, *Dasybus novemcinctus*; white-eared opossums, *Didelphis albiventris*; grey four-eyed opossums, *Philander opossum*, and other unidentified small opossums; tapeti or Brazilian cotton-tail rabbit, *Sylvilagus brasiliensis*; and brocket deer, *Mazama americana*), to compare activity patterns under different moonlight conditions.

The aim was to evaluate whether activity patterns by prey species were more easily explained by the predator-avoidance hypothesis or by the visual-acuity hypothesis. We specifically hypothesised that the relationship between moonlight and the activity patterns of predators and their prey is, at least partly, a function of the acuity of, and dependence on, night vision of the species involved (Prugh and Golden, 2013). For example, some species from predominantly diurnal lineages (e.g. red brocket deer) consistently show activity both during the day and the night (i.e. they are cathemeral, *sensu* Tattersall, 1987; Huck et al., in prep.), which could be related to the structure of their *tapetum lucidum*. The *tapetum lucidum* is a reflective tissue layer behind the retina that, by reflecting light, increases the availability of it to the photoreceptors (Lee, 1886). It has been suggested that many herbivore ungulates have *tapeta* with a relatively lower amount of light reflectance (Ollivier et al., 2004). These species may possess a *tapetum lucidum*, but the *tapeta fibrosa* of artiodactyls (which consist of extracellular collagen fibrils) are morphologically and

chemically different from the *tapeta cellulosa* (which consist of regular cells containing variable reflective materials, depending on taxa) of carnivores (Ollivier et al., 2004; Schwab et al., 2002). Thus, we formulated predictions for activity patterns under different moonlight conditions of the different species based on their visual system and general adaptations to predator avoidance.

Ocelots have highly developed night vision (Kitchener et al., 2010), and they may also use their sense of smell to locate prey (Emmons, 1988; Emsens et al., 2013). Therefore, ocelots should be able to hunt under very low light intensities. However, since even the best adapted visual system needs some light to function, we predicted that ocelots would reduce, but not completely avoid, activity during low intensity moonlight conditions.

Like ocelots, opossums also have a well-adapted night vision system, although they are rather myopic and adapted to detect insect prey species at short distances (Volchan et al., 2004, on *Didelphis* spp.). If moonlight helps opossums during foraging, but does not increase the risk of predation by ocelots, we predicted that white-eared opossums, and smaller opossums like the grey four-eyed opossum would be more active with high levels of moonlight and avoid times when the moonlight is minimal. However, if opossums have adapted their activity patterns to avoid predation by ocelots, they would show more activity at times that were avoided by their predator.

In contrast to opossums, the tapeti rabbit does not possess a *tapetum lucidum*. We therefore predicted that these rabbits would avoid times when the moon is not visible, showing increased activity during moonlit nights. Similarly, since the night vision of species with a *tapetum fibrosum* is likely to be less well developed (Ollivier et al., 2004) than the one

of feline predators, we predicted that brocket deer would show increased activity during bright nights, and reduced activity during dark ones.

Finally, nine-banded armadillos rely heavily on olfaction and have poor eyesight (Loughry and Mcdonough, 1994; Newman, 2014). We predicted that they would show no preferences at all, or more activity during nights or times of the night with less ocelot activity.

Methods

Study area and species

The study area was located in the Estancia Guaycolec ranch, 25 km from the city of Formosa in the Argentinean Gran Chaco of South America (58°11 W, 25°58 S, Fig. 1a). The climate is subtropical and seasonal with a mean annual precipitation of 1,432 mm (\pm 331, 1977-2012, Fernandez-Duque, 2016), two rain peaks in April (197 ± 166 mm) and November (186 ± 122 mm), and the lowest mean (51 ± 51 mm) for the period of June through August. Monthly mean temperatures are lowest between May and August (16-18°C) and highest between October and March (23-27°C).

The ranch includes nearly all habitat types representative of the Humid Chaco region: savannah, pasture, forest islands (forest patches surrounded by savannah), gallery forests (forests that form along rivers), and floodplains (Placci, 1995; Neiff, 2005).

There are several carnivore predators in the area, but the one most commonly caught in camera-traps is the ocelot (Huck et al., in prep.), which we therefore chose as the focus of this study. Other mammalian carnivores present are either diurnal (tayra, *Eira barbara*; jaguarondi, *Puma yagouaroundi*), at our study site not commonly found inside

the forest (crab-eating fox, *Cerdocyon thous*; maned wolf, *Chrysocyon brachyurus*) or recorded in the photographs not frequently enough for analysis (puma, *Puma concolor*; Geoffroy's cat, *Leopardus geoffroyi*; Huck et al., in prep.). Of the two large owls present, only the spectacled owl (*Pulsatrix perspicillata*) seems to hunt within the forest, while the greater horned owl (*Bubo virginianus*) has only been observed outside it (M. Rotundo, V. Dávalos, pers. comm.). Several species known to be preyed upon by ocelots (Emmons, 1987; Konecny, 1989; Sunquist et al., 1989) occur in the area. Namely, we analysed data for nine-banded armadillos, white-eared opossums, grey four-eyed opossums and other unidentified small opossums, tapeti rabbits, and brocket deer, all of which are predominantly or completely terrestrial (including the opossums; Cunha and Vieira 2002).

Data collection

In October 2010 we started long term camera-trap monitoring of the field site. We used Moultrie Game Spy I-35, Moultrie Game Spy I-45 and Cuddeback Attack IR cameras. These cameras use infrared flash, since bright flash can scare animals away and lead to trap shyness (Schipper, 2007). Since then, a variable number of cameras (1-12, median: 5.0, \bar{x} : 5.4), running 24h/day, have been installed in an area of 97 ha (minimum convex polygon; Fig. 1b). Most of the cameras were situated within the gallery forest, usually on foot trails that run at 100m distances in North-South and East-West direction through the main part of the study area (Fig. 1b), because this allowed the cameras a better detection range, and because felids are known to commonly use human tracks (e.g. Trolle et al., 2005). We have no indication whether the use of tracks influenced the likelihood to detect certain prey species. Since the purpose of the study was to determine to see whether activity levels

changed according to moonlight, a general effect of tracks would not be expected to bias the results. Differences in numbers of active cameras were fully taken into account by our approach to analysis (see below, and last column Table 1). Out of 214.6 camera-months, only 14.0 were from cameras situated just outside the gallery forest, and 11.6 were placed in a forest islands that was separated from the gallery forest by a minimum of 30m savannah. This did not allow taking habitat type into account, but there was no pattern in the data apparent that would suggest that these non-forest cameras would qualitatively change the results. While one camera was installed for eight months on a platform ca. 1.5m above ground, all other cameras were placed at ground level (20-40 cm high), since all of the investigated prey species are either exclusively, or in the case of opossums, mainly terrestrial (Cunha and Vieira, 2002). The mean distance between cameras set up during the same time period was 532m (with mean minimum distances of 103 and mean maximum distances of 1212m). We analysed photos obtained between 12th October 2010 and 8th January 2015, with interruptions between 6th Oct 2012 and 17th Mar 2013, and between 9th July and 30th Oct 2014, when no cameras were installed. The period analysed included approximately 45 moon cycles.

For the analyses presented below we only used photos taken during the night, which we defined as the period between the end of nautical twilight and the beginning of it the following morning (i.e. when the sun is more than 12° under the horizon). In other words, we limited our analyses to a period when there was no sunlight that could confound the effects of moonlight. We obtained nautical twilight times from the website of the Astronomical Department of the US Navy (USNO, 2011).

Moon phases

We determined the percentage of the moon's visible illuminated surface using a code for R 2.15.2 (Schmitt, 2013; R Core Team, 2014). Following the categorisations by Schmitt (2013), we additionally classed moon phases according to the moon's age (i.e. the number of days from new moon; Table 1). We used the times of moon rise and moon set (USNO, 2011) to determine if a photo had been taken before the moon had risen, or after it had set. In those cases, the moon phase was characterised as "not visible" (with 0% illuminated surface). This correction did not affect all moon phases equally, and resulted, for example, in a lower number of "available" hours for the first quarter of the moon, since during this phase the moon is mainly visible during daylight. Likewise, the number of active cameras varied, and we therefore estimated sampling effort calculating the hours each camera was active during each moon phase (Table 1). Since our data set was not sufficient to analyse waxing and waning phases of similar illumination separately, they were combined for some analyses (Table 1). For example, as the waxing and waning crescent periods have both 3.8 - 30.9% of the moon surface illuminated, they were then combined into a "1st quarter" phase.

Moon-light is also affected by cloud cover. Since hourly cloud cover values were not available, we used daily precipitation as a proxy for cloud cover, classing days with zero precipitation as "no cloud cover" (91% of days) and days with precipitation as "cloud cover".

Data preparation

We characterised the activity patterns of the different species using time stamped photographs and we quantified their activity using the number of photographic records over

any given observation time. Photos from the same camera station were only considered independent data points, but not necessarily different individuals, when the two closest times of photographs were at least 60 min apart. Although we cannot exclude the possibility that the same individual was recorded more than once during one night (either at the same camera station more than one hour apart or at different camera stations) this was not a common occurrence, since we rarely had more than one record per species per night. Furthermore, following the logic for home-range analyses (Blundell et al., 2001; De Solla et al., 1999; Otis and White, 1999), auto-correlated records can also convey a strong biological message because they imply higher activity. The long sampling period ensured that any remaining low levels of pseudo-replication will not have biased our data. For most species it was not possible to differentiate individuals from the photographs, but we were able to identify a minimum of five ocelots (one female, three males, and one individual of unidentified sex) based on individual coat patterns. For the smaller prey species, the duration of the study (> 4 years), and the size of the sampled area should ensure that the photos are from a larger number of individuals. We have little information to estimate the number of brocket deer individuals, but given that carnivores tend to have larger home-ranges than herbivores, it is reasonable to assume that more individual deer than ocelots were included in our study. With night-time photos it was often difficult to distinguish confidently between grey brocket deer (*Mazama gouazoubira*) and red brocket deer. However, photos for which clear identification was possible, suggested that only red brocket deer were active at night (Huck et al., in prep.). We therefore combined all deer photos, assuming that they were from red brocket deer. Likewise, for the smaller opossums it was not possible to always identify individuals to the species level, so all photographs of smaller

opossums were subsumed under the name of the most commonly identified species, the grey four-eyed opossum.

Statistical analysis

For statistical analyses we employed two approaches: We used binary logistic regression for the main analyses using R 2.15.2 (R Core Team, 2014). Additionally, we employed a visual approach accompanied by G-tests, since this provided more intuitive representation of the data than the graphics for binary logistic regression. We did not employ circular statistics, since these assume equal availability for each section of the circle. Since during the moon cycle certain phases are more commonly visible during day-time than during night-time, circular statistics were therefore clearly not applicable (Batschelet, 1981) and could lead to misinterpretation of the actual activity patterns. Both of our approaches took into account the variable availability of different moon illuminations during the moon cycle and the variable number of cameras available during the whole study period.

First, each species was analysed separately to estimate the potential effect of illumination on the probability of detection of that species. Binary logistic regression used photographic records as "presence", and per species 1,000 randomly generated data points (proportional to the availability of different moon illumination levels, see '*Moon phases*') as "absences". Preliminary analyses using fewer random data points suggested that test statistics were not affected by the imbalance of the number of random vs. true data points, except for the intercept, which was not under consideration for the research question. The percentage illumination and cloud cover were used as independent variables (without interaction effects, since there were not enough days with cloud cover) when analysing each

species separately. Additionally, we conducted a binary logistic regression to estimate the interaction effect of illumination and species, with the ocelot as the reference species and cloud cover as a third independent variable. The purpose of this analysis was to detect whether any interaction effect would suggest that moon illumination had a different effect on the activity pattern of particular species compared to the pattern shown by the predator. Binary logistic regression models assume a linear relationship between the logits of the dependent variables and continuous predictor variables, so we checked for non-linearity using a Box-Tidwell transformation test (Box and Tidwell, 1962); the tests suggested that the relationships did not deviate statistically from linearity (all p-values > 0.05).

Secondly, for the visual approach and G-tests, we calculated expected frequencies of photos (E) per moon phase as the total number of photos for a species or group of species, multiplied by the availability of a certain moon phase, divided by the total availability (i.e. the total number of trap-hours). We then compared the frequencies of photos for a specific species (or group of species) in different moon phases to the expected frequencies using a goodness of fit G-test with William's correction for small sample sizes. Graphically, we present this as the ratio of observed (O) over expected (E) frequencies for each species for each different moon phase. We gave the ratio a negative inverse value (i.e. $-E/O$) when $O/E < 1$. This adjusted ratio then ranges from +1.0 to positive infinity and from -1.0 to negative infinity, with values above +1.0 indicating a higher number of photos taken than expected, and values below -1.0 indicating a lower one. Similarly, we compared the observed activity patterns of ocelots and each of the species using a contingency table G-test with William's correction.

For some species sample sizes were relatively small for at least some moon phases. We therefore additionally analysed the data combining the phases "not visible", "new moon" and "first quarter" into a category of "low moon light" and the phases "half moon", "third quarter" and "full moon" into a category of "high moon light". Using the same type of analyses as described above, this additional classification provided a general indication of whether species preferred brighter or darker nights.

Results

The white-eared opossum, tapeti rabbit, and red brocket deer were more active on nights of higher moon illumination levels. These species were detected in brighter nights more commonly than expected (Fig. 2; for a coloured figure see Electronic supplement Fig E1). These positive relationships between activity and moonlight levels were statistically significant as indicated by the binary logistic regressions (Table 2) and the G-tests using either the detailed or the combined moon phases (Table 3, Fig 2). Post-hoc, pairwise G-tests showed that significant differences were between all low light level moon phases against all high light level phases for the tapeti rabbit, and between non-visible moon phases against half and full moon, as well as new moon against full moon for the red brocket deer (Table 4). The remaining two prey species, the grey four-eyed opossum and the nine-banded armadillo, showed no statistically significant relationship between moon illumination and activity levels (Table 2, Table 3, Fig. 2).

The ocelots showed a tendency to prefer third quarter moon nights, and to avoid full moon nights (Fig2, Table 5, Table 6). Still, the relationship between moon phase and the ocelots' activity patterns was not statistically strong (Table 2). The activity pattern of the

ocelot was not very dissimilar from most of its prey species, and only for the nine-banded armadillo did the interaction effect of species and moon illumination approach statistical significance compared to the ocelot (Table 5), although using the less powerful G-tests no statistically significant differences in the patterns of ocelot and any prey species were detected (Table 6).

Discussion

Our analyses show that the activity patterns of half of the examined species were related to moonlight. Nevertheless, all species were encountered during all moon phases at least occasionally, including times when the moon was not visible. Our findings are compatible with the hypothesis that the patterns observed are related to the acuity of the night vision system of the various species, whereas we found little evidence that any prey species, with the possible exception of the nine-banded armadillo, directly responded to the activity pattern of their predator. Thus, most of our data do not provide support for the predator-avoidance hypothesis for the prey species under investigation. Nevertheless, it should be born in mind that prey species might also shift their micro-habitat use in order to avoid predators, such as spiny rats avoiding ocelots (Emmons et al., 1989), and thus more subtly avoiding predators. However, since most of our camera-traps were situated on footpaths, a shift of prey species to different micro-habitats would have led to a change in capture frequency and hence differences in activity patterns compared to ocelots, which was not the case.

We did not find a strong relationship between moon phase and ocelot activity patterns, in general agreement with other studies (Emmons et al., 1989; Maffei et al., 2005).

Our data support partly our prediction that ocelots would show only a weak avoidance of dark nights, given their good night vision (Kitchener et al., 2010). However, ocelots showed a slightly stronger tendency for higher activity levels in brighter nights (in particular gibbous, but not full moon) than other predominantly night active carnivores (lions, *Panthera leo*, and spotted hyaenas, *Crocuta crocuta*), that used full and new moon nights similarly in a more open habitat (Cozzi et al., 2012). If, as suggested by our data and previous studies (Emmons et al., 1989; Maffei et al., 2005), ocelots do not strongly avoid or prefer any particular moon phase, prey species may not gain much by shifting their activity levels (i.e. absolute amount of time being active) in relationship to the ocelots'. However, as pointed out earlier, there may be other factors leading prey species to prefer brighter nights, in particular more efficient foraging and easier predator detection (Gursky, 2003; Prugh and Golden, 2013).

A meta-analysis to unravel the extremely variable response of different species to moonlight indicated a strong phylogenetic signal: species relying principally on vision were generally attracted by bright moon (Prugh and Golden, 2013). In particular vision-orientated primates such as owl monkeys (*Aotus azarae*; Fernandez-Duque et al., 2010), spectral tarsiers (Gursky, 2003), Southern African lesser galagos (*Galago moholi*; Bearder et al., 2006), and lemurs (see review table 8.1 in Nash, 2007) have been shown to be more active during brighter nights or parts of nights. Our findings for both deer and the tapeti rabbit are in line with this suggestion, since these species clearly showed more activity during brighter nights and avoided those times of the night when the moon was not visible, whereas the weak-sighted armadillo showed no marked preferences. At first sight, this might not be clearly concordant with rabbit and deer abilities of night vision, since while the tapeti rabbit

does not possess a *tapetum lucidum* (Lee, 1886), deer do (Schwab et al., 2002; Ollivier et al., 2004). However, there is an astonishing scarcity of information on the relative light reflection properties of various types of *tapeta lucida* and night vision abilities of different mammals (Schwab et al., 2002; Ollivier et al., 2004). All of the species we studied, except the armadillo and the tapeti rabbit (Lee, 1886; Loughry and Mcdonough, 2013), have some kind of *tapetum*, yet the chemical and anatomical features differ (Schwab et al., 2002; Ollivier et al., 2004), and it is possible that the ungulate *tapetum* is less efficient than the one of felids like ocelots. Species with a less efficient *tapetum* might therefore need higher light levels to find their food, and/or to detect potential predators. Nevertheless, it should be pointed out that this preference for bright nights by species without a *tapetum lucidum* is not universal; in fact European rabbits (*Oryctolagus cuniculus*) seem to prefer dark nights and to avoid bright ones in Spain where they are hunted by the Iberian lynx (*Lynx pardinus*; Penteriani et al., 2013).

Of the two opossum species, the larger white-eared opossum conformed to the prediction of slight preference of brighter nights. This would support the hypothesis that this species might use visual cues for foraging and predator detection. The smaller grey four-eyed opossum, however, showed no such tendency, using most other moon phases according to availability, suggesting that visual cues for foraging may be less relevant for this species. Another possibility is that, in the case of this relatively small marsupial, the ocelot might not be the relevant factor driving activity patterns, but rather other nocturnal predators, like the spectacled owl that is known to heavily prey on this species in the area (Ramírez Llorens, 2003). Given that owls in other areas have been shown to hunt more efficiently under bright moon-light (Clarke, 1983), it is possible that the smaller opossums

might be avoiding predation by spectacled owls rather than ocelots when active during darker nights. Nevertheless, opossums, including *Didelphis* and *Philander* species, were the most frequently consumed prey items of ocelots in Belize; it is therefore likely that they are also under predation pressure from ocelots in our study area (Konecny, 1989).

The nine-banded armadillo, the one prey species that relies mainly on its sense of olfaction (Loughry and Mcdonough, 1994; Newman, 2014), was clearly lacking any pattern, showing similar activity during all moon phases. Since ocelots are found moving during all moon phases, and armadillos probably do not benefit much from moonlight in terms of foraging or predator detection, there may be no selection pressure on them to shift their own activity to any particular moon phase.

All other prey species, like the opossums, might also face predation by other night-time predators, like pumas, Geoffroy's cats, or spectacled owls. Deer and armadillos are clearly too large to be preyed on by the latter two species, while the small species are unlikely to be the most preferred prey for a large predator like the puma. Both of the other cat species are much less frequently detected by the camera traps, and it is therefore unlikely that they pose a stronger force on the investigated prey species than the ocelot.

The number of photos taken of a species during a certain period is only an approximate measure of their overall activity. The activity of animals might also change in more subtle ways, for example by shifting the location of their activity, rather than the overall amount of it (Emmons et al., 1989). They might also walk more slowly, rather than for a shorter period of time, and this would also lead to a lower number of photographic records. A shift in micro-habitat use depending on moon-light levels would possibly be stronger evidence for the predator-avoidance hypothesis, while changes in absolute activity

levels would support the idea that moon-light increases foraging efficiency and helps with predator detection. Still, even after these considerations, our analyses indicate some change in the patterns of activity that are related to changes in moonlight. If all prey species strongly avoided the ocelot, this would have shown in the relative frequency of photographs in different moon-phases, regardless of whether the avoidance was achieved by a shift in the level of activity, or a shift in micro-habitat use. In order to distinguish between these possibilities additional approaches, like radio-telemetry or direct observation, are needed. Furthermore, the hypothesis that the night vision of some species is less well developed than the ocelot's highlight the need for more information on the relative performance of these species under low light conditions. This could be accomplished with studies examining the light reflection properties of various types of *tapeta lucida*.

The patterns of activity could also differ depending on whether the moon is waxing or waning, even when the percentage of illuminated moon surface may be the same. The ocelots of Misiones province in Northern Argentina showed this kind of response, reducing the use of trails previous and during full moon nights, but not after them (Di Bitetti et al., 2006). However, analyses that distinguish between a waxing and a waning crescent moon would have required larger sample sizes than we acquired during 45 months of data collection.

Our study confirms suggestions that the effects of moonlight on activity patterns are quite variable. Still, just as with cathemeral activity, this variability in response to moonlight, might partly relate to phylogenetic constraints and is less straightforwardly linked to predation than previously thought (Cozzi et al., 2012; Curtis and Rasmussen, 2006; Donati and Borgognini-Tarli, 2006; Prugh and Golden, 2013). While our data are in line with the

visual-acuity hypothesis, they obviously do not provide direct evidence for it. More investigations about the relationship of different *tapetum lucidum* types with night vision on the one hand, and with night-time activity patterns and behaviour on the other are needed for a more direct support of the hypothesis. Additionally, unless there are strong constraints like those imposed by morphological adaptations (e.g. in terms of night vision), it seems likely that predators and prey will show some tendency for oscillation between different patterns, as they cycle through periods of co-evolutionary 'arms-races' (Halle, 2000).

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References

- Batschelet, E., 1981. *Circular Statistics in Biology*. Academic Press, London.
- Bearder, S.K., Nekaris, K.A.I., Buzzell, C.A., 2002. Dangers in the night: Are some nocturnal primates afraid of the dark?, in: *Eat or Be Eaten - Predator Sensitive Foraging Among Primates*. Cambridge University Press, Cambridge, pp. 21–43.
- Bearder, S.K., Nekaris, K.A.I., Curtis, D.J., 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatol.* 77, 50–71. doi:10.1159/000089695
- Blundell, G.M., Maier, J.A.K., Debevec, E.M., 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecol. Monogr.* 71, 469–489. doi:10.1890/0012-9615(2001)071[0469:LHREOS]2.0.CO;2
- Bouskila, A., 1995. Interactions between predation risk and competition - a field-study of kangaroo rats and snakes. *Ecology* 76, 165–178.
- Box, G.E.P., Tidwell, P.W., 1962. Transformation of the independent variables. *Technometrics* 4, 531–550. doi:10.1080/00401706.1962.10490038
- Clarke, J.A., 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio tlammeus*) and deermice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* 13, 205–209. doi:10.1007/BF00299924
- Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W., Schmid, B., 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology* 93, 2590–2599. doi:10.2307/41739617

- Cunha, A., Vieira, M. V., 2002. Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil. *J. Zool.* 258, 419–426. doi:10.1017/S0952836902001565
- Curtis, D.J., Rasmussen, M. a, 2006. The evolution of cathemerality in primates and other mammals: a comparative and chronoecological approach. *Folia Primatol. (Basel)*. 77, 178–93. doi:10.1159/000089703
- De Solla, S., Bonduriansky, R., Brooks, R., 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *J. Appl. Ecol.* 68, 221–234. doi:10.1046/j.1365-2656.1999.00279.x
- Di Bitetti, M.S., Paviolo, A., De Angelo, C., 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *J. Zool.* 270, 153–163. doi:10.1111/j.1469-7998.2006.00102.x
- Donati, G., Borgognini-Tarli, S.M., 2006. From darkness to daylight: cathemeral activity in primates. *J. Anthropol. Sci.* 84, 7–32.
- Emmons, L.H., 1988. A field-study of ocelots (*Felis pardalis*) in Peru. *Rev. d'Ecologie la Terre la Vie* 43, 133–157.
- Emmons, L.H., 1987. Comparative feeding ecology of Felids in a Neotropical rainforest. *Behav. Ecol. Sociobiol.* 20, 271–283. doi:10.1007/BF00292180
- Emmons, L.H., Sherman, P., Bolster, D., Goldizen, A., Terborgh, J., 1989. Ocelot behavior in moonlight, in: Redford, K.H., Eisenberg, J.F. (Eds.), *Advances in Neotropical Mammalogy*. The Sandhill Crane Press, pp. 233–242.
- Emsens, W.-J., Hirsch, B.T., Kays, R., Jansen, P.A., 2013. Prey refuges as predator hotspots:

- ocelot (*Leopardus pardalis*) attraction to agouti (*Dasyprocta punctata*) dens. *Acta Theriol.* 59, 257–262. doi:10.1007/s13364-013-0159-4
- Fernandez-Duque, E., 2016. Social monogamy in wild owl monkeys (*Aotus azarae*) of Argentina: the potential influences of resource distribution and ranging patterns. *Am. J. Primatol.* 78, 355–371. doi:10.1002/ajp.22397
- Fernandez-Duque, E., de la Iglesia, H., Erkert, H.G., 2010. Moonstruck primates: owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. *PLoS One* 5, e12572. doi:doi.org/10.1371/journal.pone.0012572
- Gursky, S., 2003. Lunar philia in a nocturnal primate. *Int. J. Primatol.* 24, 351–367.
- Halle, S., 2000. Ecological relevance of daily activity patterns, in: Halle, S., Stenseth, N.C. (Eds.), *Activity Patterns in Small Mammals - An Ecological Approach*. Springer, Heidelberg, pp. 67–90.
- Kitchener, A.C., Van Vallkenburgh, B., Yamaguchi, N., 2010. Felid form and function, in: Macdonald, D.W., Loveridge, A.J. (Eds.), *Biology and Conservation of Wild Felids*. Oxford University Press, Oxford, pp. 83–106.
- Konecny, M.J., 1989. Movement patterns and food habits of four sympatric carnivore species in Belize, Central America, in: Redford, K.H., Eisenberg, J.F. (Eds.), *Advances in Neotropical Mammalogy*. The Sandhill Crane Press, Inc., Gainesville, FL, pp. 243–264.
- Lee, H., 1886. On the tapetum lucidum. *Med. Chir. Trans.* 69, 239–245.
- Loughry, W.J., Mcdonough, C.M., 2013. *The Nine-Banded Armadillo: A Natural History*. University of Oklahoma Press, Norman, Oklahoma.
- Loughry, W.J., Mcdonough, C.M., 1994. Scent discrimination by infant nine-banded

- armadillos. *J. Mammal.* 75, 1033–1039. doi:10.2307/1382486
- Maffei, L., Noss, A.J., Cuéllar, E., Rumiz, D.I., 2005. Ocelot (*Felis pardalis*) population densities, activity, and ranging behaviour in the dry forests of Eastern Bolivia: data from camera trapping. *J. Trop. Ecol.* 21, 349–353. doi:10.1017/S0266467405002397
- Nash, L.T., 2007. Moonlight and behavior in nocturnal and cathemeral primates, especially *Lepilemur leucopus*: Illuminating possible anti-predator effects, in: Gursky, S.L., Nekaris, K.A.I. (Eds.), *Primate Anti-Predator Strategies*. Springer, Heidelberg, pp. 173–205.
- Neiff, J.J., 2005. Bosques fluviales de la cuenca del Paraná, in: Arturi, M.F., Frangi, J.L., Goya, J.F. (Eds.), *Ecología Y Manejo de Los Bosques de Argentina La Plata*. Servicio de Difusion de la Creacion Intelectual de la Universidad Nacional de La Plata: Editorial de la Universidad Nacional de La Plata (EDULP), La Plata, pp. 1–26.
- Newman, H.H., 2014. The natural history of the ninebanded armadillo of Texas. *Am. Nat.* 47, 513–539.
- Ollivier, F.J., Samuelson, D.A., Brooks, D.E., Lewis, P.A., Kallberg, M.E., Komáromy, A.M., 2004. Comparative morphology of the tapetum lucidum (among selected species). *Vet. Ophthalmol.* 7, 11–22. doi:10.1111/j.1463-5224.2004.00318.x
- Otis, D.L., White, G.C., 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *J. Wildl. Manage.* 63, 1039–1044. doi:10.2307/3802819
- Penteriani, V., Kuparinen, A., Delgado, M. del M., Palomares, F., López-Bao, J.V., Fedriani, J.M., Calzada, J., Moreno, S., Villafuerte, R., Campioni, L., Lourenço, R., 2013. Responses of a top and a meso predator and their prey to moon phases. *Oecologia* 173, 753–66. doi:10.1007/s00442-013-2651-6

- Placci, G., 1995. Estructura y funcionamiento fenológico en relación a un gradiente hídrico en bosques del este de Formosa. La Plata.
- Prugh, L.R., Golden, C.D., 2013. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J. Anim. Ecol.* 83, 504–514. doi:10.1111/1365-2656.12148
- R Core Team, 2015. R: A language and environment for statistical computing. doi:URL: <http://www.R-project.org>.
- Ramírez Llorens, P., 2003. Ecología trófica de Strigiformes en Argentina: *Pulsatrix perspicillata* (Lechuzón Mocho Grande). Universidad de Buenos Aires.
- Schipper, J., 2007. Camera-trap avoidance by Kinkajous *Potos flavus*: rethinking the “non-invasive” paradigm. *Small Carniv. Conserv.* 36, 38–41.
- Schmitt, S.R., 2013. Lunar Phase Computation [WWW Document]. URL http://www.abecedarical.com/zenosamples/zs_lunarphasecalc.html
- Schwab, I.R., Yuen, C.K., Buyukmihci, N.C., Blankenship, T.N., Fitzgerald, P.G., 2002. Evolution of the tapetum. *Trans. Am. Ophthalmol. Soc.* 100, 187–199.
- Starr, C., Nekaris, K. a I., Leung, L., 2012. Hiding from the moonlight: luminosity and temperature affect activity of Asian nocturnal primates in a highly seasonal forest. *PLoS One* 7, e36396. doi:10.1371/journal.pone.0036396
- Sunquist, M.E., Sunquist, F., Daneke, D.E., 1989. Ecological separation in a Venezuelan Llanos carnivore community, in: Redford, K.H., Eisenberg, J.F. (Eds.), *Advances in Neotropical Mammalogy*. The Sandhill Crane Press, Inc., Gainesville, FL, pp. 197–232.
- Tattersall, I., 1987. Cathemeral activity in primates: a definition. *Folia Primatol.* 49, 200–202.

doi:10.1159/000156323

Trolle, M., Kéry, M., Consultancy, N., Allé, P., Denmark, F., 2005. Camera-trap study of ocelot and other secretive mammals in the northern Pantanal. *Mammalia* 69, 405–412.

doi:10.1515/mamm.2005.032

USNO, 2011. Sun or Moon Rise/Set Table for One Year [WWW Document]. *Astron. Appl.*

Dep. U.S. Nav. Obs. URL http://aa.usno.navy.mil/data/docs/RS_OneYear.php#notes

Volchan, E., Domingues Vargas, C., Da Franca, J.G., Pereira, A., Da Rocha-Miranda, C.E.,

2004. Tooled for the task: vision in the opossum. *Bioscience* 54, 189. doi:10.1641/0006-

3568(2004)054[0189:TFTTVI]2.0.CO;2

Figure legends:

Fig 1: a) Study area within Argentina, and b) camera-trap locations at the ranch Estancia Guaycolec, Formosa Province (Argentina). The grid lines (trails) are spaced 100m apart.



Fig. 2: Adjusted ratio of observed (O) over expected (E) frequencies of photos, during different moon phases, of ocelots (cross-hatched bars) and its prey species: a) white-eared opossum (*Didelphis albiventris*), b) grey four-eyed (and other small) opossums (*Philander opossum*), c) nine-banded armadillo (*Dasyus novemcinctus*), d) tapeti rabbit (*Sylvilagus brasiliensis*), and e) red & grey brocket deer (*Mazama americana*, *M. gouazoubira*). N.v. = non visible. For $O/E < 1$, the negative inverse value (i.e., $-E/O$) was used instead of O/E .

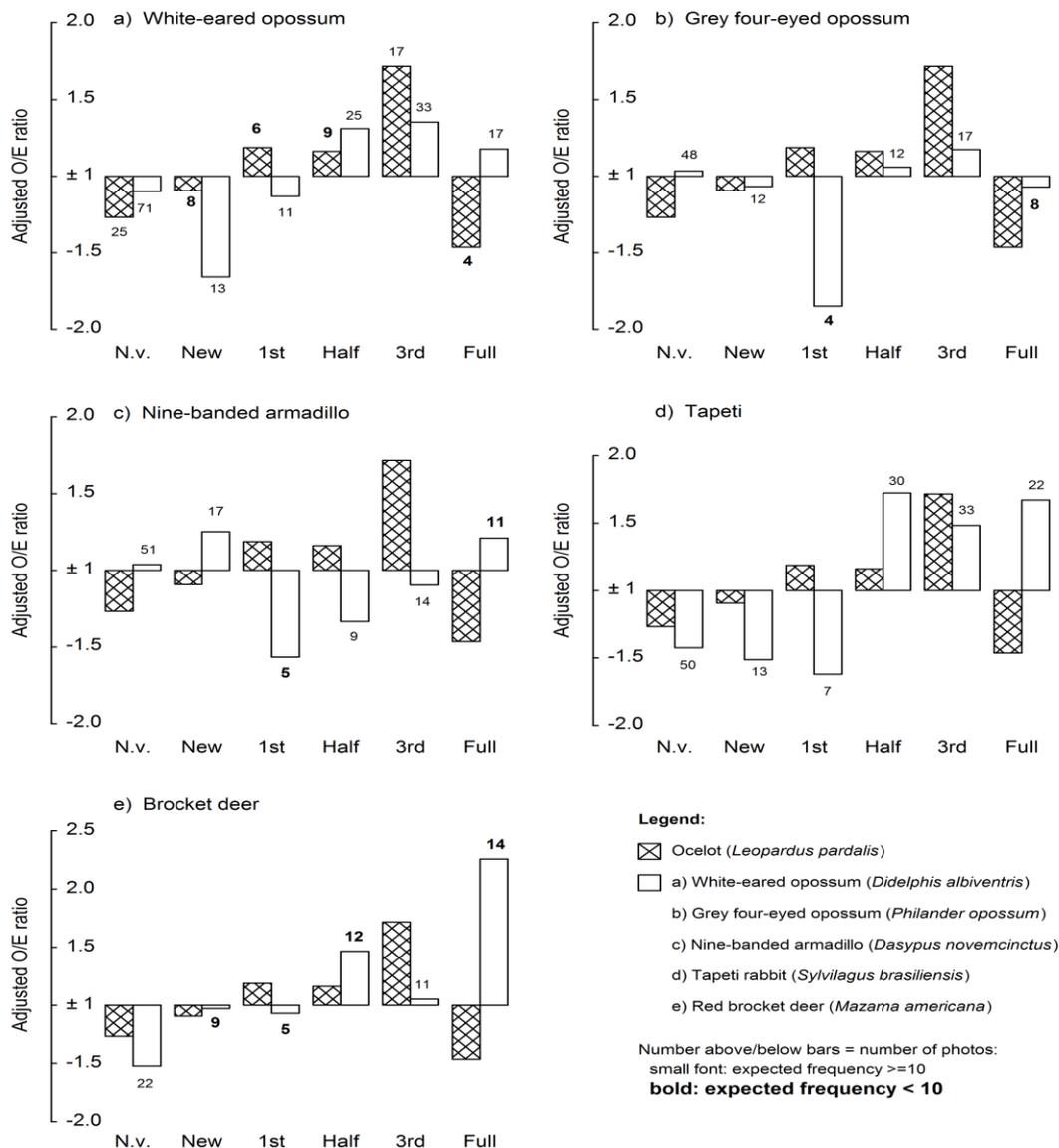


Table 1: Moon phases and sampling effort at Estancia Guaycolec (Formosa, Argentina) between October 2010 and January 2015. Moon age in days: number of days since new moon. Raw availability: number of trap hours. Availability: number of trap hours corrected for the time when the moon was not visible.

Moon phase	Combined phase	Moon age in days	% illuminated surface	Raw availability	Availability
New moon	New moon	< 1.8 or ≥ 27.7	0 – 3.8	10604	10604
Waxing crescent	1 st quarter	≥ 1.8 < 5.5	3.8 - 30.9	10378	3159
Waning crescent	1 st quarter	≥ 24.0 < 27.7	3.8 - 30.9	9876	2966
Waxing half	Half moon	≥ 5.5 < 9.2	31.0 - 69.0	10511	4756
Waning half	Half moon	≥ 20.3 < 24.0	31.0 - 69.0	10071	4634
Waxing gibbous	3 rd quarter	≥ 9.2 < 12.9	69.1 – 96.2	10473	5841
Waning gibbous	3 rd quarter	≥ 16.6 < 20.3	69.1 – 96.2	10892	6158
Full moon	Full moon	≥12.9 < 16.6	96.21 - 100	10825	7100
"Not visible"	"Not visible"	≥ 1.8 < 27.7	0	NA	38412

Table 2: Test statistics for binary logistic regressions for each species. The logit-estimate was converted to the odds for 10% changes in moon-illumination (Odds10[§]).

Species	Odds10 [§]	Z-value	P-value
Ocelot (<i>Leopardus pardalis</i>)	1.04	1.2	0.25
White-eared opossum (<i>Didelphis albiventris</i>)	1.05	2.3	0.024
Grey four-eyed opossum (<i>Philander opossum</i>)	0.99	-0.3	0.75
Nine-banded armadillo (<i>Dasypus novemcinctus</i>)	0.95	-1.5	0.14
Tapeti rabbit (<i>Sylvilagus brasiliensis</i>)	1.08	3.9	<0.001
Red brocket deer (<i>Mazama americana</i>)	1.07	2.1	0.027

§: The Odds10 value is the predicted change, when the independent variable "percentage moon illumination" increases by 10%, in the probability that a species is recorded over the probability that it is not recorded.

Table 3: Test statistics for goodness-of-fit G-tests comparing the frequency of photographic records against expected values for various species under either high and low levels of moon light, and under six different moon phases (moon not visible, new moon, first quarter, half moon, third quarter, full moon). Statistically significant values are highlighted in bold.

Species	Combined moon phases (Low vs. High) df = 1		Detailed moon phases df = 5	
	Gadj	p-value	Gadj	p-value
Ocelot	2.6	0.10	6.7	0.24
White-eared opossum	7.3	0.007	9.6	0.09
Grey four-eyed opossum	0.29	0.59	2.5	0.78
Nine-banded armadillo	0.26	0.61	3.4	0.64
Tapeti rabbit	27.9	<0.001	28.4	<0.001
Red brocket deer	8.4	0.004	13.2	0.02

Table 4: Pairwise post-hoc G-tests for activity under different moon phases for tapeti rabbit and red brocket deer.

	New		1 st quarter		Half		3 rd quarter		Full	
Tapeti	G _{adj}	p	G _{adj}	p	G _{adj}	p	G _{adj}	p	G _{adj}	p
Not visible	0.04	0.85	0.11	0.74	13.6	< 0.001	10.3	0.001	10.0	0.002
New			0.02	0.88	9.0	0.003	6.6	0.010	7.2	0.007
1 st quarter					7.2	0.007	5.2	0.022	6.0	0.014
Half							0.3	0.55	0.01	0.91
3 rd quarter									0.2	0.66
Deer										
Not visible	0.9	0.34	0.5	0.49	4.5	0.03	1.5	0.22	11.2	< 0.001
new			0.005	0.95	0.85	0.36	0.03	0.87	3.9	0.047
1 st quarter					0.73	0.39	0.05	0.83	3.1	0.08
Half							0.62	0.43	1.2	0.27
3 rd quarter									3.6	0.06

Table 5: Test statistics of binary logistic regression for interaction effects of species and moon illumination with ocelot as the reference level while taking Cloud cover into account. The logit-estimate was converted to the odds (cloud cover) or odds for 10% changes in moon-illumination (Odds10[§]).

Species:Illumination	Odds10 [§] or Odds	Z-value	P-value
White-eared opossum (<i>Didelphis albiventris</i>)	1.01 [§]	0.3	0.73
Grey four-eyed opossum (<i>Philander opossum</i>)	0.95 [§]	-1.1	0.26
Nine-banded armadillo (<i>Dasypus novemcinctus</i>)	0.91 [§]	-1.9	0.061
Tapeti rabbit (<i>Sylvilagus brasiliensis</i>)	1.05 [§]	1.2	0.23
Red brocket deer (<i>Mazama americana</i>)	1.03 [§]	0.7	0.49
Cloud cover_Yes	0.70	-2.0	0.049

§: The Odds10 value is the predicted change in the probability that a species is recorded over the probability it is not recorded when the independent variable "percentage moon illumination" increases by 10% compared to the odds for ocelots. For cloud cover, the odds give the probability of getting a record of any of the species if there is cloud cover compared to the probability if there is no cloud cover.

Table 6: Test statistics for contingency-table G-tests comparing the frequency of photographic records of various species compared to those of ocelots under either high and low levels of moon light, and under six different moon phases (moon not visible, new moon, first quarter, half moon, third quarter, full moon).

	Combined moon phases (Low vs. High) df = 1		Detailed moon phases df = 5	
	G _{adj}	p-value	G _{adj}	p-value
White-eared opossum	0.008	0.93	3.2	0.66
Grey four-eyed opossum	0.8	0.37	4.2	0.53
Nine-banded armadillo	2.4	0.12	7.7	0.18
Tapeti rabbit	2.5	0.12	6.6	0.25
Red brocket deer	0.7	0.39	7.6	0.18