

Temporal activity patterns of North China leopards and their prey in response to moonlight and habitat factors

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Abstract

The nocturnal activities of predators and prey are influenced by several factors, including physiological adaptations, habitat quality and, we suspect, corresponds to changes in brightness of moonlight according to moon phase. In this study, we used a dataset from 102 camera traps to explore which factors are related with the activity pattern of North China leopards (*Panthera pardus japonensis*) in Shanxi Tiejiaoshan Provincial Nature Reserve (TPNR), China. We found that nocturnal activities of leopards were irregular during four different lunar phases, and while not strictly lunar philic or lunar phobic, their temporal activity was highest during the brighter moon phases (especially the last quarter) and lower during the new moon phase. On the contrary, roe deer (*Capreolus pygargus*) exhibited lunar philic activity, while wild boar (*Sus scrofa*) and Tolai hare (*Lepus tolai*) were evidently lunar phobic, with high and low temporal activity during the full moon, respectively. In terms of temporal overlap, that there was positive overlap between leopards and their prey species, including roe deer (*Capreolus pygargus*) and Tolai hare (*Lepus tolai*), while leopard activity did not dip to the same low level of wild boar during the full moon phase. Generally, our results suggested that besides moonlight risk index (MRI), cloud cover and season have diverse effects on leopard and prey nocturnal activity. Finally, distinct daytime and nighttime habitats were identified, with leopards, wild boar and Tolai hare all using lower elevations at night and higher elevations during the day, while leopards and roe deer were closer to secondary roads during the day than at night.

Introduction

Worldwide, 69 % of mammals are nocturnal while 20% are exhibiting more diurnal activity patterns (Bennie et al., 2014), and this phenomena is an ancestral character stemming from the ‘nocturnal bottleneck’ in the early evolution of the clade (Hut et al., 2012). Although synapsids invaded the nocturnal niche 100 million years prior to mammals, recent studies support the essential nocturnality of ancestral mammals, by way of selection for dim-light vision (“night vision”), endothermy, and loss of UV protection (Angielczyk and Schmitz, 2014, Wu et al., 2017).

The time it takes for the moon to complete one revolution around the earth relative to the sun (29.5 days) is known as the synodic period or lunar month (Häfker and Tessmar-Raible, 2020). The familiar cycle of lunar phases is affected by alterations in the visible portion of the moon illuminated by the sun (Andreatta and Tessmar-Raible, 2020), with the intensity of lunar illumination on the Earth’s surface at night varying by three orders of magnitude over a full lunar cycle (Kyba et al., 2017). Moreover, other factors such as topography, cloud cover, latitude, and distance from the moon, each play a role in influencing the intensity of lunar illumination in any given space. Nocturnal organisms can react directly to changes in lunar illumination

as the moon cycles through the phases, and they can also anticipate variations that go along with the lunar cycle by means of an endogenous oscillator (“clock”) synchronized to the 29.5 day circalunar rhythm (Raible et al., 2017).

The primary environmental cue that changes with the lunar cycle is moonlight intensity (Andreatta and Tessmar-Raible, 2020, Häfker and Tessmar-Raible, 2020), and these cues (or ‘zeitgebers’) act on endogenous oscillators to adjust biological processes such as mating, feeding, activity, predator avoidance and many others (Andreatta and Tessmar-Raible, 2020). The idea that being afraid of the dark is an adaptation to dodge predation has a long history (Darwin, 1871), and moonlight cycles as a cue for predation risk was first studied in nocturnal desert rodents several decades ago (Lockard and Owings, 1974). Animals’ circadian activity patterns are influenced by evolution (Halle, 2000) and physiology (Heurich et al., 2014), and we find that prey species with powerful tapeta (and therefore, have superior night vision) tend to be lunar philic (light lovers) whereas species deficient a tapetum lucidum (i.e., have poor night vision) are more lunar phobic (light avoiding) or uninfluenced by lunar phase (Prugh and Golden, 2014). According to the ‘predation risk hypothesis’ (Huck et al., 2017), if predators are more successful at chasing under bright moonlight, prey species will alter activity to become “lunar phobic” or avoid brighter moon phases. On the contrary, the ‘visual acuity hypothesis’ (Huck et al., 2017, Pratas-Santiago et al., 2017) states that the brightness of a full moon provides “visually-oriented” prey species heightened chance to forage and/or detect danger, with the result that they are expected to be more active during the full moon, showing “lunar philic” activity, in other words preferring brighter moon phases.

Besides lunar illumination, the activity patterns of large carnivores, such as felids, are also influenced by anthropogenic disturbances (Gaynor et al., 2018, Van Cleave et al., 2018). For example, studies have shown that leopards (*Panthera pardus*) in Thailand (Ngoprasert et al., 2007) and Amur tigers (*Panthera tigris altaica*) and leopards (*Panthera pardus orientalis*) in China (Yang et al., 2018b, Zhao et al., 2020) shift their activity patterns under the effect of human disturbance to become more nocturnal or crepuscular and avoid human activity across spatiotemporal scales to decrease the risk of conflict with humans (Treves and Karanth, 2003, Wang et al., 2019).

Furthermore, the landscape of fear created by predator may linked to prey behavioral resource depression and their changing in temporal foraging movement (Bischof et al., 2014). Further to temporal activity patterns also altering in habitat resources selection into different seasons (Ramesh et al., 2012, Yang et al., 2018b), hence spatial separation is another strategy for the coexistence of sympatric species (Yang et al., 2018b, Zhao et al., 2020, Davis et al., 2018).

The North China leopard (*P. p. japonensis*), hereafter leopard, their distribution and ecology is very scarce or unidentified and also has been classified as Critically Endangered on the IUCN Red List (Jacobson et al., 2016). Basic information about how various ecological factors influence leopard and prey species co-occurrence under different lunar phases is still unknown in China and the current research aims to fill this gap. The aims of the current study were to examine the temporal activity patterns of leopards, prey species and human-related activities or habitat factors and the influence of lunar illumination. Specifically, we tested the following three hypotheses: 1) the effects of different moon phases on nocturnal spatio-temporal overlap intensity will be distinct among different predator-prey pairs; 2) habitat factors influence the activity response of prey to leopards during the four moon phases, and; 3) predator and prey species shift their temporal activity patterns during the full moon higher activity during the day time to counter the brightness of the moon at night time.

Materials and Methods

Study area

This study was conducted in Tieqiaoshan Provincial Nature Reserve (TPNR) in Shanxi Province, China (Figure 1). The TPNR is a federally protected area established in 2002 by the federal people’s administration, permitting local population settlement in the TPNR with strict actions of wildlife protection and the altitude ranges between 1400 m to 1700 m.a.s.l. The total protected area of the reserve is 35,351.7 ha, with a core

zone area of 13,948.6 ha and a buffer area of 7401.7 ha. There are 40 villages located in the two townships of Tie qiao Forest Bureau with approximately 30,022 inhabitants; the density is 85 inhabitants/km². The majority of people practice Buddhism and their livelihood is mainly based on agricultural crops and livestock (goat *Capra hircus*, sheep *Ovis aries* and cow *Bos indicus*) along with pet or stray dogs which are found in each village. The climate is warming temperate in summer and continental in winter. The annual rainfall is about 600 mm and the annual temperature is about 6 degC. Major threats for this reserve are tree logging at the forest edge, overgrazing, forest fire and human-carnivore conflicts (Tieliang, 1985). The area also has a high wildlife diversity containing 24 species of mammals, 6 species of reptiles, 3 species of amphibians, and 116 species of birds and sixteen wild animal species are protected there and the flora is plenty by deciduous broadleaf, coniferous, and mixed deciduous forests. The common tree species are Chinese red pine (*Pinus tabulaeformis*), Liaotung oak (*Quercus liaotungensis*), white birch (*Betula platyphylla*), and larch (*Larix principis*), and rare tree, willow (*Salix spp*), apricots (*Prunus spp*) etc and dominated shrubs such as sea buck thorn, *hippophe spp*, *Berberis spp* and *Artemisia spp* and overall the TPNR has 78 genera of wild seed plants (Hua et al., 2020).

Data collection

Camera trapping videos and photos, including pre-processing

Initially the whole area was divided into a grid system of size 4x4 km² (Figure 1) and between two and five camera-trap locations in each grid cell were selected based on the presence of carnivore sign and prey trails. Two infrared cameras (Eastern Red Hawk E1B 6210M and LTL6210MM, Manufactured by Shenzhen Weikexin Science and Technology Development Co. LTD Shenzhen, China) were set facing each other at each trap station to increase capture probabilities and capture the fur patterns on both sides of leopards, of which one was set to record short videos (10 second length) and one to record photos (3 photos per trigger event). In order to capture quality images, cameras were attached to trees 45–50 cm above the ground at a distance of 3.5–4 m from animal trails, and all vegetation or other obstacles in front of the cameras were removed (Qi et al., 2015). All photographs were automatically stamped with the time and date, moon phase and respective location ID. A total of 102 camera locations operated between March 2017 – June 2019, and among them, 78 cameras successfully functioned to collect data over three sampling stages in two different seasons (see below for details) with 131 (March–July 2017), 120 (September–December 2018), and 134 (March–June 2019) consecutive days being sampled. Each camera was visited approximately every two months to download image files and check/replace batteries. The remaining 24 cameras were stolen or damaged during the study period.

The 24-h activity patterns of all species were deduced from camera-trap photo and video records (Qi et al., 2015, Yang et al., 2018b). We analysed only photos taken at a minimum time interval of 30 minutes (Santos et al., 2019) to avoid pseudoreplication. Based on local climate characteristics, we defined two distinct periods: the winter period (snow period: Nov– Apr) and the summer period (snow-free period: May – Oct) (Table 1). The data processing was completed by specialists in Prof. Jiang Guangshun’s research teams at the Feline Research Center of National Forestry and Grassland and Administration (Northeast Forestry University) who completed species identification and data arrangement.

Influence of moonlight on temporal overlap intensity

We calculated the Relative Abundance Index (RAI) at each trap site as the number of detections per 100 camera-trap days of every species in the two seasons (Yang et al., 2019) (Table 2). Each camera trap was considered as an independent spatial point for determining animal nocturnal activity by selecting records occurring between sunset and sunrise. The clock time of sunrise and sunset varies slightly over the course of the year depending on distance from the equator and time of year. To account for these successive changes of daylight hours throughout the year (Nouvellet et al., 2012), we used the ‘sunTime’ function of the ‘overlap’ package version 0.3.2 in R to map times to radians for analysis (see (Meredith and Ridout, 2020) for details). The activity pattern of each species was fitted non-parametrically as kernel density functions with the package ‘Overlap’ using the default bandwidth parameters (Meredith and Ridout, 2014, Meredith

and Ridout, 2020), following the assumption that animals are equally likely to be ‘trapped’ throughout any period of their activity (Linkie and Ridout, 2011). Circular density curves were compared using the coefficient of overlapping (‘overlap coefficient’[?]), with values ranging from 0 (no overlap) to 1 (complete overlap), as proposed by (Ridout and Linkie, 2009). Lunar activity was categorized using Moonrise 3.5 software (Free data source <https://moonrise.informer.com>) to obtain the moon phase for each observation based on moon phase data stamped on camera trap images, location of study area and its date. Moon phase was scaled to radians so that 0 corresponds to New Moon, $\pi/2$ as First Quarter, π as Full Moon, and $3\pi/2$ as Last Quarter, as described by (Pratas-Santiago et al., 2017, Prugh and Golden, 2014) and further details to see the conceptual model in (e.g. Figure 2).

We estimated the overlap coefficient ([?]) for nocturnal activity between leopard-prey species pairs and night vs daytime for each species sets at four moon phases. In addition, to test the predictions of the predation risk and visual acuity hypotheses, we computed the number of independent records in each quarter of the moon phase for each species at the night by dividing the moon phase cycle from 0 to 2π using four identical quadrants centered on every moon phase (for illustration: First Quarter from $1/4 \pi$ to $3/4\pi$). The percentage of records in each lunar phase for each species was calculated, with the assumption that lack of any pattern would be shown by 25% of activity occurring during each of the four lunar phases. A deviation from 25% activity during the full moon phase was interpreted as follows: (1) species with less than or equal to 20% of records during full moon were classified as lunar phobic; (2) those with more than or equal to 30% of records during full moon were considered lunar philic (e.g; Figure 2), and; (3) species that did not qualify as lunar phobic or lunar philic exhibited no pattern or irregular (Prugh and Golden, 2014).

Model selection

To investigate potential factors influencing activity patterns associated with the lunar cycle, we developed two models: a mixed effects model to explore factors that might influence activity during the lunar month, and a logistic mixed effects model to examine whether the lunar cycle influences habitat preference or avoidance by leopard and prey during the lunar cycle.

For the first model that explored lunar cycle activity, we examined which factors were associated with an increase or decrease in activity closer to the full moon phase (e.g., lunar phobic versus lunar philic). To investigate this hypothesis, we used a Generalized Linear Mixed Effects Model (GLMM) using only nocturnal data (activity predominantly between 1 h after the sunset and 1 h before the sunrise), with temporal activity events occurring during the full moon’ as the response variable to check lunar phase influences on animals’ activities (Norris et al., 2010). We also categorized seasons as either summer or winter as we suspected that predators and prey may shift their activity in the different seasons (Yang et al. 2019). In addition, there is an ecologically significant factor which positively influences an animal’s night and day activity called ‘Moonlight Risk Index’ (MRI) (Gigliotti and Diefenbach, 2018, Searle et al., 2021). We calculated this index of nocturnal luminosity by multiplying together the amount of the moon illuminated, the proportion of time between sunset and sunrise that the moon was above the horizon and their information taken from moonrise software for each moon phase data stamped on camera trap images and the inverse proportion of the sky covered in clouds between 0 (overcast) and 1 (clear) as an explanatory variable; clouds cover information data for each capture event was taken from a free online data source in the Heshun county in tieqiaoshan provincial nature reserve (TPNR) in Shanxi province China (<https://m.tianqi.com/lishi/heshun/201601.html>) see for more details in Table 1.

First, for all global models used in model 1 or 2, we checked for multi-collinearity using the variance inflation factor (VIF), with covariates eliminated from our model at $VIF > 3$, and using Pearson correlation test, a variable was excluded when correlation $|r| > 0.7$ with other covariates (Yang et al., 2019). Second, we used super-ranked correlation test to check leopard and prey temporal co-occurrence or avoidance. Third, the GLMMs were fitted using the R package lme4 and MuMIn (Yang et al., 2019). We used stepAIC to select the most parsimonious model at $\Delta AICc \leq 2$ (Zaman et al., 2019, Zaman et al., 2020b).

For the second model which explored circadian activity events during the four different lunar phases for

leopard and prey linked to habitat factors, we considered four moon phase activity occurrence events of the leopards and their prey species during the night and daytime into the following three categories: (1) nocturnal, as defined above; (2) diurnal, activity predominantly between 1 h after sunrise and 1 h before sunset, and; crepuscular, 1 h before sunrise to 1 h after sunrise and 1 h before sunset to 1 h after sunset (Zhao et al., 2020). For example, if a species was less active during the full moon or other lunar phase at the nighttime (lunar phobic), we examined whether that species shifted to being more active during daylight (full moon day or other moon phases) hours to compensate for the time ‘lost’ by being less active at night during the full moon phase. For each activity during night vs day events, ROC was used to define the accuracy of a classification model at the user-defined threshold value of 0.5 (Zaman et al., 2020b), and area under the curve (AUC) score of [?] 0.7 (Jiang et al., 2015) and also ran a Shapiro–Wilk’s test and graphic examination of histograms were made to confirm that the data were normally distributed. We used a Logistic Generalized Linear Mixed Effects Model (GLMM) with the designation of day or night activity capturing events during four moon phases only set as the binary response variable (0 all moon phases of day, 1 all moon phases of night, i.e., day vs. night). Habitat factors were included as explanatory variables and the camera trap identity was considered a random effect in our model to differentiate between the effects of non-dependent variables, removing when not a random effect (Yang et al., 2019, Zaman et al., 2019, Zaman et al., 2020b) and packages rocr, lmtest, car and package lme 4 and MuMIn were used for Logistic Generalized Linear Mixed Effects Model (GLMM) and all the analysis were computed in R statistical software V.3.5.1 package (www.r-project.org, R Core Development Team 2018).

Results

In this study’s analyses, we used 102 camera traps for 3,268 trap-nights. We captured 154 events of leopards, 414 of wild boar (*Sus scrofa*), 942 of roe deer (*Capreolus pygargus*) and 1,751 of Tolai hare (*Lepus tolai*). The RAI for North China leopards in the summer (1.13) was lower than in winter (3.58), a phenomenon observed in all four species. Moreover, among the three main prey species, the RAI was highest for Tolai hare in both seasons (Table 2).

Influence of moon phase on activity and predator-prey interaction

Leopards exhibited irregular activity pattern and most camera trigger events occurred at last quarter (n = 27; 17.52 %) and full moon (n=33; 21.42%), followed by new moon (n = 20; 13.63%) and first quarter (n = 18; 11.67%; Figure 3a) at the nighttime and daytime maximum camera trigger occasions occurred at full moon (n = 34; 22.07 %), and similar results occurred during the daytime for others lunar phases; Figure 3a). For prey species, wild boar indicated lunar phobic behavior during the night events; activity declined during full moon (n=32; 10.06%), while peak activity occurred during the last quarter (n=50; 15.72 %), followed by first quarter (n=34; 10.69%) and new moon phase (n=34; 10.69 %; Figure 3b) and similar results were occurred during the daytime, activity dropped for the period of full moon (n=22; 6.91%), and similar results were consistent for other lunar phase, Figure 3b), Furthermore, roe deer were evidently lunar philic, based on percent nocturnal activity during full moon phase (n=184; 30.42%); first quarter moon (n=64; 10.72%); and last quarter (n=40; 6.61%; Figure .3c) and daytime activity was peak at full moon phase (n=190; 31.41%); was also relatively high during the first quarter moon (n=40; 6.61%) and last quarter (n=30; 4.95%; Figure .3c) and activity during the new moon was lowest during both daytime new moon (n=20; 3.30%) and nighttime new moon (n=37; 6.11%). Similar with wild boar, Tolai hare (Figure 3d) had a dip in nighttime activity during the full moon (n=103; 9.03%); into the new moon (n=115; 10.38%) and increased activity during into the first quarter (n=193; 13.08%) ; in to the last quarter (n=144; 13.00%; Figure 3d) and daytime Tolai hare dip peak in activity during the full moon and showed lunar phobic (n=122; 11.10%); and into the first quarter (n=127; 11.47 %) and increased activity during of new moon (n=187; 16.89%) in to the last quarter (n=210; 18.97%; Figure 3d).

The nocturnal temporal overlap between leopards and wild boar (Figure 3e) was low and a significant negative relationship was observed. In contrast, the temporal overlap between leopard and both roe deer (Figure 3f) and Tolai hare (Figure 3g) was relatively high and showed significant positive relationships.

Based on analyses of nocturnal activity capture occasions during the full moon, leopard activity was significantly positively linked to MRI as well as the interaction between clear cover and more active during a summer full moon (Table 3). For roe deer, clear nights did not influence temporal activity but more active during a summer full moon than a winter full moon had a negative effect on activity during the full moon. Wild boar activity during the full moon was not influenced by clear cover and MRI as independent factors, but their interaction had a significant negative effect. Finally, Tolai hare activity during the full moon had a significant negative relationship with clear nights and a significant positive relationship with season (summer), i.e., more active during a summer full moon than a winter full moon.

Influence of habitat factors on species detections at night vs. day

Using data across all moon phases combined (i.e., irrespective of moon phase), we analyzed habitat factors influencing the use of camera sites at night (1) rather than day (0), i.e., the response was a binary variable. We used nine covariates and ran seven GLMM candidate models to predict how these habitat factors altered species occurrence during night vs. day.

We found that leopards used lower elevations at night and higher elevations during the day, and activity closer to secondary roads and deciduous forest was more likely to be during the daytime while further distances from these landscape features were more likely detected at night (Table 4a, 4b). Roe deer also exhibited this relationship between distance to secondary roads and night vs. day activity, although the relationship was weaker for roe deer. As observed in the leopard data, wild boar used lower elevations during the nighttime and medium or high elevations during the daytime, and the relationship was stronger in the case of wild boar. Also, wild boar tended to be nearer to mixed forest during the daytime and further away at night. Finally, Tolai hare had a similar relationship with elevation as did leopard (i.e., weak negative association with elevation, lower elevations preferred at night), and at night tended to be far from mixed forest and grasslands while near to deciduous forest, woody savannas and villages.

Discussion

Influence of moon phase on temporal activity & predator-prey overlap

It is recognized that the response of nocturnal mammals to moonlight differs among taxa and may vary according to several determining factors, such as phylogeny, trophic level, sensory systems and human activity (Santos et al., 2019). This camera-trap based assessment has revealed both lunar phobic and lunar philic behaviors of rare and/or shy animals and contributes to building our understanding of the factors shaping activity patterns of multiple sympatric mammals under different lunar phases.

Our results indicated that leopards show no activity pattern throughout the four lunar phases, exhibiting neither a clear lunar phobic nor lunar philic activity pattern, as observed in other felid species too, such as puma (*Puma concolor*) and jaguar (*Panthera onca*) in Neotropical forests (Harmsen et al., 2011, Prugh and Golden, 2014). Due to the extraordinary reflectance of the feline tapetum cellulosum, assessed to reflect 130 times extra light than the human eye (Huck et al., 2017), we suspect that the leopards' lack of tendency to be more or less active during the full moon can be at least partly explained by visual acuity. We also suppose that the leopards' irregular temporal patterns may be influenced by mesopredators in the landscape, such as red fox (*Vulpes vulpes*) and leopard cat (*Prionailurus bengalensis*), as sympatric carnivores can drive temporal activity fluctuations (Packer et al., 2011, Hua et al., 2020). In terms of human activities, human-leopard conflict has been found to occur often in the summer in TPNR (Hua et al., 2020), and perhaps this can explain irregular activity patterns and the higher relative species abundance in winter. Human activity on foot and in vehicles mostly occurred in the day time in TPNR, so a landscape of fear induced by human activities may adjust leopard behavior, for example our earlier research work conducted by Hua et al., (2020) In TPNR concluded that grazing intensity by free roaming cattle was lower in the winter than summer and may also influence wild animal behavior.

For the herbivore prey species studied, our results are similar with previous research showing that mammals often adapt their nocturnal activity to the level of lunar illumination (e.g (Huck et al., 2017, Pratas-Santiago

et al., 2017). Here, wild boar and Tolai hare were evidently lunar phobic, while roe deer indicated lunar philic activity. Especially in the case of the wild boar and Tolai hare, the results align with the visual acuity hypothesis, as lagomorphs and suids have poor eye sight and avoid the brightness of moon to reduce predation risk (Pratas-Santiago et al., 2017, Preisser et al., 2005, Tuan, 1979, Zaman et al., 2020a). Lunar phobic behavior has also been observed in Neotropical prey species, such as armadillo (*Dasypus novemcinctus*) and paca (*Cuniculus paca*) (Harmsen et al., 2011, Prugh and Golden, 2014), while hare have also been observed to dodge the risk of predation by medium-sized felids by adjusting temporal activity (Griffin et al., 2005). Deer species however, including white-tailed deer (*Odocoileus virginianus*) and red brocket deer (*Masama temama*), have shown both lunar phobic and lunar philic behaviours, and while they have tapetum, prey can shift their night activity because the choroidal tapetum fibrosum (CTC) of carnivores has better light reflectance than the choroidal tapetum fibrosum (CTF) of ungulate herbivores (Botts et al., 2020, Brown et al., 1999).

Although felid activity patterns rarely relate with those of their potential prey (Ramesh et al., 2012) (Krittika and Yadav, 2020), in this study, leopard nocturnal activity had high overlap with that of roe deer and Tolai hare across the full lunar cycle. These results support the prediction that predators should reduce activity at times when major prey species are less active, in accordance with both the visual acuity and optimal foraging model (Pianka, 1973, MacArthur and Pianka, 1966). Conversely, prey can adjust their activity pattern or spatial distribution to avoid predators (i.e., to reduce predation risk), such as bighorn sheep (*Ovis canadensis*) spatially eluding pumas (*Puma concolor*) (Laundré et al., 2001), and roe deer and wild boar having minimal temporal overlap with tigers (Yang et al., 2019). Hence, while lunar phobia (wild boar and Tolai hare) and lunar philia (roe deer) were observed in the prey species in this study, the activity pattern of leopards observed here, we suspect, is more closely linked with the temporal behaviors of prey species than directly with moon phase *per se*.

Explicitly during the full moon phase, nocturnal activity of leopards and prey were diversely affected by clear summer nights and moon risk index (MRI). Leopards activity during the full moon showed preference for high lunar luminosity (high MRI) and showed higher activity during clear summer or winter nights. We suppose that clear summer or winter nights or active prey may either force leopards to restrict roaming behavior (and reduce hunting success) or may increase activity as they move towards a safe or warmer refuge (Türk and Arnold, 1988). For prey species, nocturnal activity events during the full moon were more for roe deer in summer or winter (seasonal effect), during clear bright nights for wild boar (clear cover and MRI interaction effect), and during clear nights (especially summer) for Tolai hare (clear cover and MRI interaction effects). Others have also revealed that cloud cover, which alters moonlight and MRI (Packer et al., 2011, Pratas-Santiago et al., 2017) and season influence nocturnality and temporal behaviours of carnivores and ungulates (Shamoon et al., 2018), as well as foraging behaviour of wild boar and roe deer (Frauendorf et al., 2016, Yang et al., 2018a). It is reasonable to assume that there is variation in nocturnal activity between seasons.

Nighttime and daytime habitat use

Based on the GLMM model results, we revealed that leopard nocturnal and diurnal activity during the four moon phases changed in response to habitat variables. Specifically, during the daytime, leopards preferred to be closer to deciduous forest and secondary roads, and to use areas of higher elevation (and *vice versa* for nighttime). We assume that these significant variables are associated with movement and hunting grounds for leopards at both day and night on a daily basis, offering higher concealment in deciduous forest while undistributed roads provide substrate for territory marking (Macdonald et al., 2010) and also facilitate leopard travel (Carroll and Miquelle, 2006). Finally, in cat species, prey movement is the primary factor influencing habitat selection (Hayward et al., 2007). While we expect that leopards move throughout the fragmented landscape by using high elevation corridors, these highest areas also may provide suitable habitat and maximum hunting opportunity for ungulates or medium sized prey (PU et al., 2019); the relationships with elevation were consistent across leopards and two of three prey species studied, while the leopards and roe deer had similar use of areas near to secondary roads during the daytime.

In addition to the results here derived from camera trap data, field observations (unpublished data) and literature sources validate some of our conclusions concerning prey activity. For example, we encountered a great number of footprints of roe deer on (snow-covered) secondary roads during winter field trips, as well as fecal pellets, footprints, and bedding sites of wild boar in mixed forest habitat. In the case of roe deer and secondary roads, we also observed that dogs used these roads and found that they may attack ungulates at nighttime, forcing these prey animals to temporally shift their use of the landscape to minimize risk (Young et al., 2018). With regards to mixed forests, (Acevedo et al., 2006) concluded that wild boar select broad-leaved mixed forest as habitat, as these environments, dominated by Chinese red pine (*Pinus tabulaeformis*) and Liaotung oak (*Quercus liaotungensis*) trees, provide foraging opportunities. While boar have been found to avoid high elevations during nights (Roberts and Bernhard, 1977) and we may have suspected that this may be to avoid the predator vantage points at high elevation, leopard and boar showed similar trends in daytime/nighttime use, though we here offer a new insight into how elevation use may vary within a daily 24-hour cycle. Finally, Tolai hare showed a preference to be near open grassland and far from human settlement during the daytime and similar results have also been found for other lagomorph species in the Karakorum range, Pakistan (Zaman et al., 2020a).

Implications for conservation

As daytime “super predators”, humans control 75% of Earth’s land surface and are driving in rise in nocturnal activity in medium- and large-bodied mammals (Clinchy et al., 2016). A recent meta-analysis of studies of 62 mammalian species on six continents (Gaynor et al., 2018), exposed a robust influence of human existence on the temporal activity of wildlife, with an average 36% increase in nocturnal activity in reaction to human stimuli. Specifically, nocturnal activity increased in response to an extensive range of human effects, lethal and nonlethal, including hunting, farming, and hiking; this proposes that wild animals recognize humans as dangers whether or not they pose a lethal risk (Gaynor et al., 2018). Free-roaming dogs also cause both lethal and non-lethal effects (Zaman et al., 2019). Even agricultural farming activities may cause mammals to shift to greater nocturnal behavior and reduced diurnal activity (Shamoon et al., 2018), and depredation on domestic livestock, which commonly occur at night, can bring about negative perceptions and conservation issues (Mishra, 1997). While the present study has achieved its goals to better understand lunar effects on animal behavior (Beale and Monaghan, 2004).

Using a variety of computational tools to analyze our vigorous dataset, this study has achieved two principal results which progress our understanding of the nocturnal and diurnal behavior of wild mammals in relation to moon phase, including predator-prey interactions and effects of habitat factors. In particular, the study has revealed that wild animal patterns of activity across the study session, display temporal flexibility in response to lunar illumination (as altered by moon phase, moonrise/set, cloud cover, night vision acuity (due to the tapetum lucidum, but not measured here), predation risk (as affected by the landscape factors plus the temporal overlap of a single predator), food availability, and potential competitive interference. Finally, recognizing that the North China leopard is a critically endangered species, to aid the conservation and management of this predator and its prey, we highly recommend further, deeper research on these focal species with a more integrated approach to understanding spatio-temporal patterns in response to natural and anthropogenic factors, aided by a live animal capture, collaring and tracking protocol in combination with scientific evaluations of the top-down and bottom-up effects of human activities and land use, including roads, villages and livestock farming . The results obtained from doing this research would likely help to scientifically – and optimally – manage the landscape for human-wildlife coexistence, restore wild animal communities and natural habitat, and increase landscape permeability and connectivity, enabling the flow of genetic material and long-term population sustainability.

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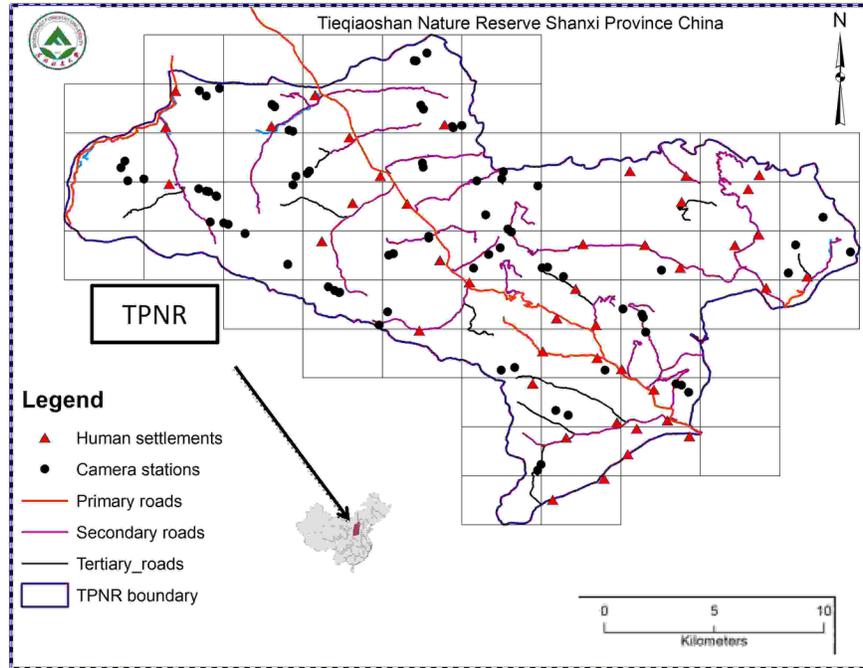


Figure 1 Map of study area showing, type of roads, human settlements and camera points, hence TPNR represented the Tiejiaoshan Provincial Nature Reserve Shanxi China.

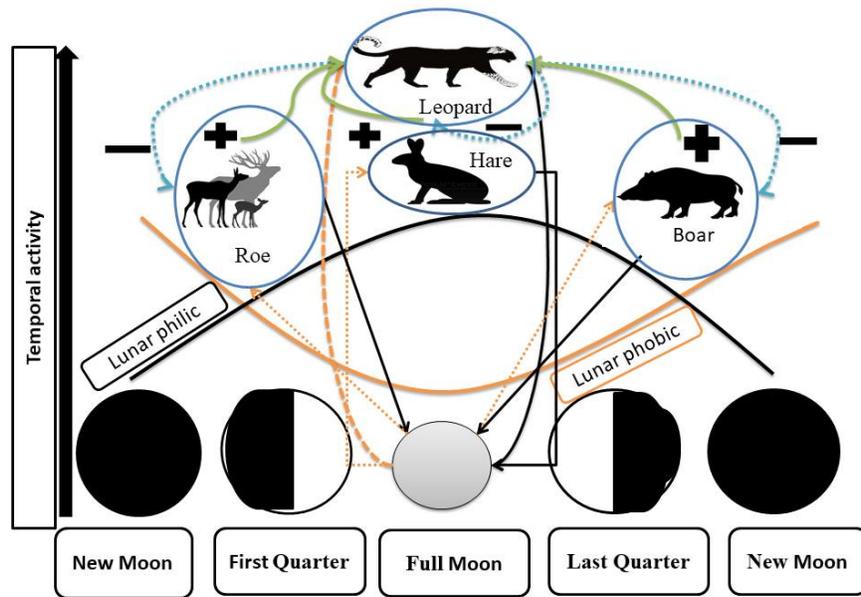


Figure 2 . A conceptual diagram to explain that the predation risk hypothesis predicts that prey species will shrink activity during bright lunar illumination, denoted by orange color (lunar phobic), while the visual acuity hypothesis reveals that prey species which have comparably good vision will increase activity during bright lunar illumination, represented by black color (lunar philic). Those species positively linked

are denoted by green solid lines, and negative interactions are represented by blue dotted lines and blue circular are exhibited temporal activity patterns of leopard and prey for different four moon phase.

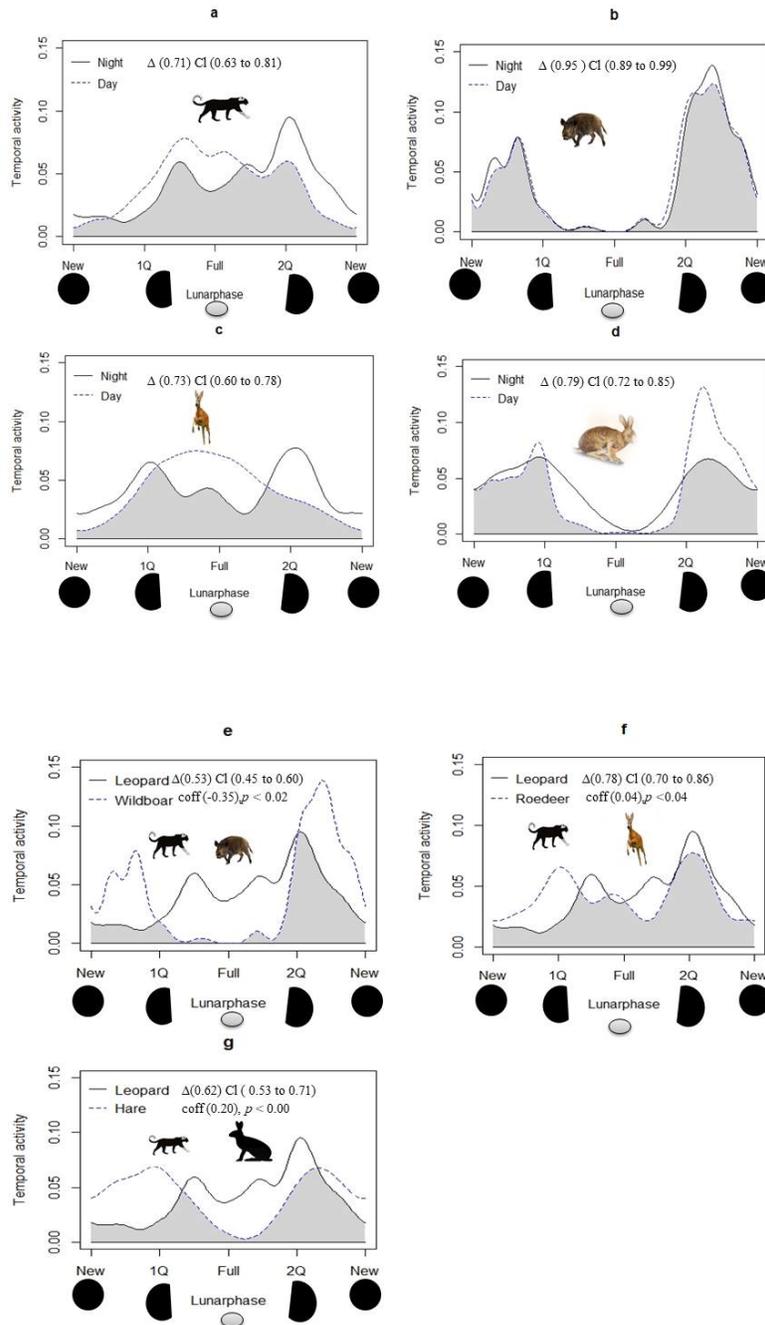


Figure 3. Temporal activity patterns of leopard (a, e, f, g), wild boar (b, e), roe deer (c, f), and Tolai hare (d, g), including diurnal and nocturnal activity intensity (a – d) and overlap of predator-prey nocturnal activity (e – f). Wild boar and Tolai hare distinctly reduce nocturnal and diurnal activity during the full moon, while leopard and roe deer increase diurnal activity during the full moon. High nocturnal activity

overlap is observed between leopard and roe deer during the full lunar cycle and low overlap is observed between leopard and wild boar. Lunar phases are new moon (new), first quarter (1Q), full moon (full), and last quarter (2Q). In each plot e – g, temporal activity density is denoted by the solid line (predator) and broken line (prey); gray shading represents the area of overlap using the coefficient of overlapping (‘overlap coefficient’[?]) and cl (Confidence intervals), and Spearman rank correlation (SRC) between the leopard and prey species from day versus night (we investigated whether diurnal activity changes due to moon phase are the same as nocturnal changes due to moon phase) and nocturnal overlap between predator-prey Coff (coefficient),P represented significant level.

Table 2 . Seasonal number of photographic capture events and relative abundance index (RAI per 100 camera trap days) for the North China leopard and prey species in Tieqiaoshan Provincial Nature Reserve, Shanxi Province, China from March 2017 to May 2019.

Common name	Scientific name	Winter RAI	Winter RAI	Summer RAI
North China leopard	<i>Panthera pardus japonensis</i>	117 (3.58)	117 (3.58)	37 (1.13)
Wild boar	<i>Sus scrofa</i>	288 (6.97)	288 (6.97)	126 (3.85)
Siberian roe deer	<i>Capreolus pygargus</i>	615 (18.81)	615 (18.81)	327 (10.00)
Tolai hare	<i>Lepus tolai</i>	1073 (32.83)	1073 (32.83)	678 (20.74)
Seasonal total	-	2093 (64.04)	2093 (64.04)	1168 (35.74)
Study total	-	3268		

Table 3 Results of the generalized linear mixed effects model of nocturnal activity capture occasions during the full moon from March 2017 to May 2019, including relation terms. a) Leopard, b) roe deer, c) wild boar, d) Tolai hare.

Variables	B	S.E	z value	P
a) (Intercept)	0.69	0.06	11.29	0.00
Clouds (clear, zero cloud)	0.06	0.10	0.60	0.54
Seasons (summer)	0.01	0.06	0.26	0.79
MRI	7.43	3.84	1.93	0.05
Clouds×seasons	-0.28	0.11	-2.55	0.01
Clouds ×MRI	-12.72	8.39	-1.51	0.13
b) (Intercept)	0.55	0.11	4.89	0.00
Clouds (clear, zero cloud)	0.02	0.20	0.01	0.99
Seasons (summer)	-0.22	0.09	-2.34	0.02
MRI	6.91	6.35	1.08	0.28
Clouds×seasons	0.04	0.16	0.25	0.80
Clouds ×MRI	2.17	14.56	0.15	0.88
c) (Intercept)	0.58	0.13	4.39	0.00
Clouds (clear, zero cloud)	0.30	0.18	1.60	0.11
Seasons (summer)	0.17	0.11	1.43	0.15
MRI	0.18	1.79	0.10	0.91
Clouds × MRI	-5.95	2.80	-2.12	0.03
d) (Intercept)	0.55	0.04	11.34	0.00
Clouds (clear, zero cloud)	-0.27	0.07	-3.78	0.02
Seasons (summer)	0.17	0.07	2.39	0.01

Variables	B	S.E	z value	P
MRI	0.20	0.50	0.41	0.67
Clouds×seasons	0.22	0.11	1.94	0.05

Table 4a Summary of generalized linear mixed-effects candidate models ([?]AIC < 2) examination the influence of both day vs. night from four moon phase activity events linked to habitat factors of leopard and prey species. AIC_C = Akaike’s information criterion adjusted for small sample sizes; K = degrees of freedom; Wi = Akaike weight.

Model (explanatory variables)

- a) Leopard~ Elevation+ distance to deciduous forest+ distance to secondary road+distance to Tertiary road
Leopard~ Elevation+ distance to deciduous forest +distance to woody savannas+distance to secondary road+distance to tertiary road
- b)Roe~ distance to deciduous forest+distance to secondary road+ distance to tertiary road
- c)Boar~ Elevation+ distance to deciduous forest+ distance to mixed forest
Boar~ Elevation+ distance to deciduous forest+ distance to mixed forest+ distance to secondary road
- d)Hare~ Elevation+ distance to deciduous forest + distance to mixed forest+ distance to woody savannas+ distance to grassland
Hare~ Elevation+ distance to deciduous forest +distance to mixed forest+distance to woody savannas+ distance to grassland

Table.4b Parameter estimates of most parsimonious best fitting models in Table 3a for leopard (a), roe deer (b), wild boar (c), and Tolai hare (d), including respective standard error (SE) and 95 % confidence intervals. Asterisk (*) indicates model parameters with a significant effect on four moon phase activity events day vs. night linked to habitat factors.

Parameter	Estimate	SE	95% CI
a) Intercept	7.38	2.24	1.51 to 2.18
Elevation*	-0.46	1.53	-0.03 to - 0.35
Distance to deciduous forest*	0.28	0.50	0.02 to 3.35
Distance to secondary road*	2.10	1.05	1.69 to 2.10
Distance to tertiary road	-0.02	0.04	-0.95 to 0.46
b) Intercept	1.10	2.41	0.16 to 0.31
Distance to deciduous forest	-0.21	0.60	-7.99 to 1.74
Distance to secondary road*	0.01	0.03	0.48 to 0.78
Distance to tertiary road	-2.21	2.95	-7.45 to 0.24
c)Intercept	3.46	3.81	2.78 to 4.29
Elevation*	-2.35	2.56	-2.90 to -1.89
Distance to deciduous forest	-0.79	2.80	-0.56 to 1.95
Distance to mixed forest*	0.73	0.90	0.24 to 0.29
d)Intercept	14.16	2.05	10.26 to 18.32
Elevation*	-0.09	0.02	-0.07 to -0.01
Distance to deciduous forest*	-0.12	1.18	-0.92 to -0.70
Distance to mixed forest*	1.62	2.25	0.42 to 1.73
Distance to woody savannas*	-2.28	3.22	-0.83 to -0.59
Distance to grassland*	0.17	2.64	0.03 to 0.55
Distance to villages*	-1.25	1.54	-1.24 to -0 .40
Distance to secondary road	-5.01	1.14	-0.03 to 4.70

Table 1 Habitat variables used for the generalized linear mixed models (GLMMs) to model the drivers of

leopard and prey species daily activity

Variable	Description	Data type	Unit/source
Habitat factors	Records were taken out from the National Geomatics Center of China (http://www.ngcc.cn/ngcc/)		
Deciduous forest	Distance to the edge of the nearest deciduous broadleaf forest (oak)	Continuous	(m)
Mixed forest	Distance to the edge of nearest mixed forest	Continuous	(m)
Woody savannas	distance to the edge of nearest woody savanna (pine tree)	Continuous	(m)
Grassland	distance to the edge of nearest grassland	Continuous	(m)
Elevation	Elevation at each camera station as described by Qi et al., (2015).	Continuous	(m) Field data
Season	Summer or winter period of capture event, determined by time stamp on camera trap image/video, summer 1 and winter 0	Binary	Camera trap
Activity times	24 hour diel activities of animals in each season calculated using independents photos as mentioned by Zhao et al., (2020)	Continuous	Moonrise
Clouds	Clear and overcast weather during capture event, 0 (overcast) and 1 (clear) from website in link (https://m.tianqi.com/lishi/heshun/201601.html)	Binary	Camera trap
Moonlight Risk Index (MRI)	We calculated MRI by multiplying the percentage of the moon illuminated, the proportion of time between sunset and sunrise that the moon was above the horizon, and the proportion of the sky covered in clouds between 0 (overcast) and 1 (clear)	Continuous	Camera trap

Variable	Description	Data type	Unit/source
Lunar phase	Moon phase was scaled to radians so that 0 relates to New Moon, $\pi/2$ as First Quarter, π as Full Moon, and $3\pi/2$ as Last Quarter for each species	Continuous	Moonrise
Anthropogenic Covariates			
Villages	Distance to the edge of nearest human settlement	Continuous	(m)
Roads	Distance to the nearest road, including secondary road (small road) and tertiary road (dirt road or logging road) and excluded primary road	Continuous	(m)