Human influence on burrow activity of the Chinese pangolin in Nepal

Ambika Pd. Khatiwada[A B C D L], Wendy Wright[E], Kyran Kunkel[F], Monsoon P. Khatiwada[A D], Carly Waterman[C G], Santosh Bhattarai[H], Hem S. Baral[I], Chiranjibi Pd. Pokheral[B] & Fredrik Dalerum[A J K]

[A] Biodiversity Research Institute (University of Oviedo, Principado of Asturias, Spanish National Research Council), Mieres Campus, University of Oviedo, 33600 Mieres, Asturias, Spain
[B] National Trust for Nature Conservation, Khumaltar, Lalitpur, Nepal
[C] IUCN SSC Pangolin Specialist Group, Zoological Society of London, Regent's Park, NW1 4RY, United Kingdom
[D] Society for Conservation Biology – Nepal Chapter, Bagdol, Lalitpur, Nepal
[E] School of Science, Psychology and Sport, Federation University Australia, Gippsland Campus, Victoria, Australia
[F] Conservation Science Collaborative, Bozeman, USA
[G] Conservation and policy, Zoological Society of London, Regent's Park, London, England NW1 4RY
[H] Nepal Conservation and Research Center, Ratnanagar-08, Chitwan 44204, Nepal
[I] Zoological Society of London, Nepal office, Bishal Nagar Marg, Kathmandu
[J] Department of Zoology, Stockholm University, Stockholm Sweden
[K] Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
[L] Corresponding author. Email: ambika.pd.khatiwada@gmail.com

Abstract

Context: People and wildlife are coming into greater contact worldwide due to the increasing human footprint. While some species tolerate certain levels of human activities, others are vulnerable to human disturbance, potentially altering their spatial or temporal patterns of activity in response to disturbance by humans.

Aims: We evaluated the influence of human activity on burrow activity of the Chinese pangolin, a Critically Endangered species that is heavily persecuted for subsistence and illegal trade.

Methods: We deployed remotely triggered camera traps at pangolin burrows located at four sites with contrasting levels of human density and infrastructure in Nepal, and estimated burrow activity patterns of pangolins using a kernel density estimator based on the time stamp of camera trap observations.

Key results: Our findings did not suggest that anthropogenic disturbance affected pangolin burrow activity, but we acknowledge that these findings were based on a limited number of observations. Peak pangolin burrow activity was observed after midnight in three of the study sites, including those with highest and lowest levels of human activity. The fourth area, which had intermediate levels of human activity, had an earlier peak in burrow activity possibly caused by prey deficiency due to intense agriculture.

Conclusions: We suggest that pangolins may tolerate human activity because of their strictly nocturnal temporal niche, but that this tolerance has made them vulnerable to poaching since it allows them to co-exist spatially with humans.

Implications: Nocturnal species may be particularly prone to non-conflict related persecution, since they may be easily accessible targets for illegal hunting activities.

Additional key words: *Manis pentadactyla*, temporal, persecution, Nepal, Asia, mammal, conservation

Introduction

The expansion of human activities has caused profound disturbances to wildlife, disrupting both spatial and temporal activity patterns across a range of scales (Gaynor *et al.* 2018; Smith *et al.* 2018; Nickel *et al.* 2020). Diel activity patterns, those that occur within a 24 hour-period (Hertel *et al.* 2017), can vary both between and within species (Ikeda *et al.* 2016; Tan *et al.* 2018). While most aspects of an animal's diel activity are regulated by circadian clocks (Takahashi *et al.* 2001), these can be affected by food availability, predation risk, competitive interactions or other disturbances (Ross *et al.* 2013; Bennie *et al.* 2014; Díaz-Ruiz *et al.* 2016). For instance, many wildlife species exhibit strong fear responses to human activities (Clinchy *et al.* 2016; Smith *et al.* 2017; Suraci *et al.* 2019), which result in increased nocturnal activity among wildlife in human-dominated areas (Gaynor *et al.* 2018; Nickel *et al.* 2020). Such human-induced shifts in diel activity may have profound consequences for resource acquisition, survival and reproductive success, and may ultimately affect the survival of animal populations (Frid and Dill 2002; Diaz-Ruiz *et al.* 2016).

Shifts in spatial and temporal distribution of animal activity can be caused by indirect disturbance to wildlife populations as humans move about predominantly during daylight hours. However, direct persecution has also been a major cause of population decline for many species. For instance, some large-bodied herbivores and many large carnivores cause intense conflicts with humans, which may drive retaliatory or pre-emptive killing (Acharya *et al.* 2016). Other species are persecuted for subsistence hunting or for commercial purposes (Bhattarai *et al.* 2016). Of particular concern is illegal persecution, i.e., poaching, which has reached critical levels for many species (Baker *et al.* 2013; Paudel *et al.* 2020). Poaching is often carried out for commercial gain, where animal parts are sold for use as medicine, luxury foods and curios (Challender 2011; Biggs *et al.* 2013; Underwood *et al.* 2013). The often high economic gain from such pursuits has resulted in overexploitation of a growing list of species that are threatened with extinction (Wyatt 2011; Eaton *et al.* 2015).

Pangolins, or scaly anteaters, are among the species most threatened by poaching (Challender *et al.* 2014; Heinrich *et al.* 2019). Heavy persecution, both for subsistence and illegal trade, has caused pangolin populations to decline rapidly in many countries and is the primary limiting factor for these species (Heinrich *et al.* 2019; Challender *et al.* 2020). Pangolins are mammals belonging to the order Pholidota, which only has one extant family, the Manidae. All eight extant species are threatened with extinction: three are listed as Critically Endangered by the International Union for Conservation of Nature (IUCN), four listed as Endangered and one listed as Vulnerable (Challender *et al.* 2020). The

extent to which indirect effects of disturbance contribute to declines of these species is currently unknown.

The Chinese pangolin (*Manis pentadactyla*) is one of the three Critically Endangered pangolin species endemic to Asia (Challender *et al.* 2020). Its persistence is primarily threatened by persecution for the use of whole animals or body parts either in local communities or in international trade (Challender *et al.* 2019). The Chinese pangolin makes extensive use of burrows for shelter and reproduction (Lin 2011). Because Chinese pangolins tend to shelter in burrows when not active, burrow exit and entrance times provide a good indication of the overall diel activity in this species. Residential burrows, i.e., burrows used for protection (Lin 2011), are excavated in the soil and usually consist of a tunnel which ends in a chamber large enough to host 2-3 adult individuals (Wu *et al.* 2020). The burrows may be used through all seasons. However, animals may include up to 80 residential burrows in their home range, with consistent use of the same burrow ranging from one day to two weeks (Lin 2011; Wu *et al.* 2004). Different individuals appear to use the same burrows, but rarely at the same time (Wu *et al.* 2020).

In this study we evaluated whether burrow activity of the Chinese pangolin was affected by human activity in Nepal. Chinese pangolins in captivity are predominantly nocturnal (Heath and Vanderlip 1988), but there is limited information on diel activity in wild Chinese pangolins. Using camera trapping data from four sites with contrasting levels of human density and infrastructure we addressed two principal questions: (i) what is the burrow activity of wild Chinese pangolins at these sites? and (ii) does pangolin burrow activity at these sites vary predictably with the levels of human activity and infrastructure? While we expected that pangolins would be predominantly nocturnal, based on observations of this species in captivity (summarized by Wu *et al.* 2020), we hypothesized that pangolins in locations with high levels of human activity would emerge from burrows later and return to their burrows earlier so as to avoid potential encounters with humans.

Materials and Methods

Study area and survey sites
We conducted camera trapping surveys of pangolins at four sites in central and eastern Nepal (Fig. 1a), two located in the Tarai and Siwalik regions (Makwanpur, 27^{0}24'59.99" N / 85^{0}01'60.00" E and Chitwan, 27^{0}34'59.99 N / 84^{0}30'59.99" E) and two in the middle hills region (Gorkha, 28^{0}28'35.02" N / 84^{0}41'23.10" E and Taplejung, 27^{0}20'59.99" N / 87^{0}39'59.99" E) (Fig. 1a). Although both Chinese and Indian pangolins (*Manis crassicaudata*) occur in Nepal (Khatiwada *et al.* 2020), only the Chinese pangolin is present at the four study sites. The sites in

Makwanpur, Chitwan and Gorkha all have tropical climates and are dominated by mixed Sal tree (*Shorea robusta*) forests, whereas the site in Taplejung has a sub-tropical to temperate climate and is dominated by broad leaved forests (Table 1). Elevation ranges from 200-400 meters above sea level (m.a.s.l.) at the Chitwan site to almost 1300 m.a.s.l. in Taplejung. Due to the relative proximity of the equator, there is a maximum of two hours variation in day length across the year. There are four distinct climatic seasons: pre-monsoon (March-May); monsoon (June-September), post-monsoon (October-November) and winter (December-February). In Makwanpur, Chitwan and Gorkha, the surveys were carried out in community forests, whereas the survey in Taplejung was carried out mainly in private forests (Table 1).

Each survey site was classed as having high, medium or low levels of human disturbance (Table 1). This classification was based on the following parameters, all calculated within a five-kilometre buffer zone extending from the camera trapping stations (Table S1): the human population density, road density, the number of human settlements and the distance to nearest protected area. The latter was calculated from the geographic center of the buffer area extending from the cameras. The camera stations in Makwanpur were in a sub-metropolitan city and a rural municipality. In Chitwan and Gorkha the camera stations were in town municipalities and in Taplejung they were both a town municipality and a rural municipality (Fig. 1b). Human population densities are lower in rural municipalities than in town municipalities, and town municipalities have lower human population densities than sub-metropolitan cities.

Camera trapping
We placed all cameras in front of pangolin burrows to optimize detection success. We identified suitable burrows for camera trap placement during searches on trails and animal paths. Burrows with signs of recent activity were prioritised, but we also placed cameras in front of older burrows if those with fresh signs were not available. We conducted camera trapping surveys from 8 March to 24 April 2018 in Makwanpur, from 8 January to 15 March 2018 in Chitwan and from 7 December 2017 to 15 August 2018 in Gorkha. In Taplejung, three surveys were conducted, one from 6 February to 17 October 2013, another from 3 February to 29 March 2014 and the last from 15 December 2019 to 17 January 2020. The cameras were active from five to 78 days, with an average duration of six days in Makwanpur and Gorkha, 11 days in Chitwan, and 28 days in Taplejung. Camera traps days in Makwanpur was for 515 days at 73 burrows, 241 days at 21 burrows in Chitwan, and 116 days at 19 burrows in Gorkha. In Taplejung, it was for 482 days at 17 burrows in 2013, 69 days at three burrows in 2014 and 32 days at two burrows in 2019/20.

We fastened the cameras with rope to available trees, shrubs and/or wooden stakes at distances of one to two meters away from the burrow. We positioned them at 50 to 100 cm above the ground, directed towards the burrow opening. In Makwanpur, Chitwan and Gorkha we used infrared E2 model Cuddeback (Non Typical, Inc., 2256 American Blvd De Pere, WI 54115, USA) camera traps, while we used a combination of Moultrie GS D40 (EBSCO Industries, Inc., Birmingham, AL 35201-1943 USA) and Campark T45A (Campark Electronics Co. Ltd, 5F, B4 Bldg., Shenzhen International Huatongyuan, Logistics Center, Minzhi Road, Shenzhen, Guangdong, China) in Taplejung. The trigger mechanism of all cameras was activated by passive movement sensors. We set the camera trap delays at one minute. The cameras were not camouflaged, and we did not use baits to attract pangolins. We visited the camera trapping station every three to four days to check camera conditions, to collect captured photos and to replace SD memory cards.

The minimum convex polygons of the cameras covered 1758 ha (Makwanpur), 1474 ha (Chitwan), 94 ha (Gorkha), and 1130 ha (Taplejung), respectively (Table 1). Sun *et al.* (2015) estimated home range sizes of the Chinese pangolin to 35.1±13.8 ha for males and 6.0±2.9 ha for female, with non-overlapping home ranges within sex classes but males overlapping their home ranges with that of several females. Hence, our areas were big enough to each contain several males and females.

Data analysis

We extracted all images of Chinese pangolins along with information about the trap station and time of the observation (Table S2). We discarded all observations made at the same camera trap within 30 minutes (O'Brien *et al.* 2003). We estimated the temporal activity patterns of pangolins at their burrows using a kernel density estimator based on the time stamp of camera trap observations, converted to radians (Ridout and Linkie 2009). We made separate activity estimations for each area. Based on these density distributions, we used a non-parametric estimation of the common area under two probability density curves as an index of temporal overlap in activity between each pair of areas (Schmid and Schimdt 2006). This estimator ranged from 0 (no overlap) to 1 (complete overlap), and was calculated numerically by taking a large number of equally spaced values between 0 and 2π, T, and summing

$$\Delta 1 = \frac{\sum_{i=1}^{T} min\{\hat{f}(t_i), \hat{g}(t_i)\}}{T}$$

where T was set to 128 and $\hat{f}(t)$ and $\hat{g}(t)$ were the two estimated density distributions of activity. This formulation has been recommended for sample sizes below 50 observations (Ridout and Linkie 2009).

Because we were more interested in differences than in similarities among sites, we have presented our result as the additive inverse of the overlap index. This value describes the joint area of both activity distributions which do not overlap with one another, and similarly range from 0 (both areas overlap perfectly) to 1 (there is no overlap between the two areas). We used permutation tests to formally evaluate if these differences deviated from random expectations. For each pair of sites, we created 1000 permuted data sets where the time stamps were randomly assigned to each observation and calculated the overlap coefficient and subsequent difference for each of these sets. We then evaluated the likelihood of the observed values using standard Z-score conversion. The two-tailed p-values were corrected for multiple comparisons according to Benjamini and Hochberg (1995).

We performed data analyses in R version 4.0.3 (http://www.r-project.org), using the contributed package "Overlap" (version 0.3.3, Ridout and Linkie 2009).

Results

We obtained a total of 56 independent observations of Chinese pangolins across the four survey sites: 16 in Makwanpur, 20 in Chitwan, nine in Gorkha and 11 in Taplejung (Table 1). These observations were made at 12 stations in Makwanpur, seven in Chitwan, seven in Gorkha and nine in Taplejung (Fig. 1b). We detected pangolins outside both fresh and old burrow entrances. These observations were located in forested areas, agricultural lands, close to human settlements and on regularly used human trails at elevations ranging from 243 m.a.s.l. at Chitwan to 1286 m.a.s.l. at Taplejung.

Both burrow exits and entrances were observed from early evening (earliest recorded exit 18:30, earliest recorded entrance 19:17) to late morning (latest recorded exit 04:51, latest recorded entrance 04:11), with the majority of burrow activity occurring during the central parts of the night (Fig 2). No pairwise comparison of differences in burrow activity between sites deviated from random expectations (Table 2). However, there were trends for significant differences in pangolin burrow activity between Chitwan and Makwanpur (z=2.34, p = 0.058), which had medium and high levels of human activity respectively, and between Chitwan and Gorkha (z=2.41, p = 0.058), which both had medium levels of human activity. Peak burrow activity was estimated after midnight in Makwanpur,

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Gorkha and Taplejung, and before midnight in Chitwan, which also had a slightly broader activity distribution than the other areas (Fig. 2).

Discussion

Despite widespread documentation of effects of human activity on diel activity of mammals (Gaynor *et al.* 2018), differences in pangolin burrow activity among sites in this study did not correspond to levels of human activity. Therefore, we argue that our results point to limited influence of human activity on pangolin diel activity at these sites. Our largest observed differences, although not statistically significant at an alpha error of 0.05, was between two sites with similar human activity, and we observed no statistically significant differences between the sites with highest and lowest human activity. Results similar to our study have been reported for several other mammals including tiger (*Panthra tigris*), bush pigs (*Potamochoerus larvatus*) and baboons (*Papio anubis*) (Carter *et al.* 2012; Mugume *et al.* 2015), suggesting that human-induced differences in diel activity may not be occurring uniformly. We detected Chinese pangolins in areas of significant human activity, which highlights that pangolins tolerate some degree of human disturbance. This has also been observed by Khwaja *et al.* (2019) and Gurung (1996), although Chinese pangolins have been reported to avoid habitat close to major highways (Wu *et al.* 2020).

Our study demonstrates that wild Chinese pangolins in Nepal are predominantly nocturnal. This nocturnal temporal niche is consistent with previous observations on this species, both in captivity and in free-ranging environments (Heath 1987; Heath and Vanderlip 1988; Wu *et al.* 2020). We suggest that this largely nocturnal temporal niche may have enabled a high level of human persecution by allowing a close spatial co-existence between pangolins and humans. Hence, this biological characteristic, which could have evolved as an anti-predator mechanism (e.g., Gerkema *et al.* 2013) or in response to prey activity (Williams *et al.* 1997), may have been a contributing factor driving the Chinese pangolin towards its current Critically Endangered state since it renders the species an easily accessible target for poachers.

Despite a generally nocturnal temporal niche, pangolins in Chitwan appear to have emerged from their burrows earlier and have had a more sustained activity at burrows than pangolins in our other study sites. We suggest that these differences could have been influenced by extensive agricultural activities in Chitwan. While this site previously consisted of a continuous forest that was connected with Chitwan National Park, since the 1960s these forests have sequentially been replaced with intense agricultural activities (Bhattarai *et al.* 2017). Increased use of chemical fertilizers and pesticides may have reduced termite and ant populations,

which may have forced pangolins towards a less nocturnal temporal niche. Such an explanation is supported by observations on aardvarks (*Orycteropus afer*) in Africa, another nocturnal myremecophage for which prey scarcity has resulted in occasional diurnality (Weyer *et al.* 2020). We recommend further studies aimed at understanding changes in land use alter the diel activity of nocturnal mammals, particularly for species sensitive to persecution such as pangolins.

While we generally regard our results as informative, we recognise some limitations in our study. First, our sample size within each area may not have been sufficient to reliably estimate pangolin burrow activity. However, activity distributions derived from as few as nine observations, i.e. approximately the lowest used in this study, have been shown to correlate well with distributions estimated from substantially more observations (Lashley *et al.* 2018). Further, the small sample size has not allowed us to consider seasonal differences in activity. While day lengths at our study locations do not vary substantially with season due to latitude, a study in Taiwan (at a similar latitude) observed captive animals emerging from burrows up to an hour earlier in winter compared to summer (Chen *et al.* 2005 cited in Wu *et al.* 2020). Second, the absence of observable effects of anthropocentric activity could have been due to a limited variation in human activity among sites, or that human activity did not reach a high enough level to influence pangolin activity. However, human population density at our sites varied by more than two-fold, and ranged from intensively used sub-metropolitan areas (Makwanpur) to a remote rural site without a major highway (Taplejung). Third, diel activities are usually adapted to local conditions (Halle 2000; Frey *et al.* 2017). Hence, we cannot rule out that the high variability among our sites in local abiotic and biotic conditions may have influenced the observed burrow activity, especially since the influence of human disturbance may interact with such factors. While the effects of environmental co-variates were not analysed in our study, the inclusion of such co-variates will likely improve evaluations of the effects of human activity of this and similar species. Nonetheless, our study demonstrates the potential use of camera traps for monitoring pangolin activity, despite a limited use of this method for pangolins previously (Khwaja *et al.* 2019).

To conclude, our study did not detect differences in pangolin burrow activity among four sites with varying levels of disturbance by humans. Further studies are required to determine whether this outcome is a result of the relatively small sample size; however if correct, our findings point towards pangolins' tolerance of human disturbance. This could be attributed to their largely nocturnal temporal niche. We consider that this nocturnality may have contributed to pangolins' vulnerability to poaching by facilitating spatial coexistence between pangolins and humans.

Data availability

The data that support this study are available in as supplementary material accompanying the article.

Conflicts of interest

The authors have no conflicts of interest to declare.

Acknowledgements

References

Acharya, K.P., Paudel, P.K., Neupane, P.R., and Köhl, M. (2016). Human-wildlife conflicts in Nepal: patterns of human fatalities and injuries caused by large mammals. *PLoS One* **11**, e0161717.

Baker, S. E., Cain, R., Van Kesteren, F., Zommers, Z. A., D'cruze, N., and Macdonald, D. W. (2013). Rough trade: animal welfare in the global wildlife trade. *Biological Science* **63**, 928–938.

Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society* **57**, 289-300.

Bennie, J.J., Duffy, J.P., Inger, R., and Gaston, K.J. (2014). Biogeography of time partitioning in mammals. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 13727–13732.

Bhattarai, B.R., Wright, W., Poudel, B.S., Aryal, A., Yadav, B.P., and Wagle, R. (2017). Shifting paradigms for Nepal's protected areas: history, challenges and relationships. *Journal of Mountain Science* **14**, 964-979.

Bhattarai, B.R., Wright, W., and Khatiwada, A.P. (2016). Illegal hunting of prey species in the northern section of Bardia national park, Nepal: implications for carnivore conservation. *Environments* **3**, 32.

Biggs, D., Courchamp, F., Martin, R.B., and Possingham, H. (2013). Legal trade of Africa's rhino horns. *Science* **339**, 1038-1039.

Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B., and Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 15360–15365.

Challender, D.W.S. (2011). Asian pangolins: increasing affluence driving hunting pressure. *TRAFFIC Bulletin* **23**, 92-93.

Challender, D.W.S., Waterman, C., and Baillie, J. (2014). Scaling up pangolin conservation. IUCN SSC Pangolin Specialist Group Conservation Action Plan. (Zoological Society of London: London, UK)

Challender, D., Wu, S., Kaspal, P., Khatiwada, A., Ghose, A., Ching-Min Sun, N., Mohapatra, R.K. and Laxmi Suwal, T. (2019). *Manis pentadactyla* (errata version published in 2020). The IUCN Red List of Threatened Species 2019. Available at https://www.iucnredlist.org/species/12764/168392151 [Assessed 2 January 2021]

Challender, D.W.S., Nash, H.C., and Waterman, C. (Eds.) (2020). 'Pangolins: science, society and conservation'. (Elsevier Academic Press: London, UK)

Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., and Macdonald, D.W. (2016). Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. *Behavioral Ecology* **27**, 1578-1586.

Díaz-Ruiz, F., Caro, J., Delibes-Mateos, M., Arroyo, B., and Ferreras, P. (2016). Drivers of red fox (*Vulpes vulpes*) daily activity: prey availability, human disturbance or habitat structure? *Journal of Zoology* **298**, 128-138.

Eaton, J.A., Shepherd, C.R., Rheindt, F.E., Harris, J.B.C., Van Balen, S.B., Wilcove, D.S., and Collar, N. (2015). Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia. *Forktail* **31**, 1-12.

Frey, S., Fisher, J.T., Burton, A.C., and Volpe, J.P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sensing in Ecology and Conservation* **3**, 123–132.

Frid, A. and Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**, 11.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., and Brashares, J.S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* **360**, 1232–1235.

Gerkema, M.P., Davies, W.I.L., Foster, R.G., Menaker, M., and Hut, R.A. (2013). The nocturnal bottleneck and the evolution of activity patterns in mammals. *Proceedings of the Royal Society Biological Science* **280**, 1-11.

Gurung, J.B. (1996). A pangolin survey in Royal Nagarjung forest in Kathmandu, Nepal. *Tiger Paper* **23**, 29-32.

Halle, S. (2000). Ecological relevance of daily activity patterns. In 'Activity Patterns in Small Mammals'. (Eds. Halle, S. and Stenseth, N.C.) Pp 67-90. (Springer: Berlin, Germany)

Heath, M.E. (1987). Twenty-four-hour variations in activity, core temperature, metabolic rate, and respiratory quotient in captive Chinese pangolins. *Zoo Biology* **6**, 1-10.

Heath, M.E. and Vanderlip, S.L. (1988). Biology, husbandry and veterinary care of captive Chinese pangolins (*Manis pentadactyla*). *Zoo Biology* **7**, 293–312.

Heinrich, S., Koehncke, A., and Shepherd, C.R. (2019). The role of Germany in the illegal global pangolin trade. *Global Ecology and Conservation* **20**, e00736.

Hertel, A. G., Swenson, J. E., and Bischof, R. (2017). A case for considering individual variation in diel activity patterns. *Behavioral Ecology* **28**, 1524-1531.

Ikeda, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K., and Koizumi, I. (2016). Seasonal and diel activity patterns of eight sympatric mammals in northern Japan revealed by an intensive camera-trap survey. *PLoS One* **11**, e0163602.

Khatiwada, A.P., Wright, W., Roe, D., Suwal, T., Thapa, S., Kaspal, P., and Poudel, K. (2020). Community conservation in Nepal – opportunities and challenges for pangolin conservation. In 'Pangolins: science, society and conservation.' (Eds. Challender, D.W.S., Nash, H.C., and Waterman, C.) pp. 395-409. (Elsevier Academic Press: London, UK)

Khwaja, H., Buchan, C., Wearn, O.R., Bahaa-el-din, L., Bantlin, D., Bernard, Bitariho, R., Bohm, T., Borah, J., Brodie, J., Chutipong, W., duPreez, B., Ebang-Mbele, A., Edwards, S., Fairet, E., Frechette, J.L., Garside, A., Gibson, L., Giordano, A., Gopi, V.G., Granados, A., Gubbi, S., Harich, F., Haurez, B., Havmøller, R.W., Helmy, O., Isbell, L.A., Jenks, K., Kalle, R., Kamjing, A., Khamcha, D., Kiebou-Opepa, C., Kinnaird, M., Kruger, C., Laudisoit, A., Lynam, A., Macdonald, S.E., Mathai, J., Sienne, J.M., Meier, A., Mills, D., Mohd-Azlan, J., Nakashima, Y., Nash, H.C., Ngoprasert, D., Nguyen, A., O'Brien, T., Olson, D.,Orbell, C., Poulsen, J., Ramesh, T., Reeder, D.A., Reyna, R., Rich, L.N., Rode-Margono, J., Rovero, F., Sheil, D., Shirley, M.H., Stratford, K., Sukumal, N., Suwanrat, S., Tantipisanuh, N., Tilker, A., Berkel, T.V., der Weyde, L.K.V., Varney, M., Weise, F., Wiesel, I., Wilting, A., Wong, S.T., Waterman, C., and Challender, D.W.S. (2019). Pangolins in global camera trap data: implications for ecological monitoring. *Global Ecology and Conservation* **20**, e00769.

Lashley, M.A., Cove, M.V., Chitwood, M.C., Penido, G., Gardner, B., DePerno, C.S., and Moorman, C.E. (2018). Estimating wildlife activity curves: comparison of methods and sample size. *Scientific Reports* **8**, 4173.

Lin, J.S. (2011). Home range and burrow utilization in Formosan pangolin (*Manis pentadactyla pentadactyla*) at Luanshan, Taitung. M.Sc.

Thesis. (National Pingtung University of Science and Technology: Neipu Township, Taiwan)

Mugume, S., Isabirye-Basuta, G., Otali, E., Reyna-Hurtado, R., and Chapman, C.A. (2015). How do human activities influence the status and distribution of terrestrial mammals in forest reserves? *Journal of Mammalogy* **96**, 998-1004.

Nickel, B.A., Suraci, J.P., Allen, M.L., and Wilmers, C.C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation* **241**, 108383.

O'Brien, T. G., Kinnaird, M. F., and Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation* **6**, 131–139.

Paudel, P.K., Acharya, K.P., Baral, H.S., Heinen, J.T., and Jnawali, S.R. (2020). Trends, patterns, and networks of illicit wildlife trade in Nepal: A national synthesis. *Conservation Science and Practice **2**,* e247.

Ridout, M.S. and Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological and Environmental Statistics* **14**, 322-337.

Ross, J., Hearn, A.J., Johnson, P.J., and Macdonald, D.W. (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *Journal of Zoology* **290**, 96-106.

Schmid, F. and Schmidt, A. (2006). Nonparametric estimation of the coefficient of overlapping-theory and empirical application. *Computational Statistics and Data Analysis* **50**, 1583-1596.

Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., and Wilmers, C.C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. *Proceedings of the Royal Society Biological Science* **284**, 0433.

Smith, J.A., Thomas, A.C., Levi, T., Wang, Y., and Wilmers, C.C. (2018). Human activity reduces niche partitioning among three widespread mesocarnivores. *Oikos*, **127**, 890–901.

Sun, C-M, Lin,J-S, Lai, C-Y, and Pei, K.J-C. (2015). Home range, density, habitat preference and modeling of the Taiwanese pangolins (*Manis pentadactyla pentadactyla*) in south-eastern Taiwan. In 'First International Conference on Pangolin Conservation, Trade and Rehabilitation'. (Eds. Jansen, R., Kotze, A. and Sibiya, L.) pp. 28. (Mabula Game Reserve: South Africa)

Suraci, J.P., Clinchy, M., Zanette, L.Y., and Wilmers, C.C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters* **22**, 1578–1586.

Takahashi, J. S., Turek, F. W. and Moore, R. Y. (2001). Handbook of Behavioral Neurobiology: Circadian Clocks. (Springer: New York, USA)

Tan, W.S., Hamzah, N.B.A., Saaban, S., Zawakhir, N.A., Rao, Y., Jamaluddin, N., Cheong, F., Khalid, N.B., Saat, N.L.M., Ee, E.N.B.Z., Hamdan, A.B., Chow, M.M., Low, C.P., Voon, M., Liang, S.H., Tyson,

M., and Gumal, M.T. (2018). Observations of occurrence and daily activity patterns of ungulates in the Endau Rompin Landscape, peninsular Malaysia. *Journal of Threatened Taxa* **10**, 11245-11253.

Underwood, F.M., Burn, R.W., and Milliken, T. (2013). Dissecting the illegal ivory trade: an analysis of ivory seizures data. *PLoS One* **8**, 1-12.

Weyer, N.M., Fuller, A., Haw, A.J., Meyer, L.C.R., Mitchell, D., Picker, M., Rey, B., and Hetem, R.S. (2020). Increased diurnal activity is indicative of energy deficit in a nocturnal mammal, the Aardvark. *Frontiers in Physiology* **11**, 637.

Williams, J. B., Anderson, M. D., and Richardson, P. R. K. (1997). Seasonal differences in field metabolism, water requirements, and foraging behavior of free-living aardwolves. *Ecology* **78**, 2588–2602.

Wu, S., Liu, N., Zhang, Y. and Ma, G. (2004). Assessment of Threatened Status of Chinese pangolin. *Chinese Journal of Applied Environmental Biology* **10**, 456-461.

Wu, S., Sun, N.C-M., Zhang, F., Yu, Y., Ades, G., Suwal, T.L., and Jiang, Z. (2020). Chinese pangolin *Manis pentadactyla* (Linnaeus, 1758). In 'Pangolins: science, society and conservation'. (Eds. Challender, D.W.S., Nash, H.C., and Waterman, C.) pp. 49-66. (Elsevier Academic Press: London, UK)

Wyatt, T. (2011). The illegal trade of raptors in the Russian Federation. *Contemporary Justice Review* **14**, 103-123.

Table 1: Descriptions of the four survey sites, including indicators of human activity within a five-kilometre buffer zone, area of the minimum convex polygons of the camera trapping stations as well as land tenure, bioclimatic zones, habitat and pangolin camera trap observations at each site.

Survey site	Makwanpur	Chitwan	Gorkha	Taplejung
Human activity	High	Medium	Medium	Low
Area (ha)	1758	1474	94	1130
Land tenure	Community forest	Community forest	Community forest	Private forest
Bioclimatic zones	Tropical	Tropical	Tropical	Sub-tropical; Temperate
Habitat	Sal mixed forest	Sal mixed forest	Sal mixed forest	Broad leaved forest
Elevation (m.a.s.l.)	456-545	243-370	485-529	848-1286
Pangolin observation	16	20	9	11

Table 2: Results from pairwise tests of differences in burrow activity of Chinese pangolins among four study sites of contrasting human activity in Nepal. Observed differences were calculated as the additive inverse of a temporal overlap index calculated on the time of camera trap observations, and represents the proportional pooled activity between two areas that do not overlap. The expected differences were calculated from 1000 random permutations of the observation times from each pair of areas. Deviations from random expectations were evaluated by Z score conversion, and the associated two-tailed p values were adjusted for multiple comparisons controlling for the false discovery rate. Each area has been coded as having high (H), medium (M) or low (L) human activity.

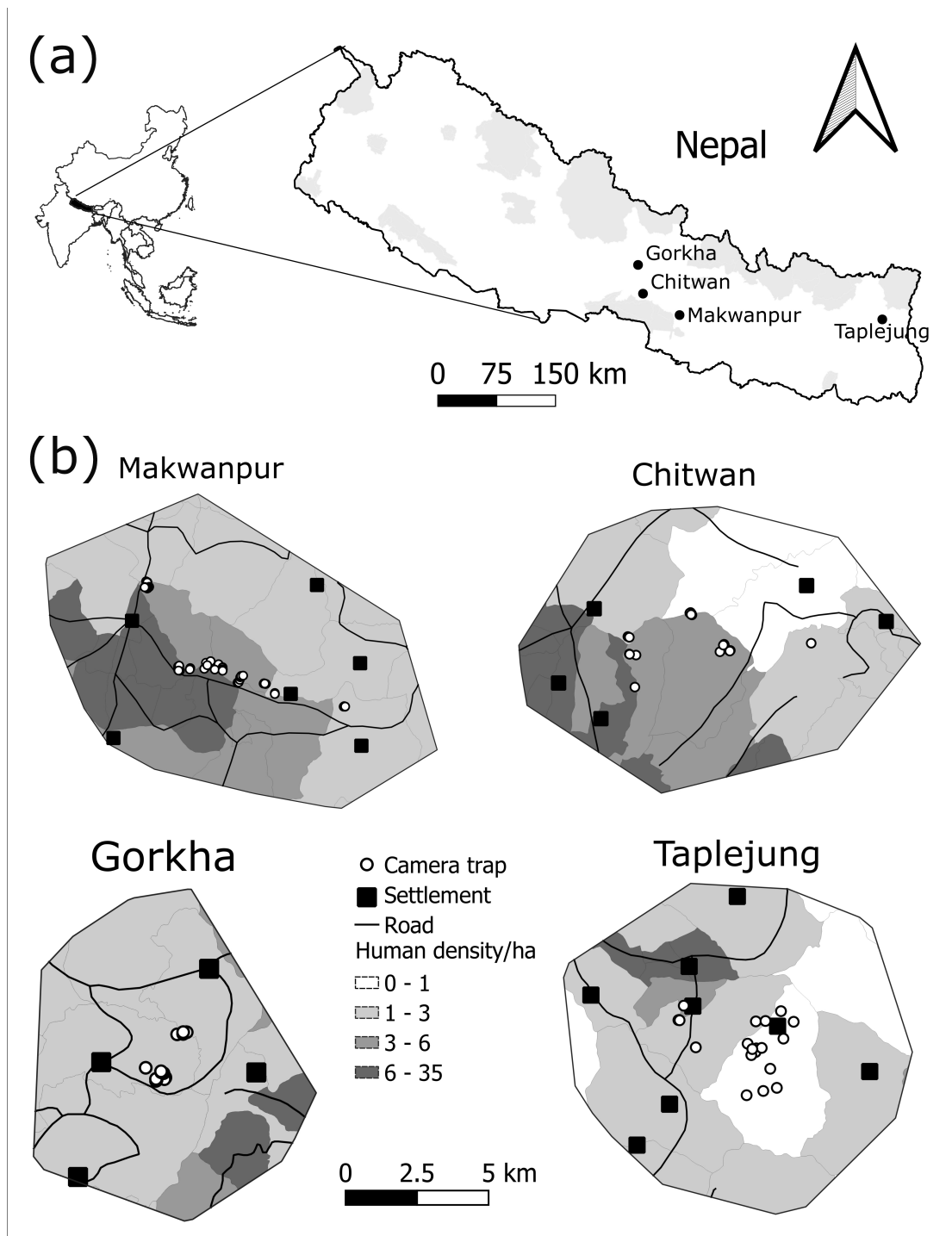| Comparison	Observed difference	Expected difference	Z	p.adj
Makwanpur (H) – Chitwan (M)	0.39	0.21	2.34	0.058
Makwanpur (H) – Gorkha (M)	0.11	0.24	1.44	0.301
Makwanpur (H) – Taplejung (L)	0.23	0.23	0.02	0.983
Chitwan (M) – Gorkha (M)	0.50	0.25	2.41	0.058
Chitwan (M) – Taplejung (L)	0.20	0.25	0.18	0.983
Gorkha (M) – Taplejung (L)	0.33	0.27	0.64	0.782

Figure 1: Locations of the study sites in Nepal (a) as well as areas surrounding the camera stations in each site, delineated as a five-kilometre buffer zone outside the minimum convex polygons of the placed cameras (b). Shaded areas in Nepal (a) represent protected land, and shaded areas surrounding camera sites (b) represents human density in local government areas (wards of municipalities).
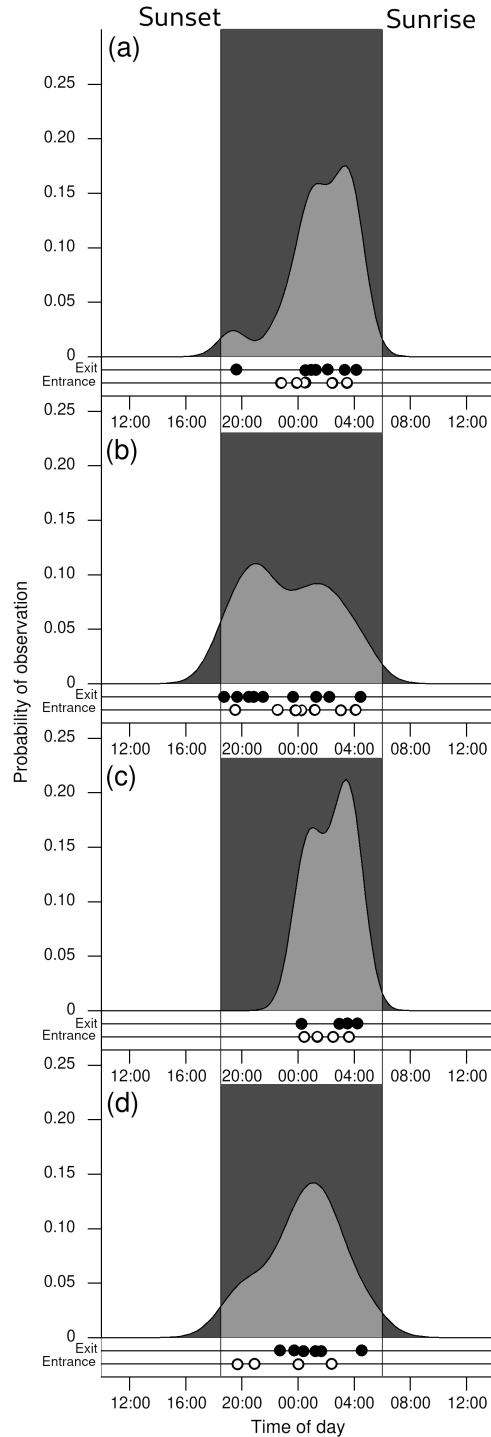
Figure 2: Probability distributions describing burrow activity of Chinese pangolins in Makwanpur (a), Chitwan (b), Gorkha (c) and Taplejung (d), estimated from 16, 20, nine and 11 camera trapping observations, respectively. Sunset and sunrise times represent annual means for Nepal. Annual variation in sunset and sunrise times in Nepal is less than 2 hours, respectively.