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Unpredictability of vigilance in two sympatric Tibetan ungulates

Yunchao Luo[1,3] | Lin Wang[1] | Le Yang[2] | Xinxin Wang[1] | Xingjun Tian[1,3] | Zhongqiu Li[1,3]

[1]Laboratory of Animal Behavior and Conservation, School of Life Sciences, Nanjing University, Nanjing, China

[2]Tibet Plateau Institute of Biology, Lhasa, China

[3]College of Eco-Environmental Engineering, Qinghai University, Xining, China

Correspondence
Zhongqiu Li, Laboratory of Animal Behavior and Conservation, School of Life Sciences, Nanjing University, Nanjing, 210023, China.
Email: lizq@nju.edu.cn

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Abstract

Vigilance is important for anti-predation, and different animals adopt different vigilance strategies. Instantaneous and sequential randomness in vigilance behavior are two main principles for the classic Pulliam model (1973). Given this context, we studied the vigilance behaviors in two wild cloven-hoofed animals, the Tibetan antelope (*Pantholops hodgsonii*) and the Tibetan gazelle (*Procapra picticaudata*) on Qinghai–Tibet Plateau, to explore if the two randomness principles work across species. The results showed that the distribution of inter-scan intervals of both Tibetan antelope and Tibetan gazelle followed the negative exponential distribution; inter-scans of both Tibetan antelope and Tibetan gazelle were unrelated with their previous scan, and most sequences of inter-scan intervals could be considered as random organized or unpredictable. In conclusion, the vigilance patterns of Tibetan antelope and Tibetan gazelle followed instantaneous randomness and sequential randomness of Pulliam model. A random vigilance strategy might be the best choice for Tibetan ungulates, and how to distinguish the social vigilance from anti-predator vigilance is an important issue for future research.

KEYWORDS
instantaneous randomness, sequential randomness, Tibetan antelope, Tibetan gazelle, vigilance

1 | INTRODUCTION

Vigilance is a state of alertness aimed at detecting predatory or competitive stimuli (Pays, Dubot, Jarman, Loisel, & Goldizen, 2009). The main function of vigilance is anti-predator (Elgar, 1989; Lima, 1987; Roberts, 1996). And it is thought to occur when animals raise their head to scan their surroundings (Beauchamp, 2014). Pulliam first proposed the theory of anti-predator vigilance strategies based on randomness in scanning behavior (Pulliam, 1973). Instantaneous randomness in scan initiation and sequential randomness across scans are two important assumptions of Pulliam model (Bednekoff & Lima, 1998; Hart & Lendrem, 1984; Pulliam, 1973).

Instantaneous randomness means that the predator is unable to predict when the prey will scan so that the predator cannot effectively time its attack (Carro & Fernandez, 2009). Consequently, the distribution of inter-scan intervals will follow a negative exponential distribution (Bednekoff & Lima, 1998). This has been found in several species, such as ostriches (*Struthio camelus*) (Bertram, 1980), yellow-eyed Junco (*Junco phaeonotus*) (Caraco, 1982), house sparrow (*Passer domesticus*) (Studd, Montgomerie, & Robertson, 1983), and black-necked Crane (*Grus nigricollis*) (Li, Yang, Luo, Wu, & Li, 2018). Instantaneous randomness is thought to be effective when facing a stalking predator (Bednekoff & Lima, 2002; Scannell, Roberts, & Lazarus, 2001), because stalking predators such as cat will take advantage of any regularity in prey scanning to advance

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closer, and break cover to attack prey after a surreptitious approach (Beauchamp, 2019).

Sequential randomness means that the duration of one inter-scan is randomly distributed and it is not influenced by the duration of previous scan (Bednekoff & Lima, 1998; Carro, Fernandez, & Reboreda, 2011; Roberts, 1994). White-lipped Deer (*Cervus albirostris*) (Wang, You, Xie, Zheng, & Li, 2018) and black-necked Crane (Li et al., 2018; Li, Che, & Yang, 2017) fitted the assumption, but purple sandpiper (*Calidris maritima*), Barbary dove (*Streptopelia risoria*), flamingo (*Phoenicopterus ruber ruber*) and greater rheas (*Rhea americana*) did not (Beauchamp, 2006; Carro et al., 2011; Desportes, Metcalfe, Brun, & Cezilly, 1990). Interestingly, marmoset (*Callithrix penicillata*) will alter sequence predictability if the experimental conditions change (Barros, Alencar, de Souza Silva, & Tomaz, 2008). Sequential randomness let the predator unable to predict the behavior of prey; therefore, it is an effective anti-predator strategy.

If the vigilance behavior is regular and predictable, the predator can use this rule to decide when to attack. Predator could watch the chance and attack at the inter-scan interval of prey. Therefore, animals need to adjust the vigilance pattern to make the alert time unpredictable. The study of instantaneous randomness and sequential randomness across scans will contribute to the theoretical knowledge of animal vigilance. However, not so many studies pay attention on this point, particularly in ungulates.

Given this context, we studied vigilance in populations of two wild ungulates, Tibetan antelope (*Pantholops hodgsonii*) and Tibetan gazelle (*Procapra picticaudata*), to explore whether their vigilance patterns are consistent with the two assumptions of Pulliam model. These two ungulates are distributed in the similar area where they can even form some mixed-species groups, but there is obvious difference in body size and group size between them. Consequently, predation risk and vigilance strategy also differ between the two species. Our recent study found that smaller Tibetan gazelles scanned environment more frequently than larger Tibetan antelopes did due to the difference of body size, and the group size effect on vigilance was also different between the two species (Luo et al., 2019). Thus, we wondered that if their vigilant randomness is also quite different.

With respect to the two assumptions of Pulliam model, namely instantaneous randomness and sequential randomness, we predict that (a) the distribution of inter-scan intervals of both Tibetan antelope and Tibetan gazelle follow the negative exponential distribution; (b) inter-scans of both Tibetan antelope and Tibetan gazelle are unrelated with their previous scans.

2 | METHODS

2.1 | Study area

This study was conducted in the Selincuo National Nature Reserve, Shenzha County (30°02′39″~32°19′33″N, 87°45′30″~89°47′49″E) of Tibet, which in the central part of Qiangtang Plateau. Elevations range from 4,530 to 6,448 m, with an average of more than 4,700 m. Local climate is characterized by extreme cold and long winters, strong winds, and high levels of solar radiation. Mean annual temperature was 0.4°C. Annual precipitation is about 330 mm, and most rain falls between June and September. Alpine meadow is the main vegetation type, and no shrubs appear in this area.

2.2 | Study species

Tibetan antelope, a flagship species to Qinghai–Tibet Plateau, belongs to Bovidae, Pantholops. They were poached terribly because of high quality cashmere, later became endangered in last century (Schaller, 1998). Tibetan antelope has been classified as a Category I (Endangered in China) National Protected Wild Animal Species in China since 1989 and as Near Threatened by IUCN since 2016. The protection of Tibetan antelope has attracted more and more attention, and the population has increased to more than 150,000 (Yang et al., 2018). However, there are still not many studies on the basic biological and behavioral information due to the extremely high elevation and cruel natural environment. Tibetan antelope is sexually segregated, males are much heavier than females (adult males with an average body weight of 39 kg; females with an average of 26 kg) (Leslie & Schaller, 2008), and they only formed mixed-sex groups in rutting season in Dec. and Jan. The resident status of Tibetan antelope can be divided into two types, the migratory population and the resident population. The population of Tibetan antelope in Shenzha is resident and does not migrate which might be up to 10,000 (Luo et al., 2018;Yang et al., 2018).

Tibetan gazelle belongs to Bovidae, Procapra, which is distributed on nearly all the Qinghai–Tibetan Plateau (Schaller, 1998). Even widely distributed, the population has been decreasing in recent decades. Tibetan gazelle has been classified as a Category II Protected Wild Animal Species in China, and Near Threatened in the IUCN Red list of Threatened Species (Zhang & Jiang, 2006). Tibetan gazelle is much smaller than Tibetan antelope, and it is also sexually segregated. The mixed-sex groups are mainly found during the rutting season in Dec. and Jan., and after then they separate and aggregate in single-sex groups (Lian, Su, & Zhang, 2004). However, the body weight is similar between sexes (average weight is 14 kg) (Leslie & David, 2010). The population of Tibetan gazelle is estimated at a few hundred in Shenzha (Yang et al., 2018).

Many natural enemies, including wolves (*Canis lupus*), snow leopard (*Panthera uncia*), lynx (*Felis lynx*), and brown bear (*Ursus arctos*), can hunt Tibetan antelope and Tibetan gazelle. Large raptors including upland buzzard (*Buteo hemilasius*) and cinereous vulture (*Aegypius monachus*) are also common (Schaller, 1998). However, besides those natural enemies, these ungulates have to be vigilant against humans (illegal hunting and human activity disturbance) and free-roaming dogs (*C. lupus familiaris*) (Yang, Cao, Li, & Dang, 2019). More attention has been paid to the potential effect of free-roaming dogs on wildlife in recent years (Atickem, Bekele, & Williams, 2010;Farrington & Zhang, 2013;Home et al., 2017;Young, Olson, Reading, Amgalanbaatar, & Berger, 2011;Zapata-Rios & Branch, 2016), and a study reported that free-roaming dogs usually formed a structured group and could use a stalking strategy to predate on Tibetan ungulates (Yang et al., 2019). We encountered free-roaming dogs at our study area frequently and witnessed those dogs utilizing grassland fence to round up and hunt a Tibetan gazelle in Shenzha County in 2015 (Yang et al., 2019). Thus, it is very important for the survival of ungulates to adopt a suitable vigilance strategy.

2.3 | Behavioral observation

Daytime observations were carried out from sunrise to sunset (Chinese standard time 9:00–20:00, equal to local time 7:00–18:00) in two summers (July & August of 2016, June & July of 2017), the childbirth period of Tibetan antelope and Tibetan gazelle. We took samples by camcorders and binoculars in this study, and individuals were observed by focal sampling method (Altmann, 1974). We recorded detailed information of focal groups and individuals, including species, sex-age, and group size.

We randomly selected encountered groups when we drove along the road. We randomly selected one focal subject in the selected group, and sometimes a few more (2–5 individuals) from different parts of the group if the group was large (Some groups have more than 400 individuals). To avoid duplicate sampling, the route was not repeated on three consecutive days. Actually, it was unlikely that the same individuals were sampled more than once on a given day given the large size of the population although the animals were not marked. It was possible that some individuals may have been sampled again, but it was very unlikely. Each individual was considered as an independent sample. Solitary individuals were also considered as a group with only one member.

Behavioral events were videotaped or dictated to a mobile phone recorder. Observations lasted for 30 min unless we lost sight of the focal individual. Actual observation duration was 5–30 min. “Vigilance” behavior was defined as an ungulate stretching its head up while scanning around (Li, 2016). Thus, a focal observation included a sequence of scans and inter-scans. Inter-scan behaviors included feeding, walking, preening, and other behaviors (Li et al., 2017).

2.4 | Ethical approval

This is an observational experiment and all observations were made at a distance of more than 200 m. All the experiment procedures in this study were approved by the Chinese Wildlife Management Authority.

2.5 | Data analysis

We totally collected 256 behavioral samples representing 4,066 min for Tibetan antelope, and 236 behavioral samples representing 3,540 min for Tibetan gazelle. A focal observation includes a sequence of scans and inter-scans. A scan refers to a bout with the head up and an inters-can refers to a bout with the head down preceding a bout with the head up (Beauchamp, 2006, 2020). Samples with less than 10 scans/ inter-scans transitions were deleted; thus, 45 samples from 36 groups of Tibetan antelope and 141 samples from 77 groups of Tibetan gazelle were effective. All these samples, timed scans, and inter-scans were reviewed to the nearest 1 s.

We used mixed linear model to compare vigilance patterns of the two ungulates. Data of scan durations and inter-scan intervals were lg10 transformed to approach normal distribution. Set species, sex-age (male, female and lamb), and group size as independent variable and group ID as a random factor since some samples were collected from the same group. All the factors (species × sex–age, species × group size, and group ID) were, respectively, nested in the model (Luo et al., 2019). For the test of instantaneous randomness, we used Kolmogorov–Smirnov test to assess whether the distribution of inter-scan intervals followed a negative exponential distribution.

In the study of sequential randomness of inter-scan intervals, parametric test needs 50 transitions of behavior at least (Roberts, 1996). In this study, not all sequence meets the requirement, so we tested it with non-parametric one-sample runs test (Beauchamp, 2006; Li et al., 2017, 2018; Wang et al., 2018). Cut point is median value. Runs test was used to assess the assumption that the elements of the sequence were mutually independent. Rejection of random test provides evidence for a non-random pattern of vigilance sequence (Li et al., 2017).

Additionally, we also used a mixed linear model to assess whether each inter-scan interval was dependent on the previous scan duration (Li et al., 2017; Pays, Blomberg, Renaud, Favreau, & Jarman, 2010). Similarly, data of inter-scan intervals were lg10 transformed and, then, set the previous scan duration as an independent variable and group ID as a random factor. Subsequently, for each individual, we evaluated whether the inter-scan intervals and the previous scan durations were closed related with Pearson correlation when data were normally distributed or Spearman rank correlation when data were not normally distributed.

We used R Language (R-3.5.1) with nlme package (Batary, Holzschuh, Orci, Samu, & Tscharntke, 2012) for mixed linear model and IBM SPSS Statistics 22 for other statistical analysis, and two-tailed probabilities of 0.05 were considered significant.

3 | RESULTS

The length of inter-scan intervals of Tibetan antelope varied from 1 to 557 s, with a median of 28.5 s, whereas the scan durations varied from 1 to 290 s, with a median of 6 s (Figure 1); the length of inter-scan intervals of Tibetan gazelle varied from 1 to 416 s, with a median of 19s, whereas the scan durations varied from 1 to 352 s, with a median of 5s (Figure 2). However, there is no significant difference in observed frequencies of inter-scan intervals between Tibetan

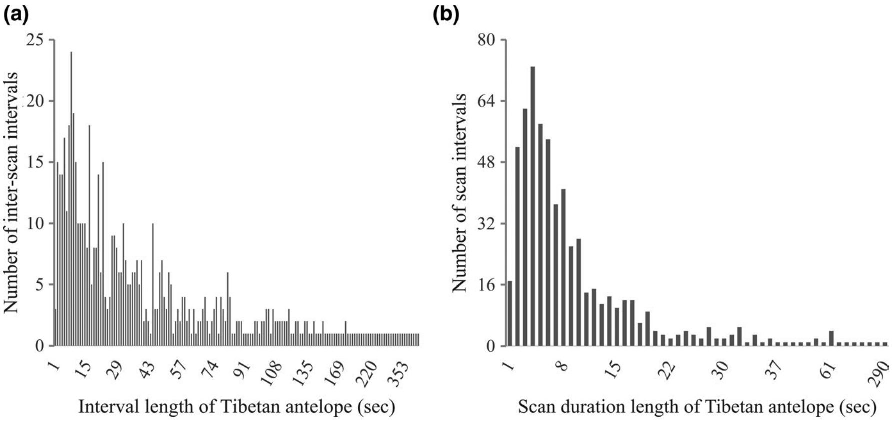

FIGURE 1 Frequency of (a) inter-scan intervals and (b) scan durations from 45 individuals of Tibetan antelope in Selincuo National Nature Reserve, Tibet

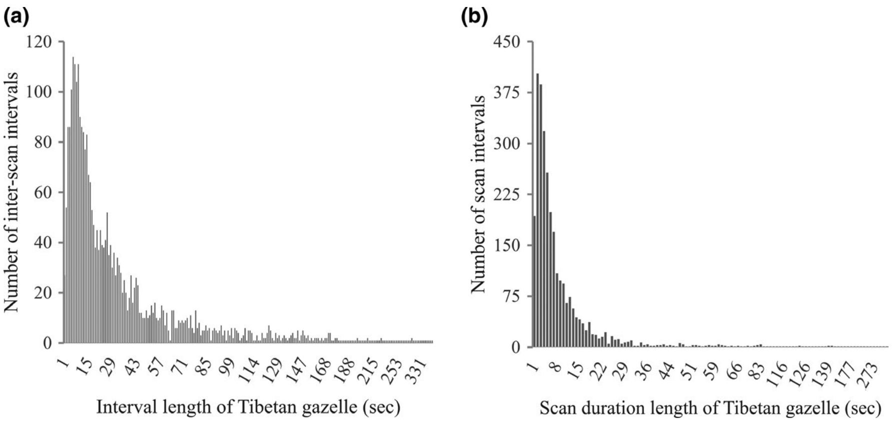

FIGURE 2 Frequency of (a) inter-scan intervals and (b) scan durations from 141 individuals of Tibetan gazelle in Selincuo National Nature Reserve, Tibet

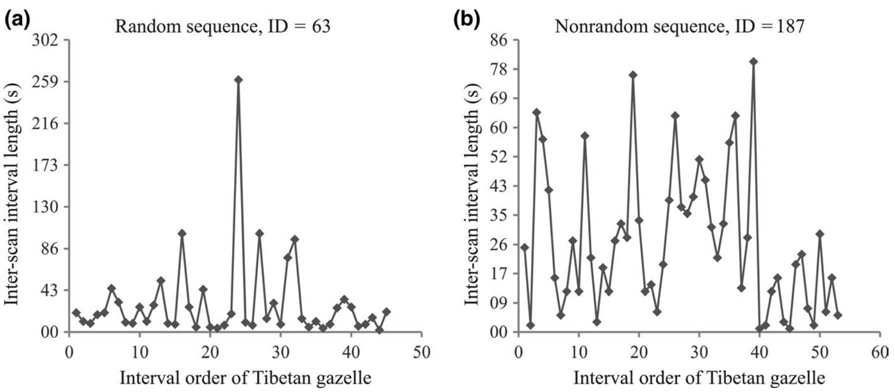

FIGURE 3 Examples of (a) random and (b) non-random sequence of inter-scan intervals in Tibetan gazelle in Selincuo National Nature Reserve, Tibet

antelope and Tibetan gazelle (df = 109, t = −1.387, p = .168, Table S1), and of scan durations between the two ungulates (df = 109, t = 0.045, p = .964, Table S2).

K-S tests showed that most inter-scan intervals fit negative exponential distribution (Tibetan antelope: 42/45, 93.33%; Tibetan gazelle: 140/141, 99.29%) (Tables S3 and S4), indicating instantaneous randomness of vigilance occurred in both species.

Through Runs tests, most sequences of inter-scan intervals (Tibetan antelope: 43/45, 95.56%; Tibetan gazelle: 135/141, 95.74%) could be considered as random organized or unpredictable, and just a few sequences were in non-random order (Tables S3 and S4). Examples of a random and non-random sequence are shown in Figure 3. The mixed linear model showed no significant relationship between the previous scan and the current inter-scan (Tibetan antelope: df = 577, t = −0.183, p = .855; Tibetan gazelle: df = 2,830, t = −0.464, p = .643). Correlation analysis left a similar result; most individuals showed no correlation between the previous scan and the current inter-scan (Tibetan antelope: 44/45, 97.78%; Tibetan gazelle: 133/141, 94.33%), and only a few showed a correlation; however, some were positive while some were negative (Tables S3 and S4). Examples of a predictable and unpredictable vigilance sequence are shown in Figure 4.

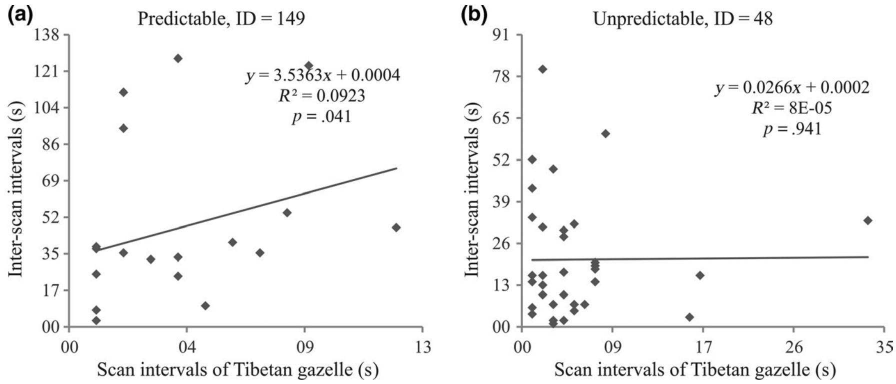

FIGURE 4 Examples of (a) predictable and (b) unpredictable correlation between the current interscan interval and the previous scan duration in Tibetan gazelle in Selincuo National Nature Reserve, Tibet

4 | DISCUSSIONS

Instantaneous randomness and sequential randomness are two important assumptions of Pulliam's model (Bednekoff & Lima, 1998;Hart & Lendrem, 1984; Pulliam, 1973). But there are few reports on vigilance randomness in ungulates. Our result indicated that Tibetan antelope had similar intervals of scan and inter-scan with Tibetan gazelle, the distribution of inter-scan intervals of both species followed the negative exponential distribution, and most sequences of inter-scan intervals could be considered as randomly organized. In other words, the vigilance patterns of both Tibetan antelope and Tibetan gazelle accorded with instantaneous and sequential randomness assumed by Pulliam model.

The living conditions of the ungulates are extremely cruel on Qinghai–Tibet Plateau where the average temperature and the oxygen content are very low due to the rarefied air (Li et al., 2018). Animals have a higher demand for energy intake but the main vegetation is alpine meadows with relatively low biomass and nutritional provision compared with plains (Wan et al., 2006). So the ungulates need more time to feed. In addition, ungulates here are facing a higher predation risk from wolf, snow leopard, free-roaming dog, etc. In summary, fixed short intervals between two successive scans are likely uninformative and time-consuming, but conversely fixed longer intervals are pretty risky. Consequently, animals have to adjust the vigilance-feeding pattern to the most reasonable state, and the random vigilance would be the best choice for anti-predator. Taking unpredictable vigilance pattern can prevent predators from predicting the potential attacking opportunities.

Animal might be facing predators with different predation strategies (Chang, Teo, Norma-Rashid, & Li, 2017). Random vigilance strategy is the best choice when facing the stalking predators that could time its attacks to coincide with relaxing periods of prey (Beauchamp, 2006; Bednekoff & Lima, 2002; Carro et al., 2011; Pays et al., 2010; Scannell et al., 2001). This also determines whether the inter-scan interval is related to the previous scan duration, and whether the distribution of inter-scan intervals follows the negative exponential distribution (Beauchamp, 2016). However, a recent study argued that animals might want to scan at regular intervals especially if stalking predators are not too common, but well-known cognitive constraints on the timing of vigilance bouts add randomness to scanning (Beauchamp, 2019). On the Qiangtang plateau, as stated above, several stalking predators exist, including snow leopard and lynx. Even the free-roaming dogs have learnt the stalking strategy to hunt wildlife (Yang et al., 2019), although they are not stalking predators in the traditional view. Therefore, keeping vigilance unpredictable is very important for the survival of these rare ungulates.

In conclusion, we found vigilance sequences were randomly organized and can be considered unpredictable in both Tibetan antelope and Tibetan gazelle. Future studies can be done on test of the third assumption of Pulliam model, the independent principle that individuals should scan environment independently of each other (Pays & Jarman, 2008; Pays et al., 2007; Podgórski et al., 2016; Scannell et al., 2001). Furthermore, in this study, we considered all the vigilance as anti-predator response, because it is hard to distinguish the specific detection targets of ungulates. However, animals are highly sensitive to the surrounding environment and vigilance may be directed at potential social competitors as well as predators (Beauchamp, 2006); thus, how to distinguish the social vigilance from anti-predator vigilance is another important issue in the future.

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ORCID

Yunchao Luo https://orcid.org/0000-0002-6102-0326
Lin Wang https://orcid.org/0000-0003-3048-1776
Xingjun Tian https://orcid.org/0000-0002-0251-2582
Zhongqiu Li https://orcid.org/0000-0003-2004-293X

REFERENCES

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3), 227–267. https://doi.org/10.1163/156853974x00534

Atickem, A., Bekele, A., & Williams, S. D. (2010). Competition between domestic dogs and Ethiopian wolf (*Canis simensis*) in the Bale Mountains National Park. *Ethiopia. African Journal of Ecology*, *48*(2), 401–407. https://doi.org/10.1111/j.1365-2028.2009.01126.x

Barros, M., Alencar, C., de Souza Silva, M. A., & Tomaz, C. (2008). Changes in experimental conditions alter anti-predator vigilance and sequence predictability in captive marmosets. *Behavioural Processes*, *77*(3), 351–356. https://doi.org/10.1016/j.beproc.2007.10.001

Batary, P., Holzschuh, A., Orci, K. M., Samu, F., & Tscharntke, T. (2012). Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agriculture Ecosystems & Environment*, *146*(1), 130–136. https://doi.org/10.1016/j.agee.2011.10.018

Beauchamp, G. (2006). Nonrandom patterns of vigilance in flocks of the greater flamingo, *Phoenicopterus ruber ruber*. *Animal Behaviour*, *71*(3), 593–598. https://doi.org/10.1016/j.anbehav.2005.06.008

Beauchamp, G. (2014). *Social predation: how group living benefits predators and prey*. London: Elsevier.

Beauchamp, G. (2016). Function and structure of vigilance in a gregarious species exposed to threats from predators and conspecifics. *Animal Behaviour*, *116*, 195–201. https://doi.org/10.1016/j.anbehav.2016.04.008

Beauchamp, G. (2019). Can scalar timing explain variability in scanning patterns? *Behavioural Processes*, *158*, 85–88. https://doi.org/10.1016/j.beproc.2018.11.006

Beauchamp, G. (2020). Predator attack patterns influence vigilance in a virtual experiment. *Behavioral Ecology and Sociobiology*, *74*(4), 49. https://doi.org/10.1007/s00265-020-02833-0

Bednekoff, P. A., & Lima, S. L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology & Evolution*, *13*(7), 284–287. https://doi.org/10.1016/S0169-5347(98)01327-5

Bednekoff, P. A., & Lima, S. L. (2002). Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance. *Journal of Avian Biology*, *33*(2), 143–149. https://doi.org/10.1034/j.1600-048X.2002.330204.x

Bertram, B. C. R. (1980). Vigilance and group-size in ostriches. *Animal Behaviour*, *28*, 278–286. https://doi.org/10.1016/S0003-3472(80)80030-3

Caraco, T. (1982). Flock size and the organization of behavioral sequences in juncos. *Condor*, *84*(1), 101–105. https://doi.org/10.2307/1367829

Carro, M. E., & Fernandez, G. J. (2009). Scanning pattern of greater rheas, *Rhea americana*: Collective vigilance would increase the probability of detecting a predator. *Journal of Ethology*, *27*(3), 429–436. https://doi.org/10.1007/s10164-008-0137-5

Carro, M. E., Fernandez, G. J., & Reboreda, J. C. (2011). Sequential predictability of the scanning behaviour of greater rheas. *Rhea Americana*. *Ethology Ecology & Evolution*, *23*(1), 27–39. https://doi.org/10.1080/03949370.2010.534326

Chang, C. C., Teo, H. Y., Norma-Rashid, Y., & Li, D. (2017). Predator personality and prey behavioural predictability jointly determine foraging performance. *Scientific Reports*, *7*, 40734. https://doi.org/10.1038/srep40734

Desportes, J.-P., Metcalfe, N. B., Brun, B., & Cezilly, F. (1990). Vigilant behaviour: Predictability or randomness? Spectral analysis of series of scan durations and their relationship with inter-scan intervals. *Ethology*, *85*(1), 43–50. https://doi.org/10.1111/j.1439-0310.1990.tb00384.x

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews of the Cambridge Philosophical Society*, *64*(1), 13–33. https://doi.org/10.1111/j.1469-185X.1989.tb00636.x

Farrington, J. D., & Zhang, X. L. (2013). The black-necked cranes of the Longbao National Nature Reserve, Qinghai, China current status and conservation issues. *Mountain Research and Development*, *33*(3), 305–313. https://doi.org/10.1659/Mrd-Journal-D-12-00134.1

Hart, A., & Lendrem, D. W. (1984). Vigilance and scanning patterns in birds. *Animal Behaviour*, *32*(4), 1216–1224. https://doi.org/10.1016/S0003-3472(84)80239-0

Home, C., Pal, R., Sharma, R. K., Suryawanshi, K. R., Bhatnagar, Y. V., & Vanak, A. T. (2017). Commensal in conflict: Livestock depredation patterns by free-ranging domestic dogs in the Upper Spiti Landscape, Himachal Pradesh, India. *Ambio*, *46*(6), 655–666. https://doi.org/10.1007/s13280-016-0858-6

Leslie, D. M., & Schaller, G. B. (2008). *Pantholops hodgssonii* (Artiodactyla: Bovidae). *Mammalian Species*, *817*, 1–13. https://doi.org/10.1644/817.1

Leslie, J., & David, M. (2010). *Procapra picticaudata* (Artiodactyla: Bovidae). *Mammalian Species*, *861*, 138–148. https://doi.org/10.7589/0090-3558-46.2.560

Li, Y., Yang, L., Luo, Y., Wu, Y., & Li, Z. (2018). Sequential vigilance is unpredictable in reproductive Black-necked Cranes. *Avian Research*, *9*(1), 44. https://doi.org/10.1186/s40657-018-0137-2

Li, Z. (2016). Datasets of vigilance behavior for three rare ungulates. *Biodiversity Science*, *24*(12), 1335–1340. https://doi.org/10.17520/biods.2016284

Li, Z., Che, Y., & Yang, L. (2017). Can sequential vigilance be predicted? *Behavioural Processes*, *145*, 81–85. https://doi.org/10.1016/j.beproc.2017.10.010

Lian, X. M., Su, J. P., & Zhang, T. Z. (2004). Grouping behavior of the Tibetan gazelle (*Procapra picticaudata*) in Hoh Xil region, China. *Chinese Biodiversity*, *12*(5), 488–493. https://doi.org/10.1007/BF02911033

Lima, S. L. (1987). Vigilance while feeding and its relation to the risk of predation. *Journal of Theoretical Biology*, *124*(3), 303–316. https://doi.org/10.1016/S0022-5193(87)80118-2

Luo, Y., Wang, L., Yang, L., Tan, M., Wu, Y., Li, Y., & Li, Z. (2018). Puppet resting behavior in the Tibetan antelope (*Pantholops hodgsonii*). *PLoS ONE*, *13*(12), e0204379. https://doi.org/10.1371/journal.pone.0204379

Luo, Y., Wang, L., Yang, L., Wang, X., Tan, M., & Li, Z. (2019). Inter- and intraspecific vigilance patterns of two sympatric Tibetan ungulates. *Journal of Mammalogy*. https://doi.org/10.1093/jmammal/gyz175

Pays, O., Blomberg, S. P., Renaud, P. C., Favreau, F. R., & Jarman, P. J. (2010). How unpredictable is the individual scanning process in socially foraging mammals? *Behavioral Ecology and Sociobiology*, *64*(3), 443–454. https://doi.org/10.1007/s00265-009-0860-0

Pays, O., Dubot, A. L., Jarman, P. J., Loisel, P., & Goldizen, A. W. (2009). Vigilance and its complex synchrony in the red-necked pademelon Thylogale Thetis. *Behavioral Ecology*, *20*(1), 22–29. https://doi.org/10.1093/beheco/arn110

Pays, O., & Jarman, P. J. (2008). Does sex affect both individual and collective vigilance in social mammalian herbivores: The case of the eastern grey kangaroo? *Behavioral Ecology and Sociobiology*, *62*(5), 757–767. https://doi.org/10.1007/s00265-007-0501-4

Pays, O., Renaud, P. C., Loisel, P., Petit, M., Gerard, J. F., & Jarman, P. J. (2007). Prey synchronize their vigilant behaviour with other group members. *Proceedings of the Royal Society B-Biological Sciences*, *274*(1615), 1287–1291. https://doi.org/10.1098/rspb.2006.0204

Podgórski, T., de Jong, S., Bubnicki, J. W., Kuijper, D. P. J., Churski, M., & Jędrzejewska, B. (2016). Drivers of synchronized vigilance in wild boar groups. *Behavioral Ecology*, *27*(4), 1097–1103. https://doi.org/10.1093/beheco/arw016

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, *38*(2), 419–422. https://doi.org/10.1016/0022-5193(73)90184-7

Roberts, G. (1994). When to scan: An analysis of predictability in vigilance sequences using autoregression models. *Animal Behaviour*, *48*(3), 579–585. https://doi.org/10.1006/anbe.1994.1277

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour*, *51*(5), 1077–1086. https://doi.org/10.1006/anbe.1996.0109

Scannell, J., Roberts, G., & Lazarus, J. (2001). Prey scan at random to evade observant predators. *Proceedings of the Royal Society B-Biological Sciences*, *268*(1466), 541–547. https://doi.org/10.1098/rspb.2000.1388

Schaller, G. B. (1998). *Wildlife of the Tibetan steppe*. Chicago: University of Chicago Press.

Studd, M., Montgomerie, R. D., & Robertson, R. J. (1983). Group-size and predator surveillance in foraging house sparrows (*Passer domesticus* L.). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, *61*(1), 226–231. https://doi.org/10.1139/z83-028

Wan, Y., Gao, Q., Lin, E., Li, Y. E, Qin, X., Jiang, C., … Li, W. (2006). Investigation of grassland growth and soil nutrient situation in Naqu prefecture of Tibet. *Pratacultural Science*, *23*(5), 10–14. https://doi.org/10.3969/j.issn.1001-0629.2006.05.003

Wang, K., You, Z., Xie, H., Zheng, T., & Li, Z. (2018). Vigilance behavior of *Cervus albirostris* during breeding season in Chaqingsongduo white-lipped deer national nature reserve. *Sichuan. Sichuan Journal of Zoology*, *37*(3), 305–310. https://doi.org/10.11984/j.issn.1000-7083.20180016

Yang, L., Cao, P., Li, Z., & Dang, W. (2019). Damage and control of free-ranging dogs in Tibet. *Journal of Biology*, *36*(2), 94–97. https://doi.org/10.3969/j.issn.2095-1736.2019.02.094

Yang, L. E., Luo, Y., Tan, M., Jiang, Z., Li, Z., & Mooring, M. (2018). Tick-defense grooming patterns of two sympatric Tibetan ungulates. *Journal of Zoology*, *307*(4), 242–248. https://doi.org/10.1111/jzo.12640

Young, J. K., Olson, K. A., Reading, R. P., Amgalanbaatar, S., & Berger, J. (2011). Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *BioScience*, *61*(2), 125–132. https://doi.org/10.1525/bio.2011.61.2.7

Zapata-Rios, G., & Branch, L. C. (2016). Altered activity patterns and reduced abundance of native mammals in sites with feral dogs in the high Andes. *Biological Conservation*, *193*, 9–16. https://doi.org/10.1016/j.biocon.2015.10.016

Zhang, F. F., & Jiang, Z. G. (2006). Mitochondrial phylogeography and genetic diversity of Tibetan gazelle (*Procapra picticaudata*): Implications for conservation. *Molecular Phylogenetics and Evolution*, *41*(2), 313–321. https://doi.org/10.1016/j.ympev.2006.05.024

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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