

25. Prokop, P. and Poreba, G. J., Soil erosion associated with an upland farming system under population pressure in northeast India. *Land Degrad. Dev.*, 2012, doi: 10.1002/ldr.2147.
26. Tiwari, B. K., Barik, S. K. and Tripathi, R. S., Biodiversity value, status, and strategies for conservation of sacred groves of Meghalaya, India. *Ecosyst. Health*, 1998, **4**, 20–32.
27. Bronk Ramsey, C., Bayesian analysis of radiocarbon dates. *Radiocarbon*, 2009, **51**, 337–360.
28. Balasubramanian, R., Metallurgy of ancient Indian iron and steel. In *Encyclopedia of the History of Science, Technology and Medicine in Non-Western Cultures* (ed. Selin, H.), Kluwer, The Netherlands, 2005, pp. 1608–1613.
29. Allen, W. J., Report on the Administration of the Cossyah and Jynteah Hill Territory, Calcutta, 1858, p. 176.
30. Hunter, W. W., *A Statistical Account of Assam*, Trubner&Co, London, 1879, vol. 2, pp. 1–490.
31. Prakash, B., Metallurgy of iron and steel making and blacksmithy in ancient India. *Indian J. Hist. Sci.*, 1991, **26**, 351–371.
32. Agarwal, D. P., *Ancient Metal Technology and Archaeology of South Asia*, Aryan Books International, New Delhi, 2000, p. 265.
33. Morton, G. R. and Wingrove, J., Constitution of bloomery slags: Part II: Mediaeval. *J. Iron Steel Inst.*, 1972, **210**, 478–488.
34. Gordon, R. B., Process deduced from ironmaking wastes and artefacts. *J. Archaeol. Sci.*, 1997, **24**, 9–18.
35. Pigott, V. C. (ed.), *The Archeometallurgy of the Asian Old World*, University of Pennsylvania Museum, Philadelphia, 1999, pp. 1–207.
36. Eerkens, J. W. and Lipo, C. P., Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. *J. Anthropol. Archaeol.*, 2005, **24**, 316–334.
37. Driem, G. V., Neolithic correlates of ancient Tibeto-Burman migrations. In *Archaeology and Language II: Archaeological Data and Linguistics Hypotheses* (eds Blench, R. and Spriggs, M.), Routledge, London, 1998, pp. 67–102.
38. Bellwood, P., *Prehistory of the Indo-Malaysian Archipelago*, University of Hawaii Press, Honolulu, 1997, pp. 1–385.
39. Higham, C. F. W., Mainland Southeast Asia from the Neolithic to the Iron Age. In *Southeast Asia. From Prehistory to History* (eds Glover, I. and Bellwood, P.), Routledge Curzon, London, 2004, pp. 41–67.
40. Bronson, B., Patterns in the Early Southeast Asian metals trade. In *Metallurgy, Trade and Urbanism in Early Thailand and Southeast Asia* (eds Glover, I. C., Suchitta, P. and Viliers, J.), White Lotus, Bangkok, 1992, pp. 63–114.
41. Wagner, D. B., The earliest use of iron in China. In *Metals in Antiquity* (eds Young, S. M. M. et al.), BAR International Series 792, Archaeopress, Oxford, 1999, pp. 1–9.
42. Gadgil, M., Joshi, N. V., Shambu Prasad, U. V., Manoharan, S. and Patil, S., Peopling of India. In *The Indian Human Heritage* (eds Balasubramanian, D. and Appaji Rao, N.), Universities Press, Hyderabad, 1997, pp. 100–129.
43. Misra, V. N., Prehistoric human colonization of India, *J. Biosci.*, 2001, **26**, 491–531.

ACKNOWLEDGEMENTS. This paper is the outcome of a bilateral project agreed between the Indian National Science Academy and Polish Academy of Sciences. We thank Prof. S. Singh and Dr H. J. Syiemlieh, Department of Geography, North-Eastern Hill University, Shillong for help in organizing our fieldwork.

Received 31 July 2012; revised accepted 6 February 2013

An adaptive system of vigilance in spotted deer (*Axis axis*) herds in response to predation

Ratna Ghosal^{1,*} and Arun Venkataraman²

¹Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

²WWF Malaysia, Petaling Jaya, Malaysia 47400

Spotted deer or chital (*Axis axis*), a major prey species in southern India, lives in large groups. To understand the benefits of group living, we carried out observations on chital herds under natural conditions. Individual and group vigilance showed a negative correlation with herd size, whereas the latter had a positive correlation with proportion of vigilant individuals. Furthermore, individual vigilance was negatively correlated with proportion of individuals vigilant and positively correlated with group vigilance. These results are explained in the context of a three-phase vigilance system, probably operative in the chital herd, under specified ecological conditions. We surmise that this system allows for adaptation to predation risk and has possibly co-evolved with the optimal hunting strategy of the predator.

Keywords: Chital, co-evolution, dhole, vigilance, predation.

‘ANTI-PREDATORY vigilance’ behaviour is often exhibited by prey species to decrease predation risk and to increase chances of survival¹. Prey animals constantly strike a balance between the amount of energy invested in vigilance and activities that enhance growth, reproduction and fitness². Solitary individuals are constrained as foraging and vigilance are mutually exclusive. The need to replenish energy reserves and the risks involved in foraging impose a trade-off on an individual³. A trade-off between the two decides where animals forage, the duration of foraging and the amount of time they invest in vigilance behaviour⁴.

An alternate strategy adopted by certain species is the formation of groups^{5,6}. During congregation, where all the individuals attempt to optimize within the same constraints, collective vigilance gives the individual an advantage of being able to spend more time in feeding without any drastic drop in the probability of survival as the tasks are shared⁶. A number of mechanisms may favour aggregation between conspecifics over solitary existence, including earlier detection of approaching predators (detection effect)^{1,7}, a greater proportion of time available for feeding because each individual needs to invest less in vigilance (‘Many-eyes’ hypothesis)¹, ‘confusion’ of attacking predators⁸ and when predators are limited in their ability to capture more than a single prey item per attack and simple numerical ‘dilution’ of risk^{4,9}.

*For correspondence. (e-mail: ratnaghosal@yahoo.com)

However, aggregation is not entirely beneficial; aggregated animals may compete for access to limited resources and larger groups of prey may also attract the predators¹⁰.

Predators also adopt specific strategies to counter such anti-predatory effects. They can either increase the number of predation attempts on larger and more conspicuous groups or resort to smaller groups for an assured reward of prey¹¹. Thus the anti-predatory vigilance behaviour is highly dynamic, being governed by several factors like group size, temperature, time of day, presence of predator, distance from cover, sex^{4,12}, group geometry¹³, dominance status¹⁴, presence of potential conspecific competitors¹⁵ and nutritional need or foraging pressure¹⁶.

Most studies on vigilance were carried out under controlled conditions¹⁷ or with artificial predators¹⁸. The results obtained from such studies may be largely influenced by experimental conditions and manipulations. Thus, how far or to what extent these results are applicable in natural/wild conditions is unknown. In this study we carried out observations on the antipredator vigilance behaviour of spotted deer or chital – the major prey species of carnivores in southern India^{19,20} under natural conditions. Chital usually form loose aggregations in large numbers, during foraging and resting^{21,22}. In the absence of social bonds, chital herds are attractive model systems to study, where presumably herd behaviour is mainly driven by the anti-predatory challenges. Thus in the current study, we attempted to understand the effect of herd size and proportion of vigilant individuals on individual as well as the group vigilance behaviour of the chital.

The study was conducted in the Mudumalai Sanctuary, Tamil Nadu, South India. The sanctuary lies to the north of the Nilgiri Plateau (11°30'–11°39'N and 76°27'–76°43'E) at an altitude of 850–1250 m amsl. The area supports large herbivores like elephant (*Elephas maximus*), gaur (*Bos gaurus*), sambar (*Rusa unicolor*), chital (*Axis axis*), wild pig (*Sus scrofa*) as well as major predators like tiger (*Panthera tigris*), leopard (*Panthera pardus*) and Asiatic wild dog (*Cuon alpinus*)²³.

In the study area three sites, namely Theppakadu, Hombetta and Jeydev Avenue were selected for observation of vigilance behaviour. The habitat types of these study site are mainly dry deciduous, moist deciduous forest patches with swampy grassland and dry thorn forest respectively. The study sites supported large herds of chital during early morning and late evening, when they aggregated for foraging.

The study area has a chital density of 28 individuals/sq. km (refs 23, 24) and it forms the major prey base. Chital frequent grasslands and open forests, seldom penetrating heavy jungles. They normally rest during the hotter part of the day and forage early in the morning and late in the afternoon when they form the largest groups^{25,26}.

Our observations indicate that chital aggregate in large herds late in the afternoon, in relatively open areas such as grasslands and river banks that remain cohesive right

through the night till mid-morning. During this period they are either resting or foraging. From mid-morning to late afternoon the herds disperse into thicker forests. They do rest during this period, but are often found foraging in smaller groups.

Chital have a tendency to form two kinds of associations²⁷: (i) buck herds or bachelor herd, and (ii) herds consisting of does with yearlings and small fawns.

The study was conducted for 4 months, from December 2003 to March 2004. Vigilance behaviour was studied by carrying out focal, group and instantaneous scans on foraging herds²⁸. Heads-up and tails-up behaviours were considered indicative that the animal was vigilant²¹. All behaviours were recorded as events. Observations were divided into sessions. The sessions lasted for 10 min or as long as the entire focal herd/individual was observable. Each session of observation comprised of one focal scan (5 min) and a group scan (5 min). To ensure independence across sampling sessions, each session began after an interval of 30 min from the preceding one. A series of instantaneous scans were performed between two sessions with an interval of 2 min between scans.

During all scans (focal, group and instantaneous) the maximum observable herd size corresponding to each observation was also recorded. All the observations were recorded during early morning, i.e. 0600–1100 h and late evening, i.e. 1600–1800 h. It was found through initial surveys that during these hours chital are out foraging in the greatest numbers. As it was desirable to see as many animals as possible, the observer used an elevated area. Observations from a distance were carried out using 7 × 50 wide-angle binoculars (Nikon, India) in an open habitat to ensure better visibility. Data were recorded only after ensuring that the herd was not disturbed by the approach of the observer. If domestic elephants or human beings appeared close to the herd, data recording was suspended until the cause of disturbance receded and the herd returned to its normal activity. A stopwatch was used to time all scans. Our observations were carried out on both the buck herds and the herds consisting of does, yearlings and fawns. Because there was a frequent fusion and fission between these two herd types, we did not include herd type as a factor in our subsequent analyses.

During group scan, a particular herd was observed for 5 min or as long as the focal herd size remained constant. The number of heads-up and tails-up exhibited by the focal herd was recorded. Group frequency (gr. freq.) is denoted as the frequency of total heads-up and tails-up recorded during each group scan.

During focal scan, a random individual was observed for 5 min or as long as the herd size of the observed individual remained constant. The number of heads-up and tails-up exhibited by the focal individual was recorded. Individual frequency (indiv. freq.) is denoted as the frequency of total heads-up and tails-up recorded during each focal scan.

A series of instantaneous scans were performed for a particular herd in intervals of 2 min. Instantaneous scans recorded the number of individuals (no. of indiv.) showing heads-up and tails-up. We calculated the proportion of individuals vigilant within herds as control and used this parameter for all subsequent analysis.

As the data followed a non-normal distribution, Spearman rank correlation (non-parametric statistics) test was used to obtain the correlation values between the given sets of parameters. All the analyses were carried out using Graph Pad Prism 5.0 software²⁹. The observations were carried out at three different locations within the sanctuary; thus the location itself may have an effect on the measured parameters (herd size, group frequency, individual frequency, no. of individuals) of the study. We also carried out a linear mixed effect (LME) model analysis (*R* version 2.7.1)³⁰, with location of chital group as a random effect, to analyse the relationship between the chosen categories. Log transformation was done for the measured parameters to follow a normal distribution and then incorporated in the LME model.

A total of 85 individuals were observed during focal scans and 56 groups were recorded for groups scans with a mean group composition of 14 (Table 1). Negative correlations of herd size (mean \pm SD, 13.7 \pm 12.14; n = 85) with individual frequency (mean \pm SD, 4.08 \pm 7.01; n = 85; Spearman r = -0.39, n = 56, P < 0.001) and group frequency (mean \pm SD, 0.39 \pm 0.49; n = 56; Spearman r = -0.71, n = 56, P < 0.001) were observed. A positive correlation of herd size with proportion of vigilant individuals (mean \pm SD, 0.19 \pm 0.2; n = 59; Spearman r = 0.3084, n = 59, P < 0.05) was also observed implying that as herd size increases, the proportion of vigilant individuals also increases. We further observed a negative correlation between individual frequency and proportion of individuals vigilant (Spearman r = -0.3419, n = 59, P < 0.001), though there was no correlation between group frequency and proportion of individuals vigilant.

We finally ran a correlation test between the group and individual frequencies to test the likelihood that individual animals were being influenced by group vigilance levels. Group frequency was found positively correlated with individual frequency (Spearman r = 0.3324, P < 0.05, n = 56). The results obtained from the LME model (positive or negative association and the corresponding P -values, P > 0.01) were similar to those obtained in the correlation analyses, thus confirming that location did not have a significant effect on the measured parameters of the study.

Table 1. Sampled individuals during the study period (December 2003–March 2004)

No. of focal individuals scanned	No. of groups scanned	Mean composition of maximum observable group size
85	56	14

The present results demonstrate the benefits of group living as an anti-predator strategy. We discuss the results in the form of three possible anti-predatory strategies (or phases) that the chital might adopt under natural conditions.

From our *ad libitum* field observations there appears to be a background level of vigilance within the herd where individuals react to random stimuli such as smells, sounds and movements from benign sources. Individuals are always vigilant to these stimuli and in larger herds this background level is high due to a higher proportion of vigilant individuals^{1,31}. Individuals possibly reassured by this high background level reduce time in vigilance to engage in other activities such as foraging³². We term this as ‘phase 1’ in the vigilance system of chital herds. This is indicated by the negative correlation of herd size with group and individual frequencies of vigilance behaviour, and a positive correlation with the proportion of individuals vigilant. Further support for phase 1 is provided by the absence of correlation and presence of negative correlation between proportion of individuals vigilant and group and individual vigilance frequencies respectively. Even though a high proportion of individuals are vigilant, they do not necessarily display a higher frequency of vigilance and group vigilance is thereby not altered. However, individual vigilance levels are significantly reduced, perhaps lending support to the ‘many-eyes hypothesis’¹.

The result that individual vigilance frequencies increase with group frequencies is perhaps evidence for a phase 2 in the system. Earlier observations establish that in response to less benign stimuli such as alarm calls from grey langur (*Semnopithecus entellus*), sambar (*Rusa unicolor*) and chital from other herds²⁴, there is a dramatic heightening of vigilance levels with a majority of individuals vigilant. The correlation between individual and group frequencies is likely to arise from this phenomenon. In the wild, phase 1 and phase 2 are two non-exclusive strategies that may operate simultaneously in the same herd. However, studies can be carried out to compare the behaviour of the herd during such sudden spurts of heightened vigilance (phase 2) with the background level of vigilance (phase 1) operative in the herd³³.

We have also observed what we believe may be a third phase in the system, in the presence of the predators³⁴. When hunting predators such as dholes are visible in close proximity to a herd, the entire herd bunches up into a tight group and all adult individuals have heads-up and tails-up. We surmise that at this stage principle within the geometry of selfish herds¹³ may be operational, but have no spatial data to support this. A study (A.V., unpublished) showed that repeated hunting by dholes on a particular herd, resulted in enhanced and sustained levels of vigilance within the herd reducing hunting success significantly. The pack was then forced to move onto other herds in other areas, which had not been hunted recently.

We speculate that this three-phase system allows for flexibility in modulating vigilance levels in response to the probability of predation. Such flexibility in the adoption of vigilance strategy is also prevalent in several other species like African herbivores², marmots (*Marmota flaviventris*)³⁵ and mustached tamarins (*Saguinus mystax*)³¹. We conclude that the above system may be optimal to allow a viable trade-off between being vigilant and foraging. Group living among chital allows for this trade-off. This system may have co-evolved with an optimal foraging strategy of dhole packs, but this may be only relevant for ecological conditions prevalent within the specific study area.

1. Lima, S. L., The influence of models on the interpretation of vigilance. In *Interpretation and Explanation in the Study of Animal Behavior: Explanation, Evolution and Adaptation* Boulder, West View Press, Colorado, 1990, vol. 2, pp. 246–267.
2. Periquet, S., Valeix, M., Loveridge, A. J., Madzikanda, H., Macdonald, D. W. and Fritz, H., Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Anim. Behav.*, 2010, **79**, 665–671.
3. Fairbanks, B. and Dobson, F. S., Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: dilution versus detection. *Anim. Behav.*, 2007, **73**, 115–123.
4. Hebblewhite, M. and Pletscher, D. H., Effects of elk group size on predation by wolves. *Can. J. Zool.*, 2002, **80**, 800–809.
5. Bertram, B. C. R., Vigilance and group size in ostriches. *Anim. Behav.*, 1980, **28**, 278–286.
6. Townsend, S. W., Zöttl, M. and Manser, M. B., All clear? Meerkats attend to contextual information in close calls to coordinate vigilance. *Behav. Ecol. Sociobiol.*, 2011, **65**, 1927–1934.
7. Pulliam, H. R., On the advantages of flocking. *J. Theor. Biol.*, 1973, **38**, 419–422.
8. Neill, S. R. St. J. and Cullen, J. M., Experiments on whether schooling by their prey affects hunting behaviour of cephalopods and fish predators. *J. Zool.*, 1974, **172**, 549–569.
9. Foster, W. A. and Treherne, J. E., Evidence of the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 1981, **293**, 466–467.
10. Pulliam, H. R., Pyke, G. H. and Caraco, T., The scanning behaviour of juncos: a game-theoretical approach. *J. Theor. Biol.*, 1982, **95**, 89–103.
11. Bertram, B. C. R., Living in groups: predators and prey. In *Behavioral Ecology: An Evolutionary Approach* (eds Krebs, J. R. and Davies, N. B.), Blackwell Scientific Publications, Oxford, 1978, pp. 64–96.
12. Elgar, M. A., Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.*, 1989, **64**, 13–33.
13. Hamilton, W. D., Geometry for the selfish herd. *J. Theor. Biol.*, 1971, **31**, 295–311.
14. Yaber, M. C. and Herrera, E. A., Vigilance, group size, and social status in capybaras. *Anim. Behav.*, 1994, **48**, 1301–1307.
15. Rose, L. M. and Fedigan, L. M., Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Anim. Behav.*, 1995, **49**, 63–70.
16. Burger, J., Safina, C. and Gochfeld, M., Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. *Acta Ethol.*, 2000, **2**, 97–104.
17. Dall, S. R. X., Kotler, B. P. and Bouskila, A., Attention, 'apprehension' and gerbils searching in patches. *Ann. Zool. Fenn.*, 2001, **38**, 15–23.
18. Leavesley, A. J. and Magrath, R. D., Communicating about danger: urgency alarm calling in a bird. *Anim. Behav.*, 2005, **70**, 365–373.
19. Karanth, K. U. and Sunquist, M. E., Prey selection by tiger, leopard and dhole in tropical forests. *J. Anim. Ecol.*, 1995, **64**, 439–450.
20. Venkataraman, A., Arumugam, R. and Sukumar, R., The foraging ecology of Dhole (*Cuon alpinus*) in Mudumalai Sanctuary, Southern India. *J. Zool.*, 1995, **237**, 543–561.
21. Schaller, G. B., *The Deer and the Tiger: A Study of Wildlife in India*, The University of Chicago Press, Chicago, 1984.
22. Guman, S., Shanker, K. and Jhala, Y. V., *A study of Vigilance Behaviour of Chital*, Lambert Academic Publishing, 978-3-8383-5803-1.
23. Varman, K. S. and Sukumar, R., The line transect method for estimating densities of large mammals in a tropical deciduous forest: an evaluation of models and field experiments. *J. Biosci.*, 1995, **20**, 273–287.
24. Ramesh, T., Snehlatha, V., Sanker, K. and Qureshi, Q., Food habits and prey selection of tigers and leopards in Mudumalai Tiger Reserve, Tamil Nadu, India. *J. Sci. Trans. Environ. Technol.*, 2009, **2**, 170–181.
25. Prasad, S., Chellam, R., Krishnaswamy, J. and Goyal, S. P., Frugivory of *Phyllanthus emblica* at Rajaji National Park, north-west India. *Curr. Sci.*, 2004, **87**, 1188–1190.
26. Sharatchandra, H. C. and Gadgil, M., On the time-budget of different life-history stages of chital (*Axis axis*). *J. Bombay Natl. Hist. Soc.*, 1980, **75**, 941–960.
27. Ramesh, T., Sanker, K., Qureshi, Q. and Kalle, R., Group size, sex and age composition of chital and sambar in a deciduous habitat of Western Ghats. *Mamm. Biol.*, 2012, **77**, 53–59.
28. Altmann, J., Observational study of behaviour sampling methods. *Behaviour*, 1974, **49**, 227–267.
29. Ghosal, R., Seshagiri, P. B. and Sukumar, R., Dung as a potential medium for inter-sexual chemical signaling in Asian elephants (*Elephas maximus*). *Behav. Process.*, 2012, **91**, 15–21.
30. Crawley, M. J., Mixed effects models. In *The R Book*. John Wiley, New Jersey, 2007, pp. 627–666.
31. Stojan-Dolar, M. and Heymann, E. W., Vigilance of mustached tamarins in single-species and mixed-species groups – the influence of group composition. *Behav. Ecol. Sociobiol.*, 2010, **64**, 325–335.
32. Blumstein, D. T., Evans, C. S. and Daniel, J. C., An experimental study of behavioural group size effects in tamar wallabies, *Macropus eugenii*. *Anim. Behav.*, 1999, **58**, 351–360.
33. Carro, M. E. and Fernandez, G. J., Scanning pattern of greater rheas, *Rhea americana*: collective vigilance would increase the probability of detecting a predator. *J. Ethol.*, 2009, **27**, 429–436.
34. Benhaiem, S. *et al.*, Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Anim. Behav.*, 2008, **76**, 611–618.
35. Bednekoff, P. A. and Blumstein, D. T., Peripheral obstructions influence marmot vigilance: integrating observational and experimental results. *Behav. Ecol.*, 2009, **20**, 1111–1117.

ACKNOWLEDGEMENTS. This work was supported by the Asian Nature Conservation Foundation, Bangalore, India. We thank the Forest Department of Tamil Nadu for providing permission to conduct research. We also thank Mr K. Siddhan and Mr P. Maran for their help and support in the field and (late) Mr Narendra Babu for valuable suggestions during the analyses of the data.

Received 4 May 2012; revised accepted 30 January 2013