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Keep calm and carry on: reactive indifference to predator encounters by a gregarious prey species

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Strategies that mitigate predation, whether proactive or reactive, can nevertheless impose significant 'nonconsumptive' costs on prey species. Here we used data from two wild vervet monkey, *Chlorocebus pygerythrus* groups to assess whether the detection of predators affected their subsequent behaviour to the detriment of their short-term foraging effort. Encounters with the three predator classes present at our study site were frequent and there was evidence that animals were more likely to shift to predator-focused vigilance, which was modulated by alarm call intensity, but not predator type, in the hour following detection. Nevertheless, and against expectation, there was no detectable shift in overall levels of vigilance, which remained low, interindividual distances, travel bearing and, consequently, effort put into foraging. We consider this surprising imperturbability by our study groups in the context of population group size, as our groups are large and have correspondingly lower levels of individual vigilance, as well as in terms of the constraints imposed by small, overlapping territories and frequent predator encounters. Finally, we advocate for increased consideration of the responses of the predators themselves to detection by their prey.

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Predation is a fundamentally powerful shaper of the morphology, social organization and individual behaviour of prey species. Notably, predation exerts its influence not only when it is successful but also via selection for prey strategies that reduce its success (Creel & Christianson, 2008; Taylor, 1984). These 'nonconsumptive' effects of predation are hypothesized to select for strategies that either mitigate risk proactively, by lowering the probability of encountering predators, or reactively, by reducing the likelihood of successful predation in the wake of such encounters (Creel, 2018).

In both cases, as Lima and Dill (1990) and, more recently, Creel (2018) have outlined, mitigation requires trade-offs, and therefore carries costs. In Creel's (2018) view, we might expect proactive responses, such as vigilance (Fortin et al., 2004) and habitat selection (Brown, 1999), to incur nutritional or energetic costs. In contrast, reactive responses, such as alarm calling and escape, should be more likely to incur direct physiological costs through the mobilizing of stress responses. However, reactive responses may also carry more proximate foraging costs if, for example,

predator encounters are followed by the persistence of elevated levels of vigilance, short-term habitat shifts, and corresponding adjustments to the activity budget. A better understanding of the consequences of reactive responses therefore requires an appreciation of the extent to which energetic costs might exacerbate any physiological consequences of predator encounters.

Among primates, as for other mammals (Isbell, 1994), predation is thought to be the main driver of gregariousness (van Schaik, 1983) and the subsequent facultative setting of group size (Hill & Lee, 1998). There is also good evidence that predation risk influences proactive responses, such as the trade-off between vigilance and foraging (Gaynor & Cords, 2012; Campos & Fedigan, 2014) and habitat selection (Cowlishaw, 1997; Willems & Hill, 2009; Makin et al., 2012; for representative reviews, see also Miller, 2002). Much less is known about reactive responses in the wake of nonconsumptive predator encounters, where only primate alarm calls have been well studied. Here, experimental evidence suggests that alarm calls serve to deter felid predators by causing them to move away from the calling group (Zuberbühler et al., 1999; Adams Kitchen, 2018; Isbell & Bidner, 2016), although the subsequent behaviour of the monkeys themselves has been far less well documented. Of those that have investigated such responses,

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Shultz et al. (2003) have shown that, in a mixed assemblage of African forest primates, alarm calls reduced both group spread and nearest-neighbour distances and increased travel and association rates in a manner that reduced foraging efficiency. In similar vein, van Schaik and Mitrasetia (1990) concluded that the presentation of a model python to long-tailed macaques, *Macaca fascicularis*, led to an increased cohesion that lasted for several days while Heymann (1987) noted that successful predation by an anaconda, *Eunectes* sp., led tamarin monkeys, *Saguinus mystax*, subsequently to avoid the predation site.

These representative observations (see also Boinski et al., 2000) underpin the following plausible and empirically testable predictions. In the wake of an encounter, group members will be more (1) cohesive and (2) vigilant. While coherence and vigilance may both be directly implicated in foraging efficiency, vigilance is also especially informative as an index of the general disquiet and disruptiveness associated with predator encounters. If so, (3) its levels should reflect both the type of predator and the intensity of the alarm calling it provokes. More particularly, (4) we anticipate an increase in environmental (or predator-directed) vigilance rather than vigilance directed at other group members (Allan & Hill, 2018). Following this, our central prediction (5) is that predator encounters will lead to a reduction in levels of foraging, regardless of whether this is associated with concerted evasive action (Shultz et al., 2003) or the increased socialization associated with stress (Cheney & Seyfarth, 2009). In all of this, where the sexes differ in size, we expect (6) the increased relative vulnerability of the smaller sex to drive more marked responses. Finally, (7) groups should adjust their travel bearing at the time of detection to reduce the likelihood of a second encounter in the short term. This prediction is based on available evidence indicating that mammalian predators back away after detection but perhaps not all that far (Isbell et al., 2018). This suggests that they will remain somewhere in the vicinity, and ahead of the monkeys' current direction of travel. If so, the most prudent response, if only to terrestrial, mammalian predators, would be to retreat and so reduce the probability of encountering this same predator again. Empirically, this should be detectable as larger turn angles than those recorded in the absence of interactions with predators (Henzi et al., 1998). The trade-off here would be the increased probability of revisiting areas through which the group had recently foraged, and, therefore, a reduction in foraging efficiency (Berger-Tal & Bar-David, 2015).

We tested these predictions with behavioural and ranging data from free-ranging, sexually dimorphic vervet monkeys, *Chlorocebus pygerythrus*, in South Africa. Vervets, both generally and at our study site, are subject to predation, or the risk of mortality, from three predator classes (mammalian, avian and snakes), the severity of which has shaped both their patterns of vigilance and the structure of their alarm calls (Struhsaker, 1967; Baldellou & Henzi, 1992; Enstam, 2007; Seyfarth et al., 1980). As the longer-term disruptive consequences of nonconsumptive predator encounters depend on the frequency with which these occur, we also provide information on encounter rate.

METHODS

Study Site and Subjects

The data for these analyses were collected from two habituated groups of vervet monkeys (RBM: $N_{\text{Total}} = 48$; $N_{\text{Males}} = 4-9$; $N_{\text{Females}} = 18$; RST: $N_{\text{Total}} = 72$; $N_{\text{Males}} = 12-14$; $N_{\text{Females}} = 23-26$) occupying semiarid riparian woodland in the Samara Game Reserve, Eastern Cape Province, South Africa (see Pasternak et al., 2013, for greater detail). Animals were fully habituated to human

presence and all adults were individually recognizable from natural markings.

Predators

In respect of the vervets, the study site held stable populations of both mammalian (cheetah, *Acinonyx jubatus*, caracal, *Caracal caracal*, black-backed jackal, *Canis mesomelas*) and avian (Verroux's eagle, *Aquila verreauxii*, Verroux's eagle owl, *Bubo lacteus*) predators. While monkeys alarm called at them, we have no evidence that they were ever targeted by cheetah. Nevertheless, predation was a common source of mortality (Ducheminsky et al., 2014) and both during the study period and subsequently we frequently observed caracal and jackal hunting and catching vervets (see also Van de Ven et al., 2013). Although not known to be vervet predators in east Africa (L. Isbell, personal communication 2019), it is likely that, in the absence of leopard, *Panthera pardus*, these two species have experienced mesopredator release (Ritchie & Johnson, 2009). Both the eagle and the eagle owl have been seen to hunt our vervets. In the absence of large constrictors, there is no snake predation on vervets at our site. There are, however, at least two large, venomous snake species (Cape cobra, *Naja nivea*, and puff adder, *Bitis arietans*) to which the vervets alarm call, and post mortem examination of several monkeys has identified snake bite as the cause of mortality.

Data Collection

The troops were followed by one or more observers for 10 h each study day over a 10-month period (February–November) in 2010 ($N_{\text{Total}} = 166$ days; $N_{\text{RBM}} = 82$ days; $N_{\text{RST}} = 84$ days). Scan samples (Altmann, 1974) were collected on all visible adult animals ($N_{\text{Total}} = 73$) across a 10 min window every 30 min ($N_{\text{Total}} = 9785$). We recorded the animal's identity, activity in one of four mutually exclusive categories (foraging, moving, resting, socializing), its location (ground under tree, ground in the open, tree), the identity and distance of its nearest adult neighbours (NND) and whether it was vigilant or not. Vigilance, a sustained gaze of more than 2 s in a nonfood-processing context, was classified as being directed at either another group member or members of other groups (social) or at some nonsocial environmental feature (environmental). The focus of the latter was often not identifiable but could include other species such as antelope, birds, baboons (not vervet predators in this population), as well as identified predators. A global positioning system (GPS) reading of the location of the estimated centre of mass of the group was taken at the beginning of each 30 min scan period. Predator alarm calling episodes, and their durations, were recorded on an all-occurrence basis, as was the group's location at the time of the incident. When sighted, we recorded the predator's identity. When we could not sight the predator, we used the alarm call type, together with the direction of vigilance, to allocate the animal eliciting calling to the three predator categories (mammalian, avian and snake). The monkeys also frequently alarm-called to antelope (principally kudu, *Tragelaphus strepsiceros*) when these ran past or burst from the undergrowth. We recorded these episodes as well, to use them as a reference category in analyses. We also used ad libitum data collection on the daily occurrence of alarm calls from these two troops over a later 4-year period (2015–2018), for which we have extensive and consistent data coverage, to assess the representativeness of the frequency of predator encounters recorded during this study. All data collection was conducted using electronic data loggers and proprietary software.

Statistical Analysis

We analysed our data in a Bayesian framework, using the ‘brms’ package (Bürkner, 2017; Stan Development Team, 2020) in R 3.5.0. (R Core Team, 2018), running four chains for 2000 iterations, with convergence of the chains ($R = 1.0$) confirmed in each case. We set weakly informative priors centred on zero (i.e. normal (0,1)) for the main effects. We used the ‘posterior predictive check’ (pp_check) and ‘leave one out’ (loo_compare) functions to determine model performance and allow model comparisons, respectively. For model comparisons we report the differences in the expected log predictive density (elpd). Posterior density distributions and other graphical outputs were generated with the ‘ggrridges’ (<https://wilkelab.org/ggrridges/index.html>) and ‘ggplot2’ (Wickham, 2009) packages. Although there is no necessity to set these as the limits (McElreath, 2016), we specified the 95% credible intervals (CI) in tables and plots, given their interpretative familiarity. Similarly, we used the ‘bayestestR’ package (Makowski et al., 2019) to generate ‘probability of direction’ (PD) estimates for the independent variables. These estimates, which range from 0.5 to 1.0, are generated from the posterior distributions and indicate the certainty of the direction (negative or positive) of an effect. They are interpretively helpful because they are closely correlated with commonly used frequentist P values (Makowski et al., 2019), with PD~97.5%, PD~99.5% and PD~99.95% corresponding to what Colquhoun (2014) considered to indicate weak, moderate and strong evidence for an effect, respectively. We present pd estimates in the Appendix model tables, and use them, along with the posterior probability density distributions, which indicate uncertainty about the estimated magnitude of the effect, to interpret outcomes.

We ran one linear mixed model (LMM), a series of generalized linear mixed models (GLMM) and a generalized additive mixed model (GAMM) to assess our predictions. In the first (m1), run as an LMM, we entered NND as the response variable with Occurrence (Before/After predator encounter), Sex and their interaction as the predictors. We also entered Activity, Location and Troop Identity as statistical controls to account for natural variation in interindividual distances. We entered animal ID and Date as crossed random effects (RE) to deal with clustering and repeated measures.

We considered the impact of predator encounters on vigilance via two GLMMs. In the first (m2a), we entered Vigilance (Yes/No) as the response variable and Occurrence (Before/After predator encounter), Sex and their interaction as the predictors, specifying the ‘bernoulli’ family and a logit-link function. We also entered NND, Activity, Location and Troop Identity as statistical controls. We specified animal ID and Date as crossed random effects (RE). We then reran this model (m2b) after expanding Vigilance to allow us to differentiate between Social and Environmental vigilance, and the absence of vigilance. To do so, we specified the ‘categorical’ family with a logit-link function. Note that it is not yet possible to estimate R^2 values for categorical models.

We addressed the question of the determinants of levels of postdetection vigilance (m3) through a GLMM by entering Vigilance (Social, Environmental, Not vigilant) as the response variable and Predator Type (Antelope, Land, Avian, Snake), Response Intensity (Duration of alarm calling) and Sex as predictors. We specified an interaction between Intensity and Sex. We entered Activity, Location, NND and Troop ID as statistical controls, and animal ID and Date as crossed REs. We specified the ‘categorical’ family, with a logit-link function.

To assess the influence of predator encounters on foraging effort (m4), we entered Foraging (Yes/No) as the response variable in a GLMM and Occurrence (Before/After predator encounter), Sex and their interaction as the predictors, specifying the ‘bernoulli’ family and a logit-link function. We also entered NND, Activity, Location

and Troop Identity as statistical controls. We specified animal ID and Date as crossed random effects (RE).

We present the full population level outcomes of models 1–4 as Appendix tables. In general, the relationships between the statistical controls and the response variables were unsurprising, allowing us to focus on the central predictors in the main text.

To determine whether interactions with predators were associated with a shift in the predicted direction of travel, we used the GPS data to estimate travel bearings in both the hour before and after the encounter (m5a). Subsequent assessment of positional accuracy and rejection of anomalous records allowed us to do so for 181 encounters. As we were not interested in absolute or cardinal direction, we established the change in bearing degree as a turn angle from 0^0 to 180^0 (for a full description of the approach, see Henzi et al., 1998). We then compared the observed data with 200 randomly drawn sets of bearings across two consecutive hours during which there had been no encounters with predators. We reran this model after restricting the comparison to responses to Land predators (m5b), as these were predicted to manifest the strongest adjustments in bearing.

The unusual distribution of turn angles is best described by a Gaussian mixture model (see Fig. 7 in the Results). However, neither a mixture nor any appropriate unimodal model could reproduce it adequately in posterior predictive checks. Consequently, we modelled the effect of predator interactions on changes in travel bearing as a GAMM. Our observed turn angles were marked as ‘observed’ (coded as 1) and we generated a second set of ‘control’ turning angles (coded as 0) by randomly sampling from a uniform distribution spanning the range from 0 to 180 degrees. As we had two types of turning angle in our observed data (i.e. those observed following a predator encounter and those that occurred in the absence of a predator encounter), we generated the equivalent number of predator-present and predator-absent turning angles for our control data set (i.e. we first generated a set of turning angles equivalent to the number of predator-present turning angles observed, and we then generated a set of angles equivalent to the number of predator-absent turning angles observed). This control data set thus acts as a reference distribution that allows us to estimate whether the distribution of observed values differs. As we were most interested in the shape of the probability of observing particular turn angles, and less interested in the absolute probability of detecting a 1, we set the density (i.e. number of zero values) such that the overall probability of observing a 1 was approximately 0.5. To model these 1s and 0s, we used a Bernoulli distribution with a logit link function, and a spline on the effect of the turn angle on the probability of getting a 1 or a 0. We specified Troop and Date as crossed random effects. We used a weakly informative prior centred on zero for the linear component of the spline (i.e. normal(0,1)), starting the model off by assuming that there was an equal probability of observing all turn angles. By fitting this model with a single spline for turn angle degree, and then comparing it to a second model where a spline was specified for each condition (Predator encounter: Yes/No), we were able to estimate whether the probability of observing specific turn angles was contingent on whether or not a predator had been encountered.

Finally, as it assists our subsequent interpretation of the outcomes, we compared individual levels of overall environmental vigilance in our two study groups with those recorded from a smaller group of vervets, occupying a different habitat and subject to different specific predators across the same three predator classes (WR: Windy Ridge Nature Reserve: $N_{\text{Males}} = 5$, $N_{\text{Females}} = 8$; data extracted from Table 1 in Baldellou & Henzi, 1992). To do so (m6), we specified the summed counts of environmental vigilance for each animal as the dependent variable in a Poisson regression,

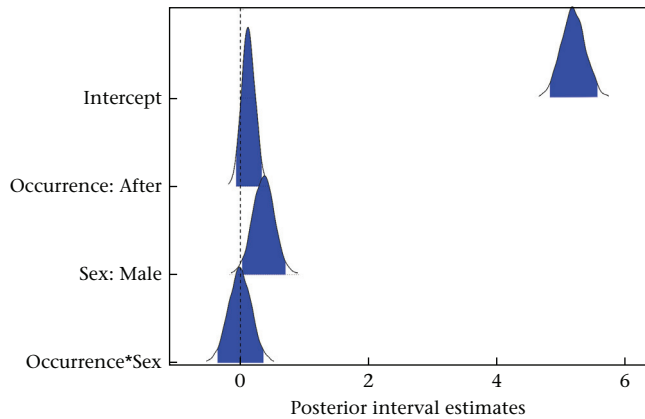


Figure 1. Posterior estimates of population level changes in Nearest-neighbour distance in relation to Occurrence (reference: Before a predator encounter), Sex (reference: Female) and the interaction of these two variables. Note that variables entered in the model principally as controls are not depicted. The blue fill is truncated to indicate the 95% credible interval.

with the total number of scans for each as the offset variable, and Troop ID as the predictor. Following Harrison (2014), we specified an observational level RE. We set the smallest group (WR) as the reference.

Ethical Note

All protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocol 0702). This study also adheres to the ASAB/ABS Guidelines for the Use of Animals in Research.

RESULTS

Encounter Frequency

We recorded 302 encounters with predators over 166 troop study days (RBM: $N_{\text{Days}} = 82$; $N_{\text{Encounters}} = 145$; daily mean = 1.79 ± 0.88 SD; range 1–4; RST: $N_{\text{Days}} = 84$;

$N_{\text{Encounters}} = 157$; daily mean = 1.87 ± 1.19 SD; range 1–5). Corresponding daily mean values for 2015–2018 were: RBM: 3.00 ± 1.83 SD; RST: 2.70 ± 1.68 SD. Of the 302 encounters, 16 were with antelope, 42 were with avian predators, 160 were with land predators and 84 were with snakes.

Does NND Decrease After Predator Encounters ($m1$)?

We found that predator encounters had little effect on subsequent NNDs (Fig. 1, Appendix Table A1; PD = 88.9%). While there was evidence that males generally maintained larger NNDs than females (PD = 98.25%), there was no differential response by the sexes to predator encounters (PD = 51.73%). All three posterior estimates were precise. The full model performed better than the RE-only model (elpd difference = 160.2 ± 18.6 SE) but accounted for relatively little variance in the data ($R^2_{\text{Marginal}}: 0.04 \pm 0.004$ SE; $R^2_{\text{Conditional}}: 0.08 \pm 0.005$ SE).

Is Vigilance Affected by Encounters With Predators ($m2a, m2b$)?

The mean proportion of scans per individual in which vigilance of either kind was recorded was 0.27 ± 0.11 SD (Environmental vigilance: mean = 0.07 ± 0.09 SD; Social vigilance: mean = 0.196 ± 0.08 SD).

When vigilance was considered simply as a binary category ($m2a$), we found good evidence (Fig. 2, Appendix Table A2) that vigilance increased in the wake of predator encounters (PD = 99.33%), that males were generally more vigilant than females (PD = 99.98%) and that the sexes responded differently (PD = 99.9%). Fig. 2b indicates that, relative to females, which became more vigilant, male vigilance declined after predator encounters, with the net effect that their subsequent levels of vigilance did not differ. All three posterior estimates were small and moderately precise. The full model performed better than the RE-only model (elpd difference = -1729.8 ± 47.3 SE) and accounted for a reasonable amount of the variance in the data ($R^2_{\text{Marginal}} = 0.35 \pm 0.006$ SE; $R^2_{\text{Conditional}} = 0.42 \pm 0.004$ SE).

With the model expanded to differentiate social from environmental vigilance ($m2b$; Fig. 3, Appendix Table A3), there was strong evidence that environmental (PD = 100%), but not social (PD = 52.3%), vigilance increased in the wake of predator encounters. Generally, the sex difference in vigilance could be attributed to

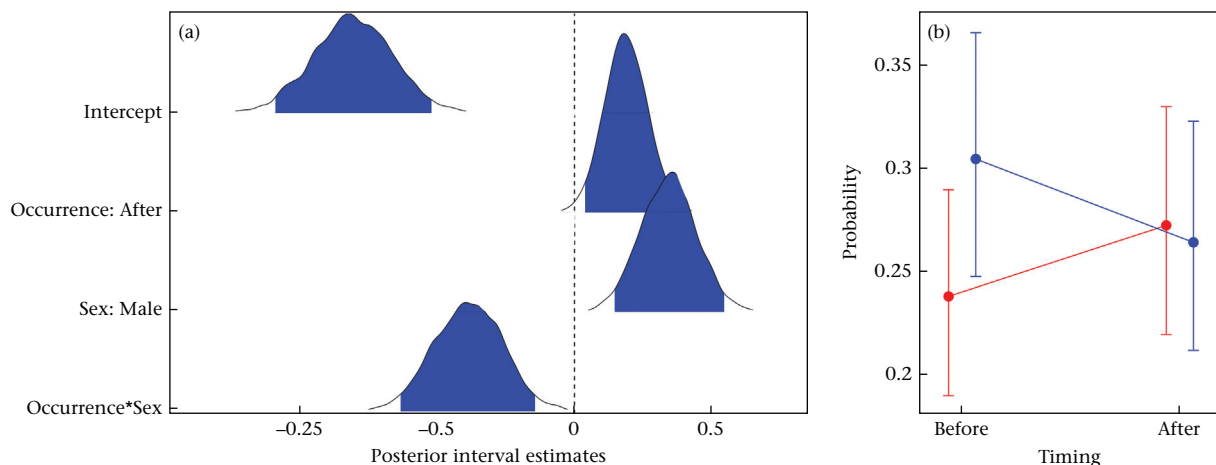


Figure 2. (a) Posterior estimates of population level changes in Vigilance (reference: Not vigilant) in relation to Occurrence (reference: Before a predator encounter), Sex (reference: Female) and the interaction of these two variables. Note that variables entered in the model principally as controls are not depicted. The blue fill is truncated to indicate the 95% credible interval, CI. (b) Predictive marginal means (\pm 95% CI) for the interaction between the occurrence of vigilance and the sex of the respondent (female: red; male: blue).

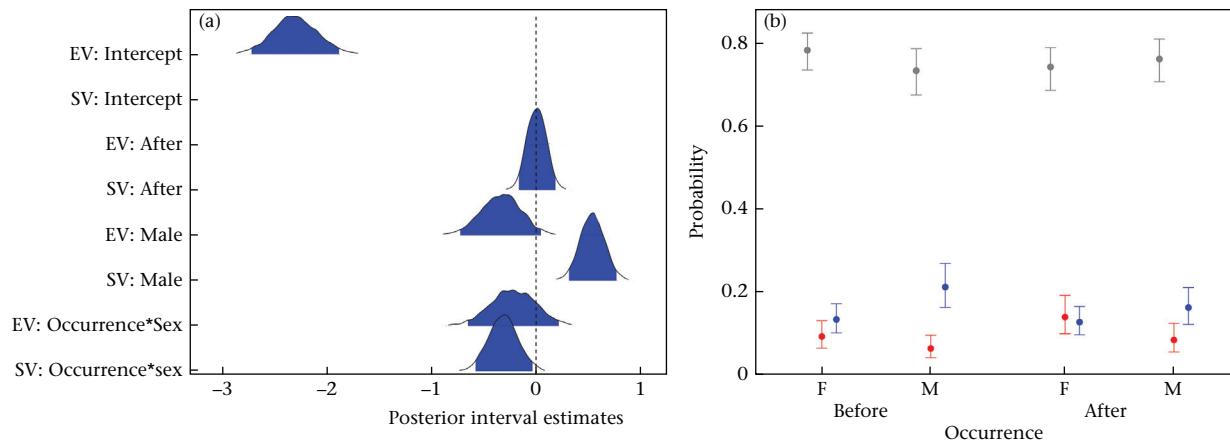


Figure 3. (a) Posterior estimates of population level changes in Environmental and Social vigilance (reference: Not vigilant) in relation to Occurrence (reference: Before a predator encounter), Sex (reference: Female) and the interaction of these two variables. Note that variables entered in the model principally as controls are not depicted. The blue fill is truncated to indicate the 95% credible interval, CI. (b) Predictive marginal means (\pm 95% CI) for the interaction between the occurrence of vigilance and the sex of the respondent in relation to the nature of the vigilance (Environmental vigilance: red; Social vigilance: blue; Not vigilant: grey).

a greater propensity for males to be socially vigilant (PD = 100%), with little indication of a meaningful sex difference in environmental vigilance, neither generally (PD = 96.62%) nor after predator encounters (PD = 83.08%). The overall increase in environmental vigilance after predator encounters, as well as the weaker interaction between occurrence, sex and social vigilance (PD = 98.8%), are therefore best interpreted (Fig. 3b) as reflecting slight increases in the relative allocation to environmental vigilance by both females and males, and a stronger reduction in the relative allocation to social vigilance by males in the aftermath of predator encounters. In this regard, Fig. 3b also highlights the important point that a lack of vigilance, which is overwhelmingly the case for both sexes, is not affected by predator encounters. In essence, then, the decomposition of vigilance into its constituent parts points to adjustments in the focus of ongoing vigilance, rather than to a generally heightened sense of risk.

Is vigilance responsive to predator type and response intensity (m3)?

The full model performed better than the RE-only model (elpd difference = -1106.9 ± 39.9 SE), providing weak evidence for an increase in environmental vigilance with increasing response intensity (PD = 97.7%) but no equivalent evidence for a corresponding decline in social vigilance (PD = 94.9%), nor for an interaction between sex and response intensity for either environmental (PD = 75.08%) or social (PD = 86.7%) vigilance (Figs. 4 and 5, Appendix Table A4). Relative to their response to antelope, the animals provided no indication (Fig. 5a) that they were more likely to be vigilant after avian (PD_{Environmental} = 54.77%; PD_{Social} = 87.62%) or land (PD_{Environmental} = 66.97%; PD_{Social} = 82.8%) predator encounters, or to snakes (PD_{Environmental} = 54.93%; PD_{Social} = 57.6%).

Do Predator Encounters Reduce Foraging Effort (m4)?

The short answer to this question is 'no' (Fig. 6, Appendix Table A5). The full model ($R^2_{\text{Marginal}} = 0.08 \pm 0.007$ SE; $R^2_{\text{Conditional}} = 0.12 \pm 0.006$ SE) performed better than the RE-only model (elpd difference = -365.7 ± 25.7 SE) but provided little support for a decline in foraging (PD = 61.15%). Nor, despite a general propensity for reduced foraging effort in males (99.98%), was there a detectable sex difference in foraging after predator encounters (PD = 95.85%).

Do Predator Encounters Increase Travel Bearing (m5)?

As is also evident from Fig. 7, which presents the observed bearings of travel, m5a provides no indication that predator encounters, in general, are associated with disproportionate changes in travel bearing (Appendix Table A6). The model with a spline by condition does slightly worse than the simple model with a spline only on turning angle (elpd difference = -1.7 ± 0.6 SE) and explains the same amount of variance ($R^2_{\text{Simple}} = 0.20$; $R^2_{\text{Spline}} = 0.21$). Rerunning the model for responses only to land predators (m5b) generates a very similar outcome (Appendix Table A7), with the simple model not performing detectably

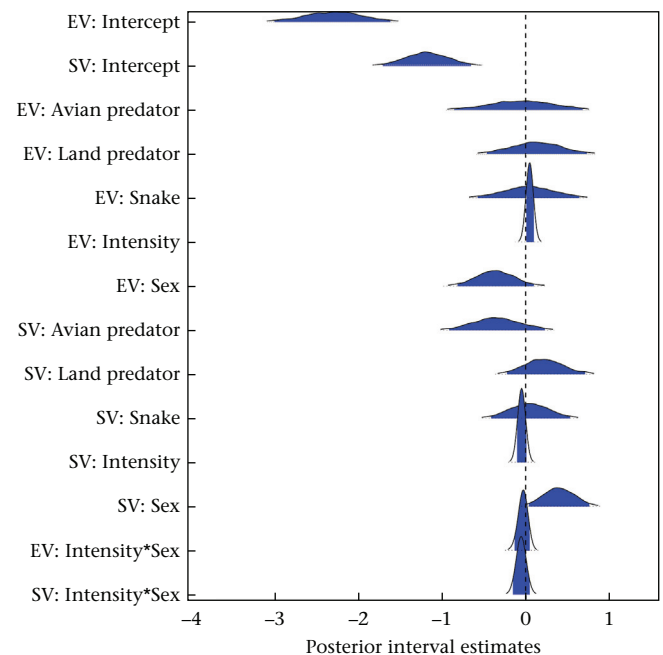


Figure 4. Posterior estimates of population level changes in Environmental and Social vigilance (reference: Not vigilant) in relation to Predator type (reference: Antelope), Intensity of the alarm calls (min) and Sex (reference: Female). We also specified an interaction between Intensity and Sex. Note that variables entered in the model principally as controls are not depicted. The blue fill is truncated to indicate the 95% credible interval.

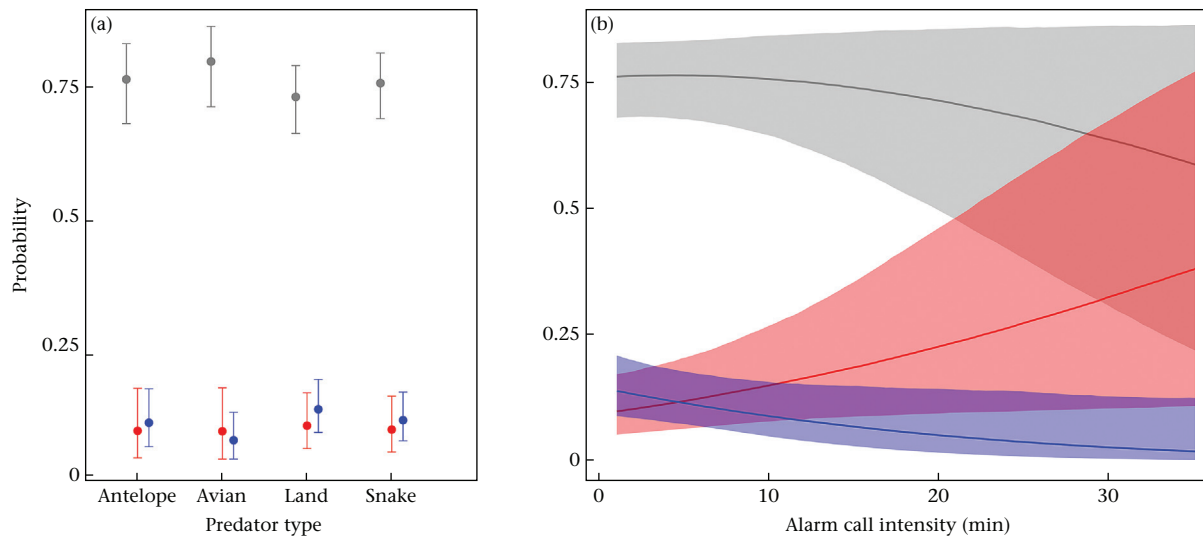


Figure 5. Predictive marginal means (\pm 95% credible interval) for the relationship between (a) Predator type and (b) Response intensity, and the likelihood of Environmental (red) or Social (blue) vigilance. Grey: Not vigilant.

worse than the model with a spline by condition (elpd difference = -1.2 ± 1.3 SE), and with each explaining the same amount of variation ($R^2_{\text{Simple}} = 0.19$; $R^2_{\text{Spline}} = 0.19$). In neither m5a nor m5b did the CIs suggest any directionality to the posterior distributions (pd range 61.45%–70.17%).

Is Vigilance Sensitive to Group Size (m6)?

Our model indicates that, relative to the smallest group (WR), individual vigilance declined with group size (Fig. 8, Appendix Table A8; $R^2_{\text{Marginal}} = 0.18$; $R^2_{\text{Conditional}} = 0.99$), corroborating the separate outcome for our two study groups, as specified in Table A3).

DISCUSSION

Aside from the alarm calling that initially alerted group members to the presence of a predator, our study animals offered little evidence that they subsequently adjusted their nearest-neighbour distances or their overall levels of vigilance in response to predator detection. They were similarly unaffected by encounters with the different predator classes, accommodating neither their vigilance nor their subsequent travel to account for the potential differences in risk posed by each. As a consequence, there was no meaningful short-term reduction in their ability to forage.

While there was no change in total levels of vigilance, its recalibration towards environmental scanning, together with weak evidence of its sensitivity to response intensity, makes it difficult to argue that the animals were simply oblivious to the prospect of any continuing or residual risk. A better conclusion might be that, rather than retaining no trace of the encounter, they were simply collectively unperturbed by it. This is reinforced by the fact that nonvigilance was the predominant state both before and after an encounter (Fig. 3b). As a practical side issue, our ability to detect appropriate changes in the focus of vigilance despite an absence of change in its overall levels confirms the value of differentiating social monitoring from environmental scanning, even though methodologically precise or unambiguous attribution may not be achievable (Allan & Hill, 2018).

The general indifference displayed by our vervets is surprising, given the animals' evolutionary, as indicated by the elaboration of

their alarm calls (Struhsaker, 1967), and current situational exposure to predation risk, as well as the comparative evidence from other studies of primates. Nevertheless, there are some readily testable possibilities that may account for this outcome.

Our study groups are considerably larger than the reported modal group size of ca. 20 for the species (Henzi et al., 2013), and is a feature of the population (Pasternak et al., 2013) that, inter alia, has been argued to account for their responses to predator alarm calls. These consist, in the main, of directing attention to the caller rather than initiating the active evasion that has been described for smaller groups elsewhere (Ducheminsky et al., 2014; Seyfarth et al., 1980). The relative equanimity to risk therefore extends back to the start of the encounter itself. In this context, being a member of a large group carries advantages, from earlier detection to the fact that most group members are at greater remove from the predator. This reduces the immediacy of risk, which, in concert with a small adjustment to the focus of vigilance, may provide sufficient cover to allow the animals to continue with their normal routine. Some

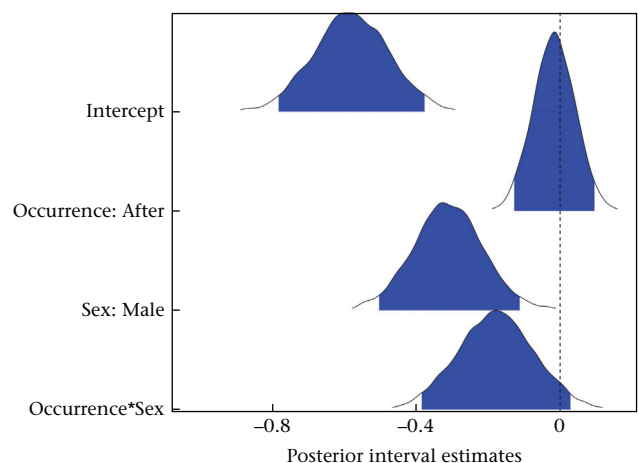


Figure 6. Posterior estimates of population level changes in Foraging (reference: Not foraging) in relation to its Occurrence (reference: Before a predator encounter), Sex (reference: Female) and the interaction of these two variables. Note that variables entered in the model principally as controls are not depicted. The blue fill is truncated to indicate the 95% credible interval.

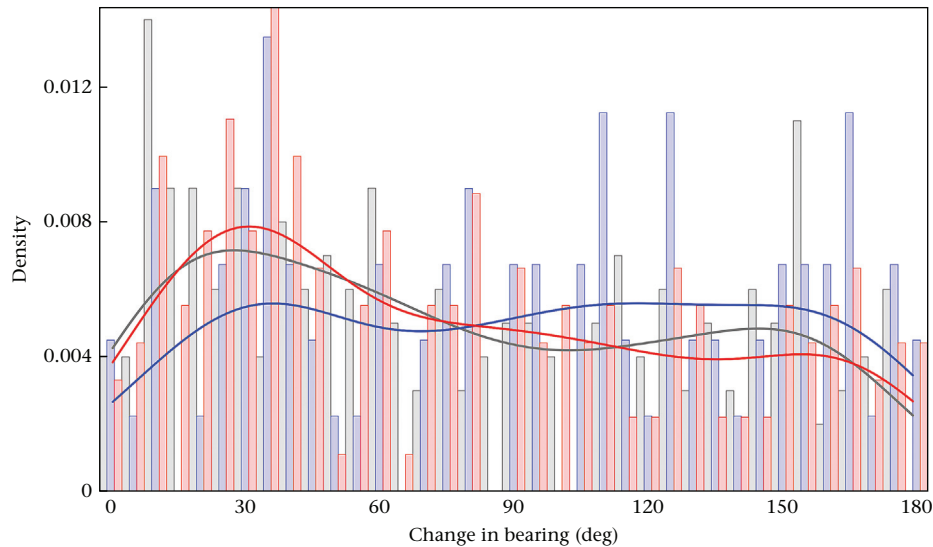


Figure 7. Kernel density estimates and underlying frequency distributions (scaled to density) of changes in the bearing of travel in the hour after all predator encounters (red line, red bars), terrestrial predator encounters (blue line, blue bars) and in the absence of encounters (grey line, grey bars).

sense that this might be so comes from the fact that we found a negative relationship between group size and overall environmental vigilance by adults in three groups from two populations, with the smallest group, from Windy Ridge, being distinctively more vigilant than the two larger ones (m4; Fig. 6). Assessing whether this is due to group size alone or is mediated by additional factors, such as specific predator identities, remains a task for the future. Similarly, any immediate evasive changes of direction by different individuals, if occurring at all, are likely to have been attenuated by the problems of coordinating large numbers of widely spaced group members. If so, they effectively cancel one another out and result in a short-term movement profile that is not distinguishable from one generated in the absence of predator encounters.

There are two other features of the study population and environment that may also play a role in determining the response to predators. First, these large groups occupy small territories (Pasternak et al., 2013) that overlap substantially with those of other groups (Dostie, n.d.), which may constrain their options, at least with respect to space use, since any short-term relocation is both unlikely to take them very far from either land or avian predators and more likely to increase their contact with neighbouring groups. Aggressive intertroop interactions are very frequent at our site, both during this study period (Freeman et al., 2012) and over the longer term (RBM: daily mean = 2.45 ± 1.79 SD; RST: daily mean = 2.13 ± 1.59 SD; Barrett & Henzi [n.d.]), and any disruptive consequences of these (LaBarge et al., 2020) would be exacerbated by an increase in contact frequency.

Second, the frequency of predator interactions may well structure the pattern of the response, especially if predators are encountered at a rate sufficiently high to mean that increased vigilance and evasion carry unmanageable costs. Our animals interacted with predators, across the short and long term, from between one to three times a day. This rate is at least four times higher than that recorded for vervets in Amboseli, Kenya (monthly daily mean = ca. 0.48 ± 0.22 SD, extracted from Fig. 4 in Hauser, 1988), which are the only comparative data to hand. While it is difficult to determine a priori what constitutes an encounter rate that is too high to respond to, it is reasonable, overall, to suggest that smaller groups, living at lower densities, and encountering

predators relatively infrequently, and possibly at closer distances (Ducheminsky et al., 2014), will be more likely to behave in ways that match theoretical expectation.

A counterpoint to the possibility that responses to predators are primarily situational is the argument that selection on gregarious prey species has resulted in alarm calls that, in and of themselves, serve as a deterrent to predators (Zuberbühler et al., 1999; Adams & Kitchen, 2018; Isbell & Bidner, 2016). To the extent to which these calls are effective at ending a hunting episode, at least by land or avian predators, this may be sufficient to allow resumption of normal behaviour in the short term. Predictively, one might expect that where alarm calls serve this purpose, group size would be less influential in determining the group's subsequent response.

Finally, as recent studies make clear, a better understanding of a prey species' responses to predators will benefit markedly from a better understanding of how this intersects with the behaviour of their particular predators (Courbin et al., 2016; Adams & Kitchen, 2018; Isbell & Bidner, 2016; Martin & Owen-Smith, 2016).

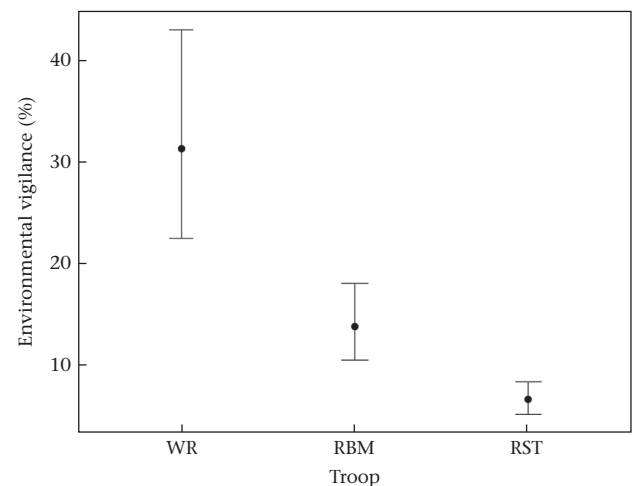


Figure 8. Predictive marginal means (\pm 95% credible interval) for the percentage of scans allocated to environmental vigilance by adults in three troops across two sites.

Author Contributions

S.P.H. and L.B. contributed to the study concept/design, data analysis, funding acquisition, supervision and the drafting and critical revision of the manuscript. T.B. contributed to data analysis, supervision and helped draft the manuscript. G.M.P. and N.J.F. contributed to data collection and the manuscript. M.J.D., S.K. and C.V. contributed to data analysis and drafting the manuscript. All authors approved the final version of the manuscript.

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Appendix

Table A1

Model 1: posterior estimates of population level changes in Nearest-neighbour Distance in relation to Occurrence (reference: Before predator detection), Sex (reference: Female) and their interaction

	Estimate	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept	5.18	0.19	4.82	5.56	1734	100.00
Occurrence (reference: Before)	0.13	0.11	-0.07	0.33	4320	88.90
Sex (reference: Female)	0.37	0.17	0.03	0.69	2568	98.25
Activity Forage (reference: Resting)	0.52	0.11	0.29	0.73	4339	100.00
Activity Move	0.98	0.12	0.74	1.22	4983	100.00
Activity Social	-1.80	0.15	-2.10	-1.51	4808	100.00
Location Open (reference: Ground)	0.48	0.15	0.20	0.76	6220	99.90
Location Tree	0.43	0.10	0.23	0.63	5581	100.00
Troop (reference: RBM)	-0.20	0.16	-0.52	0.12	2533	89.85
Occurrence*Sex	-0.01	0.18	-0.38	0.34	3680	51.73

Activity (reference: Resting), Location (reference: Ground) and Troop (reference: RBM) were entered as statistical controls. Subject ID and Date were entered as crossed random effects (RE). β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction. Interaction model performs better than RE-only model: elpd difference: RE-only: -160.2 ± 18.6 . R^2_{Marginal} : 0.04; $R^2_{\text{Conditional}}$: 0.08.

Table A2

Model 2a: posterior estimates of population level changes in vigilance (Y/N; reference: Not vigilant) in relation to Occurrence (reference: Before predator detection), Sex (reference: Female) and their interaction

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept	-0.81	0.15	-1.10	-0.51	779	100.00
Occurrence (reference: Before)	0.19	0.08	0.04	0.34	3731	99.33
Sex (reference: Female)	0.34	0.10	0.15	0.55	2929	99.98
Activity Forage (reference: Resting)	-1.21	0.08	-1.37	-1.07	5184	100.00
Activity Move	-0.87	0.08	-1.04	-0.72	5724	100.00
Activity Social	9.00	1.34	7.01	12.17	2610	100.00
Nearest-neighbour Distance	-0.05	0.01	-0.06	-0.03	6139	100.00
Location Open (reference: Ground)	0.43	0.10	0.23	0.62	5231	100.00
Location Tree	0.07	0.07	-0.07	0.21	4860	83.45
Troop (reference: RBM)	-0.09	0.10	-0.29	0.10	2460	82.78
Occurrence*Sex	-0.39	0.12	-0.63	-0.14	3352	99.90

Activity (reference: Resting), Nearest-neighbour distance, Location (reference: Ground) and Troop (reference: RBM) were entered as statistical controls. Subject ID and Date were entered as crossed random effects. β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction. R^2_{Marginal} : 0.35; $R^2_{\text{Conditional}}$: 0.42.

Table A3

Model 2b: posterior estimates of population level changes in vigilance (reference: Not Vigilant) in relation to Occurrence (reference: Before predator detection), Sex (reference: Female) and their interaction

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept: Environmental vigilance (EV)	-2.30	0.22	-2.73	-1.90	1462	100.00
Intercept: Social vigilance (SV)	-1.23	0.17	-1.56	-0.90	998	100.00
EV: Occurrence (Reference: Before)	0.47	0.11	0.25	0.70	4506	100.00
EV: Sex (Reference: Female)	-0.34	0.19	-0.73	0.03	2689	96.62
EV: Forage (Reference: Resting)	-1.74	0.12	-1.98	-1.50	5366	100.00
EV: Move	-1.64	0.15	-1.95	-1.35	5680	100.00
EV: Social	4.61	1.35	2.62	7.97	1382	100.00
EV: Nearest-neighbour distance	0.02	0.01	0.00	0.04	6474	99.33
EV: Open (Reference: Ground)	1.11	0.15	0.80	1.41	5460	100.00
EV: Tree	0.71	0.12	0.48	0.94	5602	100.00
EV: Troop (Reference: RBM)	-0.73	0.17	-1.07	-0.40	2629	100.00
EV: Occurrence*Sex	-0.21	0.22	-0.64	0.20	3625	83.08
SV: Occurrence (Reference: Before)	0.01	0.09	-0.17	0.19	3924	52.30
SV: Sex (Reference: Female)	0.54	0.12	0.32	0.77	3272	100.00
SV: Forage (Reference: Resting)	-0.92	0.09	-1.10	-0.75	4368	100.00
SV: Move	-0.54	0.09	-0.72	-0.36	4882	100.00
SV: Social	9.70	1.32	7.84	13.05	1440	100.00
SV: Nearest-neighbour distance	-0.11	0.01	-0.13	-0.09	6981	100.00
SV: Open (Reference: Ground)	0.14	0.11	-0.08	0.37	4610	89.48
SV: Tree	-0.26	0.09	-0.42	-0.10	5591	99.88
SV: Troop (Reference: RBM)	0.16	0.12	-0.08	0.39	2653	91.27
SV: Occurrence*Sex	-0.32	0.14	-0.61	-0.04	3434	98.80

Activity (reference: Resting), Nearest-neighbour distance, Location (reference: Ground) and Troop (reference: RBM) were entered as statistical controls. Subject ID and Date were entered as crossed random effects. β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction.

Table A4

Model 3: posterior density estimates of population level changes in environmental and social vigilance (reference: Not vigilant) in relation to Predator Type (reference: Antelope), Alarm call intensity (min) and Sex (reference: Female)

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept: Environmental vigilance (EV)	-2.30	0.35	-3.00	-1.62	2307	100.00
Intercept: Social vigilance (SV)	-1.18	0.27	-1.71	-0.65	2435	100.00
EV: Avian predator (reference: Antelope)	-0.06	0.39	-0.86	0.68	2196	54.77
EV: Land predator	0.13	0.30	-0.46	0.73	2037	66.97
EV: Snake	0.04	0.31	-0.58	0.63	2148	54.93
EV: Response intensity	0.05	0.02	0.00	0.10	2483	97.70
EV: Sex (reference: Female)	-0.36	0.23	-0.82	0.10	3407	94.35
EV: Forage (reference: Rest)	-1.68	0.16	-2.01	-1.36	5143	100.00
EV: Move	-1.84	0.20	-2.24	-1.45	5899	100.00
EV: Social	25.39	14.45	5.18	58.14	1073	100.00
EV: Open (reference: Ground)	1.18	0.20	0.78	1.58	5027	100.00
EV: Tree	0.75	0.16	0.45	1.07	4746	100.00
EV: Nearest-neighbour distance	0.04	0.01	0.01	0.06	6273	99.72
EV: Troop (reference: RBM)	-0.81	0.19	-1.20	-0.43	3520	100.00
EV: Intensity*Sex	-0.03	0.05	-0.13	0.05	3631	75.08
SV: Avian predator (reference: Antelope)	-0.34	0.29	-0.92	0.23	2677	87.62
SV: Land predator	0.22	0.23	-0.22	0.71	2429	82.80
SV: Snake	0.05	0.24	-0.41	0.53	2414	57.60
SV: Response intensity	-0.05	0.03	-0.11	0.01	3756	94.90
SV: Sex (reference: Female)	0.40	0.19	0.03	0.76	3092	98.22
SV: Forage (reference: Rest)	-0.96	0.13	-1.22	-0.70	5835	100.00
SV: Move	-0.77	0.14	-1.03	-0.50	4325	100.00
SV: Social	30.94	14.44	10.61	63.69	1072	100.00
SV: Open (reference: Ground)	0.07	0.17	-0.26	0.39	4748	65.90
SV: Tree	-0.38	0.12	-0.62	-0.15	5261	99.95
SV: Nearest-neighbour distance	-0.08	0.01	-0.11	-0.06	7772	100.00
SV: Troop (reference: RBM)	0.18	0.15	-0.11	0.47	2833	88.42
SV: Intensity*Sex	-0.05	0.05	-0.15	0.04	3254	86.70

We specified an interaction between Intensity and Sex. Activity (reference: Resting), Nearest-neighbour distance, Location (reference: Ground) and Troop (reference: RBM) were entered as statistical controls. Subject ID and Date were entered as crossed random effects. β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction. The Interaction model performs better than RE-only model: elpd difference: RE-only: -1106.9 ± 39.9 .

Table A5

Model 4: posterior density estimates of population level changes in Foraging (Y/N; reference: Not foraging) in relation to Occurrence (reference: Before), Sex (reference: Female) and their interaction

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept	-0.58	0.11	-0.80	-0.38	1595	100.00
Occurrence (reference: Before)	-0.02	0.06	-0.13	0.10	4984	61.15
Sex (reference: Female)	-0.31	0.10	-0.50	-0.12	2728	99.98
Environmental vigilance (reference: Not vigilant)	-1.18	0.11	-1.40	-0.96	5703	100.00
Social vigilance	-1.59	0.08	-1.74	-1.45	8221	100.00
Nearest-neighbour distance	0.00	0.01	-0.01	0.02	9339	79.72
Location: Open (reference: Ground)	0.43	0.08	0.28	0.59	6552	100.00
Location: Tree	0.47	0.05	0.37	0.58	6045	100.00
Troop (reference: RBM)	-0.09	0.09	-0.27	0.10	2060	83.33
Occurrence*Sex	-0.18	0.10	-0.38	0.03	4490	95.85

Vigilance (reference: Not vigilant), Nearest-neighbour Distance, Location (reference: Ground) and Troop (reference: RBM) were entered as statistical controls. Subject ID and Date were entered as crossed random effects (RE). β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction. R^2_{Marginal} : 0.08; $R^2_{\text{Conditional}}$: 0.12. The full Binary Forage model performs better than the RE-only model: elpd difference: RE-only: -365.7 ± 25.7 .

Table A6

Model 5a: a comparison of changes in travel direction in the absence of predator encounters (Control) to those after encounters with predators (Predator detection)

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept	0.48	0.62	-0.91	1.91	911	87.42
Control	-0.50	0.97	-2.32	1.49	2623	70.17
Predator detection	-0.30	0.96	-2.12	1.60	2773	62.92

β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction. The Simple model performs better than the Spline model: elpd difference: -1.7 ± 0.6 . R^2_{Simple} : 0.20; R^2_{Spline} : 0.21.

Table A7

Model 5b: a comparison of changes in travel direction in the absence of predator encounters (Control) to those after encounters with terrestrial predators (Land predator detection)

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept	0.28	0.61	−1.12	1.57	1.00	78.47
Control	−0.38	0.96	−2.16	1.57	1.00	65.8
Land predator detection	−0.26	0.87	−1.94	1.44	1.00	61.45

β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction. The two models performed similarly (elpd difference_{SIMPLE}: -1.2 ± 1.3). R^2_{Simple} : 0.19; R^2_{Spline} : 0.19.

Table A8

Model 6: posterior estimates of the population level effects of Location (reference: Windy Ridge) and the proportion of scans for which the subject was environmentally vigilant

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept	1.17	0.17	0.85	1.49	1346	100
Troop (RBM)	−0.81	0.21	−1.21	−0.40	1527	100
Troop (RST)	−1.54	0.20	−1.94	−1.14	1548	100

β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction.