



## Research

**Cite this article:** Stears K, Schmitt MH, Wilmers CC, Shrader AM. 2020 Mixed-species herding levels the landscape of fear. *Proc. R. Soc. B* **287**: 20192555. <http://dx.doi.org/10.1098/rspb.2019.2555>

Received: 1 November 2019

Accepted: 7 February 2020

**Subject Category:**

Behaviour

**Subject Areas:**

behaviour, ecology

**Keywords:**

herding behaviour, predation, social information, vigilance, zebra

**Author for correspondence:**

Keenan Stears

e-mail: [keenanstears@ucsb.edu](mailto:keenanstears@ucsb.edu)

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4860606>.

# Mixed-species herding levels the landscape of fear

Keenan Stears<sup>1,2,3</sup>, Melissa H. Schmitt<sup>2,3,4</sup>, Christopher C. Wilmers<sup>5</sup> and Adrian M. Shrader<sup>2,6</sup>

<sup>1</sup>Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA

<sup>2</sup>School of Life Sciences, University of KwaZulu-Natal, Scottsville 3209, South Africa

<sup>3</sup>South African Environmental Observation Network, Ndlovu Node, Phalaborwa 1390, South Africa

<sup>4</sup>Department of Ecology and Evolutionary Biology, and <sup>5</sup>Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA

<sup>6</sup>Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0028, South Africa

KS, 0000-0003-1012-5838; MHS, 0000-0002-5544-7673; CCW, 0000-0003-2063-1478; AMS, 0000-0002-6451-6132

Prey anti-predator behaviours are influenced by perceived predation risk in a landscape and social information gleaned from herd mates regarding predation risk. It is well documented that high-quality social information about risk can come from heterospecific herd mates. Here, we integrate social information with the landscape of fear to quantify how these landscapes are modified by mixed-species herding. To do this, we investigated zebra vigilance in single- and mixed-species herds across different levels of predation risk (lion versus no lion), and assessed how they manage herd size and the competition–information trade-off associated with grouping behaviour. Overall, zebra performed higher vigilance in high-risk areas. However, mixed-species herding reduced vigilance levels. We estimate that zebra in single-species herds would have to feed for approximately 35 min more per day in low-risk areas and approximately 51 min more in high-risk areas to compensate for the cost of higher vigilance. Furthermore, zebra benefitted from the competition–information trade-off by increasing the number of heterospecifics while keeping the number of zebra in a herd constant. Ultimately, we show that mixed-species herding reduces the effects of predation risk, whereby zebra in mixed-species herds, under high predation risk, perform similar levels of vigilance compared with zebra in low-risk scenarios.

## 1. Introduction

Predators can influence populations, communities and, ultimately, ecosystem function through the combination of consumptive and non-consumptive effects [1,2]. To understand the effects of predation risk and fear on prey species, these concepts have been developed into a model that represents relative levels of perceived predation risk across a landscape (i.e. landscape of fear [3]). By using social information to obtain more accurate information about the presence/location of a predator, prey species can mitigate the effects of predation risk, thereby, influencing the landscape of fear. Social information is information gleaned from observing the positions or behaviours of other animals including both heterospecifics or conspecifics (e.g. signals and cues [4,5]). It is well documented that social information gained through mixed-species herding can reduce predation risk [6,7]. Because of the effects of mixed-species herding on the landscape of fear, these two concepts are intimately linked. However, to our knowledge, no study has quantified how landscapes of fear in different areas varying in predation risk (e.g. high risk versus low risk) are modified by mixed-species herding. Thus, the current paradigm fails to incorporate this critical aspect of reducing predation risk. Understanding this relationship is critical because the behavioural response of prey species to predators can have

substantial cascading effects within ecosystems and can constrain species coexistence and biodiversity maintenance [8,9].

Predation is a selective force, thus behavioural decisions made by prey species to avoid predation can greatly alter their probability of survival. Social information regarding predators can elicit important collective behaviours such as grouping and group vigilance [10]. While *per capita* risk can vary inversely with group size (i.e. dilution and detection; see [7]), competition for resources can increase with the number of individuals in a herd [11]. Frequently, predator–prey models focus on single pairs of predator and prey species (e.g. mule deer–puma [12]), whereas landscapes typically contain multiple prey species and multiple predators that pose different levels of threat [13]. Thus, it is important to evaluate responses to perceived risk in the context of the diverse, multispecies assemblages within which an individual lives [14]. For example, an individual could attempt to reduce risk by grouping with conspecifics, or by joining a group that contains both conspecific and heterospecific individuals. Not only does social information influence grouping behaviour as a whole but it also affects how individuals select herd members. For example, in some species, individuals select for the quality rather than the quantity of group members [7]. However, the value and reliability of information from heterospecifics is contingent on whether they share a common predator (i.e. they are diluting partners [7,15]).

In addition, different prey species often have different sensory modalities and therefore differ in their ability to detect shared predators [14]. As a result, valuable information about predation risk can be gleaned from alarm calls [15] and body posture [16] by heterospecific herd mates. Thus, by forming mixed-species groups, individuals can obtain a more comprehensive assessment of threat, and at times even better information about predation risk from a heterospecific than from a conspecific [16]. A species that provides information that is disproportionately more valuable than the information from other members of a mixed herd is considered a keystone informant (*sensu* [17]). Consequently, social information about predation risk plays an important role in vigilance and grouping behaviour, both of which can ultimately influence individual fitness [18,19], as well as population and community dynamics through indirect effects [17].

A major cost associated with grouping behaviour, and larger herd sizes, is increased competition for resources [11]. Competition is likely to be greatest between conspecifics compared with heterospecifics because of the potential for greater niche overlap [20]. Thus, if social information regarding predation risk is an important driver for grouping and vigilance behaviour, then changes in predation risk are likely to influence the behaviourally mediated responses of prey species because of the inherent competition–information trade-off associated with herding [21]. This means that grouping behaviour observed across different levels of risk should reflect trade-offs being made by individuals balancing potential costs of competition (increased herd size) with the benefits of predator detection [22]. Therefore, under high levels of predation risk, we would expect prey to form large herds by ideally herding with heterospecifics because of better predator detecting abilities and reduced competition compared with herding with conspecifics. By contrast, we would expect that predator removal would result in a

collapse of anti-predator responses (e.g. [23]) and the breakdown of larger herd formations in an attempt to reduce potential competition [11].

Plains zebra (*Equus quagga*) frequently form mixed-species associations and use herding behaviour to obtain social information about perceived predation risk [7,16,24]. Thus, to better understand the potential of social information to modulate the landscape of fear of prey species, we investigated zebra vigilance in single- and mixed-species herds across different levels of predation risk based on the presence or absence (high risk versus low risk) of lions (*Panthera leo*). First, we measured zebra vigilance, as a proxy for the effectiveness of their anti-predator grouping behaviours (i.e. single- versus mixed-species herding) [7], to determine if mixed-species herding elicited any potential benefits across different levels of predation risk. Then, we quantified the difference in vigilance as a function of grouping behaviour and predation risk to determine if mixed-species herding can lower vigilance to similar levels obtained under low-risk scenarios (i.e. level the landscape of fear). We then assessed how zebra grouping behaviour influenced herd size and the competition–information trade-off across different levels of predation risk. Finally, we model and discuss the implications of the investment cost of anti-predator responses to predation risk on prey species and equate these investment costs to time lost to foraging.

## 2. Methods

We conducted fieldwork in four protected areas in South Africa that have varying levels of predation risk for zebra based on the presence or absence of lions during August–September (late dry season) in 2011 (three sites) and 2015 (one site). Lions are the main predator of zebra and approximately 15% of lion kills comprise zebra [25]. We deemed Hluhluwe–iMfolozi Park (HiP) and Kruger National Park (KNP) as ‘high risk’ because of the presence of lions. Both sites have an intact large predator guild, which consists of similar densities of lion (HiP: 13 lions/100 km<sup>2</sup> [26] and KNP: 8 lions/100 km<sup>2</sup> [27]) as well as secondary predators that include leopard (*Panthera pardus*), African wild dog (*Lycan pictus*), cheetah (*Acinonyx jubatus*) and spotted hyena (*Crocuta crocuta*)—all of which also can prey on zebra, although they are not a preferred prey item [28–31]. Ithala Game Reserve and the Cape Vidal section of the Isimangaliso Wetland Park were considered to be ‘low risk’ because they lacked lions altogether, although they do have populations of both leopard and spotted hyena.

To minimize spatial and temporal differences in perceived predation risk, we limited observations to herds feeding in savannas and only collected data 2 h after first light and 2 h before last light [7,16]. All observations occurred from a stationary vehicle using binoculars. To avoid potential behavioural changes due to vehicles, we only collected data when no other vehicles were present and when the zebra were more than 20 m from the road. We focused our observations in open-canopy savanna habitats, which had approximately 40–60% tree cover. These open-canopy savannas are widely represented across all of our study sites. While differences in percentage tree cover could influence local vigilance levels, we were more interested in approximating vigilance at the landscape scale (i.e. open-canopy savannas across our study sites).

Schmitt *et al.* [7] found that predator detection, rather than dilution effects, was the main factor in reducing zebra vigilance in small and medium herd sizes (2–30 individuals). Furthermore, these smaller herds occurred more frequently at the landscape scale (for more information, see [7]). Thus, we limited data

collection to herd sizes of fewer than 30 individuals because we were more interested in the active use of social information to avoid predators (detection) rather than the passive use of dilution to minimize predation risk. Additionally, we only collected data from mixed-species herds comprised of species that share lions as a common predator. Thus, our mixed-species herds comprised of zebra and one or more of the following ungulate prey species: wildebeest (*Connochaetes taurinus*; partial competitor), kudu (*Tragelaphus strepsiceros*; non-competitor) and waterbuck (*Kobus ellipsiprymnus*; partial competitor). All of these species were present across all of our study sites and are either preferred prey items of lions (wildebeest) or are eaten in relation to their availability (kudu, waterbuck) [25]. Importantly, because all of these species share a common predator, they are all able to reduce predation risk via both dilution and detection [7,32]. The mechanism through which each heterospecific conveys information (i.e. alarm calls), or how differences in species' detection abilities (i.e. sensory modalities), influenced herding preference was beyond the scope of the study.

Following Schmitt *et al.* [16], zebra-only herds comprised a group of zebra that fed within six body lengths of their nearest conspecific (approx. 12 m), while mixed-species herds contained at least one heterospecific individual within 12 m of a zebra. We limited our data collection to single- and mixed-species herds that comprised only adult individuals. All vigilance observations started when a focal zebra had its head down and was grazing. We considered a zebra vigilant when it lifted its head above grazing height and scanned for predators, or focused its gaze and actively listened (as per [7]). Within a herd, we did not record data from the same individual twice. For each herd, we sampled more than 75% of herd members.

### (a) Anti-predator behaviour

The type and quality of social information gleaned from herd mates plays an important role in herding behaviour. Thus, to determine the efficacy of mixed-species herding as a function of predation risk, we compared zebra vigilance across different predation risk and herd compositions (i.e. single- versus mixed-species herds). To determine vigilance behaviour, we observed a zebra for 3 min and recorded: (1) the number of vigilance events, (2) total time vigilant, (3) the type of each vigilance event (i.e. general or focused scan [16]) and (4) the amount of time devoted to general versus focused scans (see electronic supplementary material for sample sizes). As per Schmitt *et al.* [16], we defined a general scan as a zebra scanning without fixing its attention (vision or ears) in a particular direction. A focused scan comprised a zebra staring in a fixed direction, with its ears pricked, either to another herd mate (i.e. zebra or other herding species) or out to the environment. Finally, we compared zebra herd size for single- and mixed-species herds in both low- and high-predation risk areas.

Focal zebra were randomly selected and anti-predator data were collected sequentially from different individuals. Because we sampled the majority of the herd, there is some variation in the spatial location of each zebra within the herd (centre versus edge), which can affect anti-predator responses [33]. However, for the analyses (see below), we created a herd average to represent perceived risk at the herd level. Finally, throughout the study period, the same observer recorded and scored zebra anti-predator responses directly in the field. We sampled both single- and mixed-species herd types in all reserves (HiP: mixed:  $n=30$  herds, zebra-only:  $n=58$  herds; Kruger: mixed:  $n=12$  herds, zebra-only:  $n=12$  herds; Ithala: mixed:  $n=15$  herds, zebra-only:  $n=15$  herds; Isimangaliso: mixed:  $n=8$  herds, zebra-only:  $n=8$  herds; for detailed sample sizes, see electronic supplementary material).

### (b) Time lost and the feeding cost of vigilance

To quantify the implications of mixed-species herding to time invested in vigilance by zebra, we created a function that represents the percentage investment cost of vigilance. Because we statistically controlled for herd size in the analyses that generated the empirical data used in this function, our projected values reflect the costs associated with anti-predator behaviour (i.e. vigilance) and not costs associated with social behaviour (i.e. competition). For this function, we only used time spent by zebra conducting a focused scan, because during these scans, zebra cease feeding (i.e. these behaviours are mutually exclusive). We extended this function to explore how the cost of vigilance may influence zebra feeding behaviour. To do this, we used empirical data on zebra foraging behaviour (i.e. bite rates) collected by [34]. Using their estimate of the time taken for a single bite, and assuming all bites are of equal quality, we were able to calculate the difference (due to vigilance) in the daily number of bites that zebra take within each herd type within a risk category. These differences in the number of bites and feeding time, reflect the benefits of mixed-species herding. See electronic supplementary material for detailed calculations.

### (c) Data analysis

#### (i) Number of vigilance events and time spent vigilant

Prior to analyses, we calculated mean individual vigilance per herd and used herds as replicates to avoid possible pseudoreplication after testing for and finding no herd effect (we therefore could pool data on individuals to create a herd average). We assessed, using two separate models, how herding behaviour (single- versus mixed-species) and predation risk (high versus low) influenced: (1) the number of vigilance events and (2) the mean duration individuals within a herd were vigilant per 3 min observation. For both models, we used a generalized linear model with a Tweedie distribution and log-link function. We used a Tweedie distribution because our dataset contained a range of zero and positive values [35]. For each model, we included 'herd type' (mixed species versus single species) and 'risk' (high or low) as the main factors as well as their interaction. To control for variation in herd size as well as for a site effect, we used number of zebra, number of non-zebra ungulates, and site as covariates. For both the mean duration of vigilance and the number of vigilance events models, the number of non-zebra ungulates was non-significant and thus removed from the model.

In our study, we found a mixed-species effect (i.e. lower vigilance levels in mixed-species herds; see Results). To quantify the degree to which mixed-species herding can reduce vigilance behaviours of zebra and modify landscapes of perceived risk, we assessed whether the average time spent vigilant by zebra in a mixed-species herd in a high-risk area was comparable to the average time spent vigilant by zebra in single-species herds in low-risk areas. To do this, we used a generalized linear model (Tweedie distribution and log-link function). We included the average time spent vigilant by zebra as the dependent variable and herd type as the independent variable. To control for variation in herd size as well as for a site effect, we used number of zebra, number of non-zebra ungulates, and site as covariates in the models. Site was non-significant and thus removed from the model.

#### (ii) General versus focused scans

We assessed how herd type and predation risk influenced the duration and proportional use of focused scans (mutually exclusive from other behaviours and therefore costlier to zebra). We included duration as the dependent variable in a generalized linear model (Gamma distribution and log-link function) with herd type, predation risk, and their interaction as independent

variables. To determine the proportional use of focused scans across treatments, we calculated the proportion of focused scans for each herd and transformed these values using an arcsine square root transformation for proportional data. The transformed values for the proportions of focused scans were then used as the dependent variable in a general linear model. Herd type, risk and their interaction were included as independent variables. In both models, we included the number of zebra, number of non-zebra ungulates, and site as covariates. The number of non-zebra ungulates was non-significant and thus removed from the model. For the second model, the number of zebra and number of non-zebra ungulates were non-significant and removed from the model. Data were back-transformed for graphical representation.

### (iii) Herd size

To determine the mechanism by which zebra reduce vigilance in high- and low-risk areas, we examined their herding behaviour, specifically the herd sizes that are maintained in high- and low-risk areas in mixed- and single-species herds. First, we ran a generalized linear model (gamma distribution and log-link function) with total herd size as the dependent variable with herd type, risk, and their interaction as independent variables. We initially included site as a covariate, but found that it was non-significant, and therefore, removed it from the model. We then ran a generalized linear model (gamma distribution and log-link function) that focused on the number of zebra only in a herd as the dependent variable, with herd type, risk, and their interaction as the main variables. We initially included site as a covariate, but found that it was non-significant, and therefore, removed it from the model. Upon finding that zebra maintain a constant number of conspecifics in both single- and mixed-species herds in high- and low-risk areas (see Results), we explored how this might vary across seasons, and thus changes in resource availability (see electronic supplementary material, methods for more details). All data were analysed and back-transformed for graphical representation using SPSS v. 25.

## 3. Results

### (a) Antipredator behaviour

Mixed-species herding and predation risk influenced the number of vigilance events, the mean duration individuals within a herd were vigilant, the proportional use of general versus focused scans and, finally, the proportion of time devoted to general versus focused scans. Zebra in mixed-species herds conducted approximately 48% fewer vigilance events ( $\chi^2=20.518$ ,  $p<0.0001$ ; figure 1a) and spent approximately 55% less time being vigilant compared with zebra in single-species herds ( $\chi^2=35.171$ ,  $p<0.001$ ; figure 1b). In addition, zebra in mixed-species herds not only conducted proportionally fewer focused scans ( $F_{1,149}=19.624$ ,  $p<0.001$ ; figure 1c) but those that they did make were approximately 20% shorter than zebra in single-species herds ( $\chi^2=6.398$ ,  $p=0.011$ ; figure 1d).

Zebra in low-risk areas conducted approximately 61% fewer vigilant events ( $\chi^2=44.746$ ,  $p<0.001$ ; figure 1a) and spent approximately 64% less time being vigilant compared with zebra in high-risk areas ( $\chi^2=59.500$ ,  $p<0.001$ ; figure 1b). Furthermore, zebra in low-risk areas also had proportionally fewer focused scans ( $F_{1,149}=4.174$ ,  $p=0.043$ ; figure 1c) of shorter duration compared with high risk-areas ( $\chi^2=29.826$ ,  $p<0.001$ ; figure 1d). For all the above analyses, we

found non-significant interaction effects between risk and herd type (i.e. the response slopes were homogeneous). This indicates that the observed differences in all the vigilance metrics (interaction terms for: number of vigilance events:  $\chi^2=0.165$ ,  $p=0.685$ ; the time spent vigilant:  $\chi^2=1.211$ ,  $p=0.271$ ; the proportional use:  $F_{1,149}=0.066$ ,  $p=0.797$ , and duration of focused versus general scans:  $\chi^2=3.333$ ,  $p=0.068$ ) between single- and mixed-species herds were independent of risk (i.e. mixed-species herding reduced zebra anti-predator behaviours by the same amount at both levels of predation risk).

Finally, with respect to the mean duration individuals within a herd were vigilant, mixed-species herding essentially levels the landscape of fear. As such, there was no difference in the time that zebra spent vigilant in mixed-species herds in high-risk areas compared with single-species herds in low-risk areas ( $\chi^2=0.001$ ,  $p=0.985$ ; figure 1b). Zebra in mixed-species herds in high-risk areas spent 17.45 s out of 3 min (approx. 10% of the time) being vigilant (down from approx. 20% of time spent vigilant out of 3 min in zebra-only herds at high risk), whereas zebra in single-species herds in low-risk areas spent 17.53 s out of 3 min (approx. 10% of the time) being vigilant.

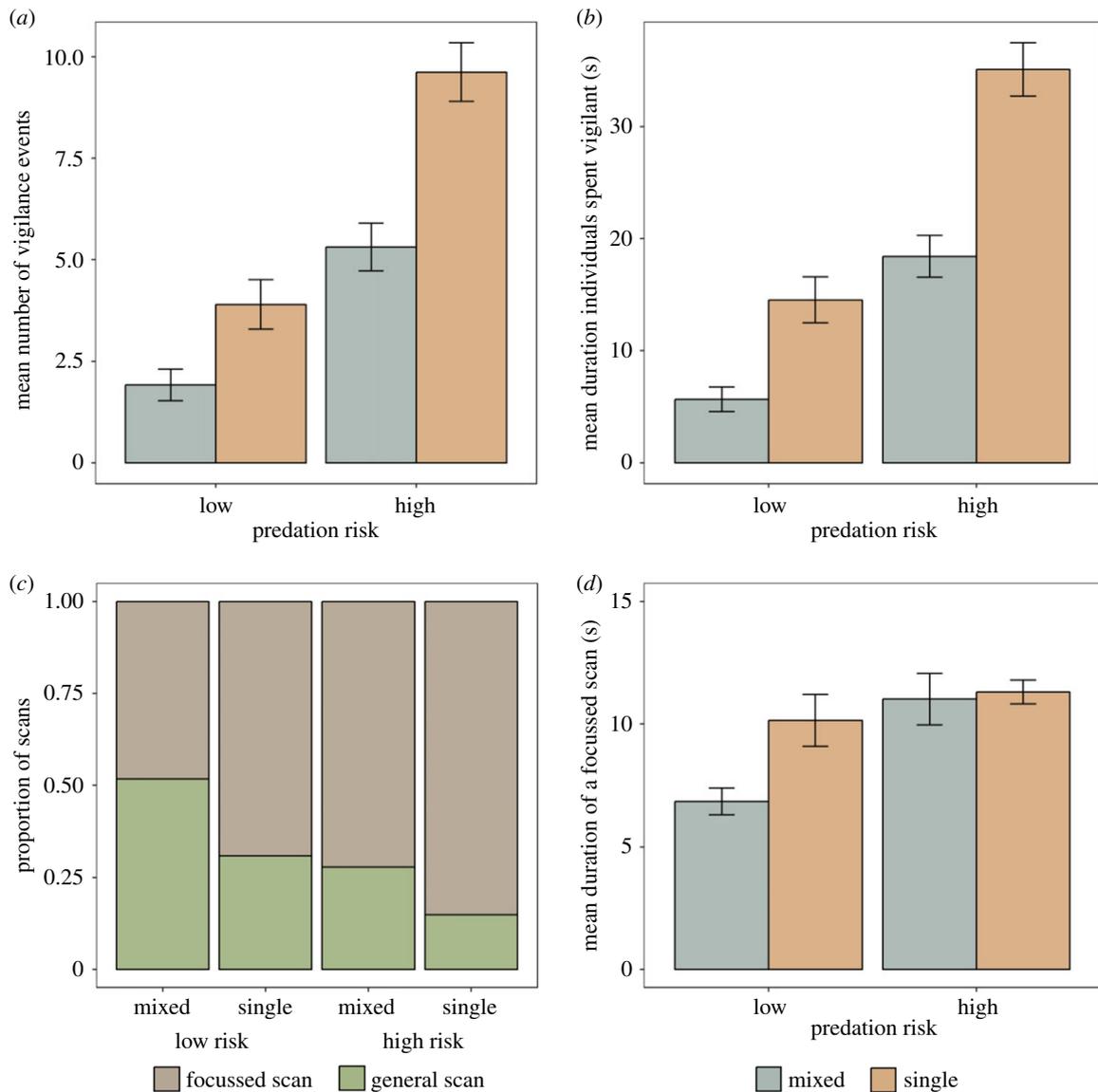
### (b) Herd size

The only factor that influenced herd size was whether the herd was a single- or mixed-species herd ( $\chi^2=91.559$ ,  $p<0.001$ ). Neither predation risk, nor the interaction between predation risk and herd type influenced herd size (predation risk:  $\chi^2=1.316$ ,  $p=0.251$ ; interaction term:  $\chi^2=1.750$ ,  $p=0.186$ ). Mixed-species herds were greater than 2 times larger than single-species herds in both high- and low-risk areas (figure 2a). However, further analyses revealed that there was no significant difference in the average number of zebra found in single- and mixed-species herds ( $\chi^2=0.066$ ,  $p=0.797$ ; figure 2b), or between the different predation risk areas ( $\chi^2=0.943$ ,  $p=0.332$ ; figure 2b). The lack of difference in zebra numbers between herd types can be inferred across both predation risks (non-significant interaction:  $\chi^2=1.312$ ,  $p=0.252$ ; figure 2b). Finally, when we explored how number of conspecifics varied across seasons in a high-risk area, we found that zebra maintained the same number of conspecifics (approx. 6) in both herd types irrespective of season (non-significant interaction:  $\chi^2=2.480$ ,  $p=0.115$ ).

### (c) Time lost and feeding cost of vigilance

Our model showed that the percentage investment cost of vigilance decreased by approximately 60% and 41% in mixed-species herds in low- and high-risk areas, respectively (figure 3). This potentially allows zebra to invest more time in other activities besides costly anti-predator behaviour. Furthermore, our model predicts that mixed-species herding in high-risk areas reduced the percentage investment cost of vigilance to a similar level obtained by zebra herding in single-species herds in areas with low levels of predation risk.

We also estimate that zebra in mixed-species herds are able to take more bites per day than zebra in single-species herd while foraging. Specifically, we found the difference in the number of bites between herd types to be approximately 917 bites per day in low-risk areas compared with approximately 1192 bites per day in high-risk areas. For zebra in single-species herds to achieve the same number of bites as zebra in mixed-species herds, they would have to feed for



**Figure 1.** Differences in zebra anti-predator responses in mixed- and single-species herds in areas of low- and high-predation risk for: (a) mean ( $\pm$  s.e.) number of individual vigilance events per 3 min observation, (b) mean ( $\pm$  s.e.) duration individuals within a herd were vigilant per 3 min observation, (c) the proportional use of general versus focussed scans and (d) the mean ( $\pm$  s.e.) duration of focussed scans. We found significant differences in the main effect of predation risk and herd type (single versus mixed) on zebra anti-predator responses. We did not find an interaction effect. (Online version in colour.)

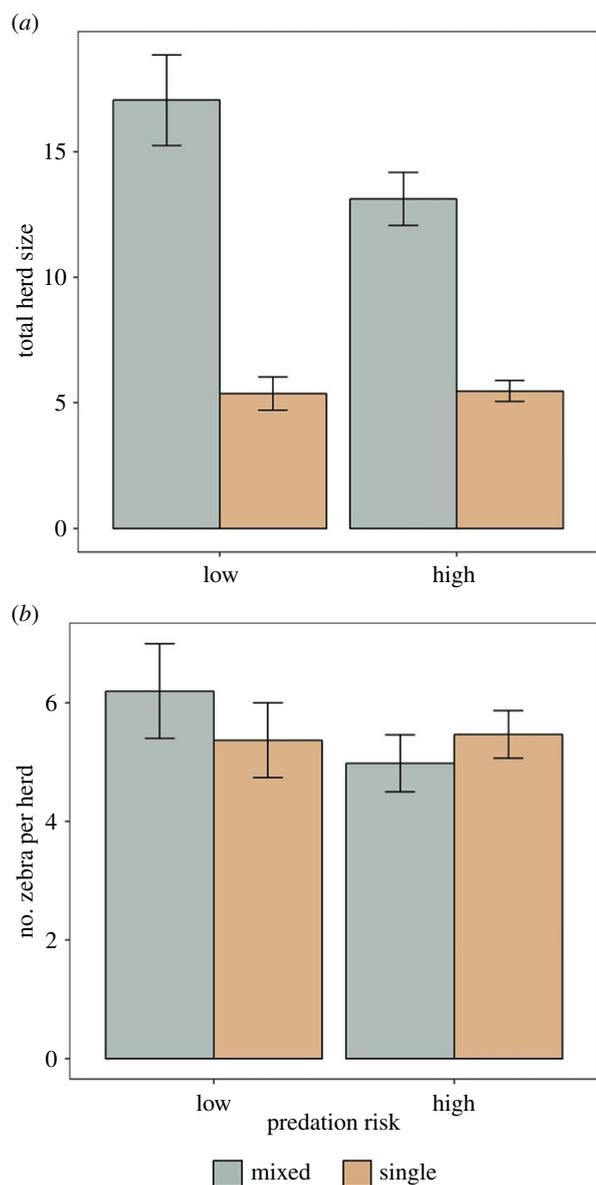
approximately an additional 35 min in low-risk areas, and 51 min in high-risk areas, per day.

#### 4. Discussion

African savannas consist of diverse predator and prey guilds [36,37]. This diversity plays an important role in determining the effect that predators have on prey populations [38]. We found that the removal of a main predator (i.e. lions) altered the anti-predator behaviour of their common prey species (i.e. zebra). However, the eradication of the top predator did not completely eliminate the perception of risk [23]. Instead, we found that zebra still maintained, and benefitted from, mixed-species herding under low predation risk scenarios. Thus, we speculate that top-down control by secondary predators still elicited a fear response from zebra, even when the main predator of zebra was removed. Thus, in predator-diverse systems, secondary predators (e.g. hyena and leopard) appear to still elicit important top-down regulation on prey species and thereby uphold a landscape of fear, albeit it

perhaps with lower peaks and shallower valleys of perceived predation risk (e.g. the multipredator hypothesis [39]).

It is plausible that we did not see a complete collapse of anti-predator behaviour under low predation risk because prey anti-predator responses may be innate and evolutionarily ingrained so that the total loss of anti-predator behaviour never occurs (see [40]). If this was the case, we would expect similar levels of anti-predator behaviours between single- and mixed-species herds under low levels of risk. However, in our study, we observed a mixed-species effect even under low levels of predation risk (i.e. there are anti-predator benefits of mixed-species herding). In addition to lions, secondary predators are also present at all of our study sites. Secondary predators (e.g. leopard and hyena) are typically not the main predators of zebra; however, they have been shown to consume zebra fairly regularly [28,29,31]. Thus, when exposed to secondary predators, zebra still exhibited anti-predator responses and benefitted from mixed-species herding. The difference in the magnitude of anti-predator responses of zebra as well as the estimated feeding costs between the two



**Figure 2.** Differences in: (a) mean total (both zebra and non-zebra ungulates) herd size for single- and mixed-species herds in high- and low-risk areas, and (b) mean number of zebras in single- and mixed-species herds in areas of high- and low-risk. Only herd type significantly influenced total herd size. We found no effect of risk, nor an interaction between risk and herd type, on total herd size. We also found no significant differences in the number of zebra per herd across both herd types and risk categories. (Online version in colour.)

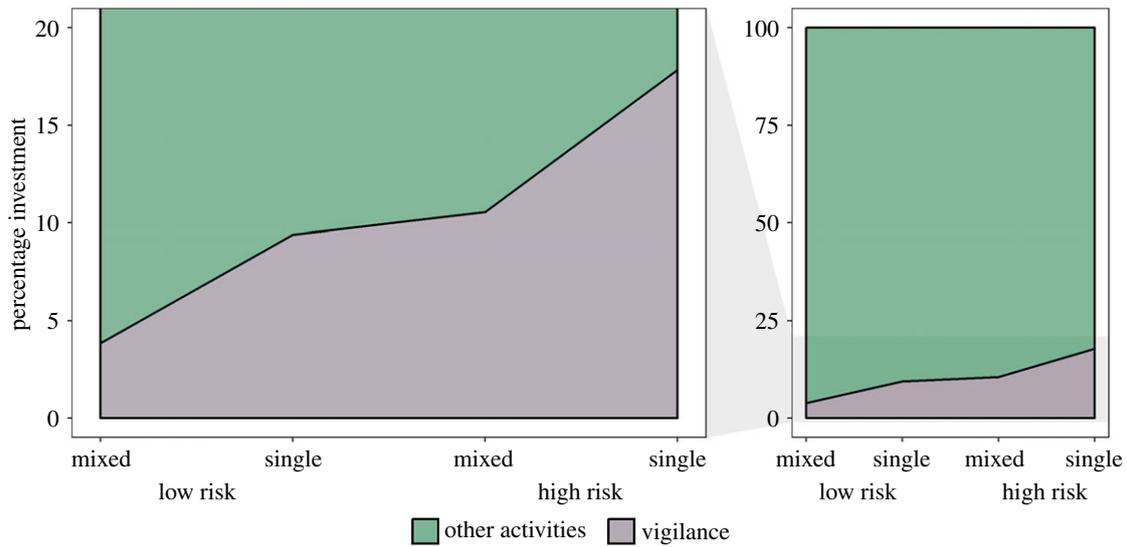
risk categories can be attributed to the greater predatory risk imposed by lion compared with secondary predators in low-risk areas [13]. However, by maintaining at least some top-down control on prey species, it appears that secondary predators are important in regulating ecosystem structure, functioning and resilience [13,41].

For predator detection, we were mainly interested in focussed scans because this vigilance event was mutually exclusive from feeding. Both mixed-species herding and predation risk influenced the duration of these focussed scans. Although, we did not find a significant interaction ( $p = 0.068$ ) between predation risk and herd type, it seems that under high levels of risk, zebra in both herd types conducted focussed scans of similar duration (figure 1*d*), albeit in different frequencies (figure 1*c*). Under high levels of risk, zebra in

both herd types may have conducted focussed scans of similar duration because that is what is needed to be able to detect cryptic, ambush predators (lion) in the landscape. However, when we combined the frequency and duration of focussed scans into a single metric (percentage investment cost; figure 3), we ultimately found that mixed-species herding lowered predation risk.

Using empirical data, where we statistically controlled for herd size (effectively removing the costs associated with increased herd size and competition), we were able to estimate the percentage investment cost of vigilance as a function of grouping behaviour. From the function we created, we found that mixed-species herding in high-risk areas reduced the cost of investing in vigilance by approximately 41%. Somewhat unexpectedly, we further found that increases in mixed-herding also decreased percentage investment in costly vigilance under low-levels of predation risk (approx. 60%). Thus, when zebra formed mixed-species herds, they invested less in costly vigilance, thereby, allowing more time to be allocated to other activities such as feeding. Barnier *et al.* [18] found that zebra obtained a low-quality diet when foraging under predation risk by lions. One of the mechanisms driving this nutritional cost is an increase in intense vigilance scans as a result of lions. Increased vigilance reduces bite rates and ultimately food intake rates [42]. When we estimated the cost of vigilance in terms of feeding, we found that zebra in single-species herds need to feed approximately 35 min more per day in low-risk areas and approximately 51 min more in high-risk areas to achieve the same number of bites as zebra in mixed-species herds. Thus, when zebra form single-species herds, it is plausible that the cost of investing more time in vigilance and less time feeding compared with zebra in mixed species herds, could have fitness consequences [42,43]. Furthermore, Gil *et al.* [19] used dynamic state variable modelling to elucidate the effects of social information on grouping behaviour and individual fitness. Under all modelling scenarios, they found that social information and mixed-species herding were not detrimental to individual fitness because the fitness benefits always exceeded the potential competition costs.

In less complex systems (i.e. systems with single predator-prey pairs), the removal of top predators results in a breakdown of anti-predator responses with strong cascading effects [3,44]. However, in African systems, the diverse predator and prey guilds results in higher trophic redundancy (i.e. the number of species at each trophic level). With an increase in trophic redundancy, there is a greater chance that the effects of removing a given species, in our case lion, on the dynamics of other species will be compensated for by the effects of other species with links to the same prey [45]. Lion and secondary predators, such as leopard, have similar hunting styles (both are sit-and-pursue predators), which has been shown for some prey species to be more important in evaluating risk than the relative predation threat of a specific predator (i.e. threat-sensitive predator avoidance hypothesis [36]). The redundancy provided by the secondary predators in our system, and the overlap in prey preference between lion and these secondary predators, prevented the removal of the main predator in our system (lion) from resulting in a complete collapse of anti-predator behaviour shown by zebra. This compensation from species redundancy is counter to predictions of simple models of intra-guild predation (IGP), where removal of a top predator should theoretically have



**Figure 3.** Modelled response showing the percentage investment cost of vigilance as a function of predation risk and herd type. The higher the percentage investment cost to vigilance, the less time that is available to zebra to conduct other activities such as foraging, moving and maintenance. The panel on the left is a zoomed-in portion of the panel of the right. The zoomed-in panel highlights the change in percentage investment cost of vigilance across herd types and risk levels. (Online version in colour.)

cascading effects to lower trophic levels. Thus, the relationship between food-web complexity and the stability of ecosystems is important when considering the outcome of predator removal on prey species [46,47]. However, these cascading effects can be precluded, for example, by structural heterogeneity of the environment [e.g. 48]. Structural heterogeneity can influence the success of the contrasting hunting styles (ambush versus cursorial) between apex and secondary predators (see [13] and references therein) as well as the ability for prey species to detect and avoid predators [49,50].

Linking trophic level redundancy and social information of prey species provides a powerful tool to understand community-level interactions in response to predation risk. A diverse prey guild has potentially different sensory abilities with certain species providing more accurate information about predation risk [15,16]. Thus, improved social information about predation risk could be an important driver of mixed-species herding and individual fitness of herd members [7,19]. Leuthold & Leuthold [51] found that zebra formed mixed-species herds more frequently than expected by chance. Furthermore, Ireland & Ruxton [52] hypothesize that zebra form the nucleus of mixed-species herds, which is supported by the social networking analyses of Kiffner *et al.* [24]. The effect of mixed-species herding in reducing predation risk is well documented [7,53]. However, we extend the effects of mixed-species herding in reducing predation risk by quantifying the degree to which mixed-species herding can reduce perceived predation risk across different levels of predation risk. We found that mixed-species herding effectively levels the landscape of fear for zebra that is created by lions, meaning that when zebra form mixed-species herds in areas of high predation risk, they are able to achieve similar levels of anti-predator vigilance that zebra herding with only conspecifics have in areas of low predation risk.

Despite the benefits obtained from mixed-species herding, grouping behaviour does not come without its costs—primarily increased competition [11]. We found that mixed-species herds were larger than single-species herds,

potentially leading to competitive effects (which we did not measure) outweighing the benefits of reduced anti-predator behaviours that we observed. However, we found that the number of zebra remained constant (approx. 6 individuals) across all herd categories (i.e. mixed versus single in high- and low-risk areas). Moreover, when we examined the mean number of zebra in single- and mixed-species herds in a high-risk area across the seasonal cycle (i.e. wet and dry season), which reflects dramatic changes in resource availability, we found that the number of zebra in a herd remained consistent at an average of six individuals. Thus, the increase in total herd size that we observed in mixed-species herds was a result of zebra herding with heterospecifics. Zebra do have the option of forming larger conspecific aggregations (sometimes up to 400 individuals [54]), but by selecting for heterospecifics, rather than conspecifics, zebra simultaneously increase detection abilities while reducing the potential for competition for mates and food resources (lower niche overlap between heterospecifics). Thus, zebra are not merely balancing the competition-information trade-off, but by selecting for quality of herd member rather than quantity of herd members, they are maximizing the benefits of mixed-species herding while reducing potential costs, which is consistent with the information quality–competition trade-off [19,21]. Additionally, we found that mixed-species herd sizes were similar in both low and high-risk areas (approx. 18 individuals). Total herd size may be limited by the potential for larger herds to be more easily detected by predators in the landscape [55].

Our finding that zebra maintain an average of six individuals in a herd is consistent with average herd sizes of zebra found in other studies (table 4.1. in [56]) and is probably the number of females in a harem that a dominant male can suitably defend against other male competitors [57]. Ultimately, the diversity of the prey trophic guild provides zebra with multiple opportunities to form mixed-species herds, and thus, reduce the strength of predator-induced risk effects. This reduction in the strength of predator impacts have the potential to cause fear-based niche shifts in gregarious

herbivore species [58], whereby these grouping associations allow gregarious prey species to forage in riskier areas, potentially explaining why strong predator-induced cascading effects are often not observed in complex systems (e.g. [59]).

We used zebra as our focal species to highlight the benefits of using social information to reduce predation risk. However, these benefits are likely to also extend to heterospecifics, which herd with zebra (as long as they share a common predator). For example, Meise *et al.* [14] used weighted directed affinity networks to reveal how different species in African savannas prefer to herd with specific species. The degree to which a specific species benefits and the directionality of these benefits depends on the vulnerability of the herding partner to predators as well as their detection abilities [14]. Although we showed that zebra benefitted from herding with species such as wildebeest, it is possible that wildebeest could be benefitting more from herding with zebra because zebra have been shown to be reliable detectors of predation risk [14,15].

In our study, for mixed-species herds, there is a positive relationship between herd size and reduced investment to costly vigilance as well as an increase in the time available for feeding (e.g. Allee effects [60]) compared with single-species herds. This further demonstrates the importance of

grouping as an option within the arsenal of anti-predator responses of prey species. Moreover, grouping benefits extend beyond regulating populations (e.g. improved survivorship) when information about predators spans multiple species, thereby influencing community-level interactions. Ultimately, our findings suggest that mixed-species herding can effectively reduce the perceived risk of predation, whereby it essentially removes the influence of the primary predator on the anti-predator responses of prey species.

**Ethics.** All aspects of the research design were approved by our institution (Ethics code: 13/11/Animal).

**Data accessibility.** The data supporting this article can be obtained from the Dryad Digital Repository: <https://dx.doi.org/10.25349/D96S3G> [61].

**Authors' contributions.** K.S. and M.H.S. conceived the study, collected and analysed the data, and wrote the manuscript. C.C.W. and A.M.S. critically revised the manuscript.

**Competing interests.** We declare we have no competing interests.

**Funding.** This research was funded by the University of California Santa Cruz (College 8), the University of California Education Abroad Program, the Claude Leon Foundation Fellowship and the National Research Foundation (IPRR and grant no. 116665).

**Acknowledgements.** We thank S. Ferreira, N. Govender and D. Druce for facilitating access to field sites.

## References

- Ripple WJ, Beschta RL. 2004 Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* **54**, 755–766. (doi:10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2)
- Orrock JL, Grabowski JH, Pantel JH, Peacor SD, Peckarsky BL, Sih A, Werner EE. 2008 Consumptive and non-consumptive effects of predators on metacommunities of competing prey. *Ecology* **89**, 2426–2435. (doi:10.1890/07-1024.1)
- Laundré JW, Hernández L, Altendorf KB. 2001 Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Can. J. Zool.* **79**, 1401–1409. (doi:10.1139/cjz-79-8-1401)
- Danchin E, Giraldeau L, Valone TJ, Wagner RH. 2004 Public information: from nosy neighbours to cultural evolution. *Science* **305**, 487–491. (doi:10.1126/science.1098254)
- Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193. (doi:10.1016/j.tree.2005.01.010)
- Templeton CN, Greene E. 2007 Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proc. Natl Acad. Sci. USA* **104**, 5479–5482. (doi:10.1073/pnas.0605183104)
- Schmitt MH, Stears K, Shrader AM. 2014 Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. *Anim. Behav.* **96**, 151–158. (doi:10.1016/j.anbehav.2014.08.012)
- Breviglieri CPB, Oliveira PS, Romero GQ. 2017 Fear mediates trophic cascades: nonconsumptive effects of predators drive aquatic ecosystem function. *Am. Nat.* **189**, 490–500. (doi:10.1086/691262)
- Pringle RM *et al.* 2019 Predator-induced collapse of niche structure and species coexistence. *Nature* **570**, 58–64. (doi:10.1038/s41586-019-1264-6)
- Jackson AL, Ruxton GD. 2006 Towards an individual-level understanding of vigilance: the role of social information. *Behav. Ecol.* **17**, 532–538. (doi:10.1093/beheco/arj060)
- Krause J, Ruxton GD. 2002 *Living in groups*. Oxford, UK: Oxford University Press.
- Laundré JW, Hernández L. 2003 Winter hunting habitat of pumas *Puma concolor* in northwestern Utah and southern Idaho, USA. *Wildlife Biol.* **9**, 123–129. (doi:10.2981/wlb.2003.034)
- Makin DF, Chamaillé-Jammes S, Shrader AM. 2017 Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. *Anim. Behav.* **127**, 225–231. (doi:10.1016/j.anbehav.2017.03.024)
- Meise K, Franks DW, Bro-Jørgensen J. 2019 Alarm communication networks as a driver of community structure in African savannah herbivores. *Ecol. Lett.* **23**, 293–304. (doi:10.1111/ele.13432)
- Palmer MS, Gross A. 2018 Eavesdropping in an African large mammal community: antipredator responses vary according to signaller reliability. *Anim. Behav.* **137**, 1–9. (doi:10.1016/j.anbehav.2017.12.018)
- Schmitt MH, Stears K, Shrader AM. 2016 Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. *Behav. Ecol. Dev.* **27**, 1073–1077. (doi:10.1093/beheco/aru015)
- Gil MA, Hein AM, Spiegel O, Baskett ML, Sih A. 2018 Social information links individual behavior to population and community dynamics. *Trends Ecol. Evol.* **33**, 535–548. (doi:10.1016/j.tree.2018.04.010)
- Barnier F, Valeix M, Duncan P, Chamaillé-Jammes S, Barre P, Loveridge AJ, Macdonald DW, Fritz H. 2014 Diet quality in a wild grazer declines under the threat of an ambush predator. *Proc. R. Soc. B* **281**, 20140446. (doi:10.1098/rspb.2014.0446)
- Gil MA, Emberts Z, Jones H, St. Mary CM. 2017 Social information on fear and food drives animal grouping and fitness. *Am. Nat.* **189**, 227–241. (doi:10.1086/690055)
- Kartzinel TR, Chen PA, Coverdale TC, Erickson DL, Kress WJ, Kuzmina ML, Rubenstein DI, Wang W, Pringle RM. 2015 DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proc. Natl Acad. Sci. USA* **112**, 8019–8024. (doi:10.1073/pnas.1503283112)
- Seppänen J-T, Forsman JT, Monkkonen M, Thomson RL. 2007 Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* **88**, 1622–1633. (doi:10.1890/06-1757.1)
- Creel S, Schuette P, Christianson D. 2014 Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav. Ecol.* **25**, 773–784. (doi:10.1093/beheco/aru050)
- Atkins JL, Long RA, Pansu J, Daskin JH, Potter AB, Stalmans ME, Tarnita CE, Pringle RM. 2019 Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* **364**, 173–177. (doi:10.1126/science.aau3561)
- Kiffner C, Kioko J, Leweri C, Krause S. 2014 Seasonal patterns of mixed species groups in large East African mammals. *PLoS ONE* **9**: e113446. (doi:10.1371/journal.pone.0113446)

25. Hayward MW, Kerley GIH. 2005 Prey preferences of the lion (*Panthera leo*). *J. Mammal.* **267**, 309–322. (doi:10.1017/S0952836905007508)
26. Somers MJ, Becker PA, Druce DJ, Graf JA, Gunther MS, Merneweck DG, Trinkel M, Moleón M, Hayward MW. 2017 Reassembly of the large predator guild into Hluhluwe-iMfolozi Park. In *Conserving Africa's mega-diversity in the anthropocene* (eds JPGM Cromsigt, S Archibald, N Owen-Smith), pp. 286–310. Cambridge, UK: Cambridge University Press.
27. Ferreira S, Funston PJ. 2010 Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. *Wildlife Res.* **37**, 194–206. (doi:10.1071/WR09030)
28. Hayward MW. 2006 Prey preferences of the spotted hyaena *Crocuta crocuta* and evidence of dietary competition with lion *Panthera leo*. *J. Zool.* **270**, 606–614. (doi:10.1111/j.1469-7998.2006.00183.x)
29. Hayward MW, Henschel P, O'Brien J, Hofmeyr M, Malmé G, Kerley GIH. 2006 Prey preference of the leopard (*Panthera pardus*). *J. Zool.* **270**, 298–313. (doi:10.1111/j.1469-7998.2006.00139.x)
30. Hayward MW, Hofmeyr M, O'Brien J, Kerley GIH. 2006 Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *J. Zool.* **270**, 615–627. (doi:10.1111/j.1469-7998.2006.00184.x)
31. Hayward MW, O'Brien J, Hofmeyr M, Kerley GIH. 2006 Prey preferences of the African wild dog *Lycaon pictus* (Canidae: Carnivora): ecological requirements for conservation. *J. Mammal.* **87**, 1122–1131. (doi:10.1644/05-MAMM-A-304R2.1)
32. Dehn M. 1990 Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* **26**, 337–342. (doi:10.1007/BF00171099)
33. Hamilton WD. 1971 Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311. (doi:10.1016/0022-5193(71)90189-5)
34. Okello MM, Wishitemi REL, Muhoro F. 2002 Forage intake rate and foraging efficiency in free-ranging zebra and impala. *S. Afr. J. Wildl. Res.* **32**, 93–100. (doi:10.520/EJC117155)
35. Jørgensen B. 1987 Exponential dispersion models. *J. R. Stat. Soc.* **49**, 127–162. (doi:10.1111/j.2517-6161.1987.tb01685.x)
36. Thaker M, Vanak AT, Owen CR, Ogden MB, Niemann SM, Slotow R. 2011 Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* **92**, 398–407. (doi:10.1890/10-0126.1)
37. Visser SN, Freymann BP, Olff H. 2011 The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *J. Anim. Ecol.* **80**, 484–494. (doi:10.1111/j.1365-2656.2010.01787.x)
38. Sinclair ARE, Mduma SAR, Brashares JS. 2003 Patterns of predation in a diverse predator–prey system. *Nature* **425**, 288–290. (doi:10.1038/nature01934)
39. Blumstein DT. 2006 The multipredator hypothesis and the evolutionary persistence of antipredator behavior. *Ethology* **112**, 209–217. (doi:10.1111/j.1439-0310.2006.01209.x)
40. Berger J, Swenson JE, Persson I-L. 2001 Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science* **291**, 1036–1039. (doi:10.1126/science.1056466)
41. Duffy JE. 2002 Biodiversity and ecosystem function. *Oikos* **99**, 201–219. (doi:10.1034/j.1600-0706.2002.990201.x)
42. Fortin D, Boyce MS, Merrill EH, Fryxell JM. 2004 Foraging costs of vigilance in large mammalian herbivores. *Oikos* **107**, 172–180. (doi:10.1111/j.0030-1299.2004.12976.x)
43. Houston AI, McNamara JM, Hutchinson JMC. 1993 General results concerning the trade-off between gaining energy and avoiding predation. *Trans. R. Soc. B* **341**, 375–397. (doi:10.1098/rstb.1993.0123)
44. Terborgh J, Holt RD, Estes JA. 2010 Trophic cascades: what they are, how they work, and why they matter. In *Trophic cascades: predators, prey, and the changing dynamics of nature* (eds J Terborgh, JA Estes), pp. 1–18. Washington, DC: Island Press.
45. Sanders D, Thébault E, Kehoe R, van Veen FJF. 2018 Trophic redundancy reduces vulnerability to extinction cascades. *Proc. Natl Acad. Sci USA* **115**, 2419–2424. (doi:10.1073/pnas.1716825115)
46. Pimm SL. 1984 The complexity and stability of ecosystems. *Nature* **307**, 321–326. (doi:10.1038/307321a0)
47. Finke DL, Denno RF. 2004 Predator diversity dampens trophic cascades. *Nature* **429**, 407–410. (doi:10.1038/nature02554)
48. Schmitt RJ, Holbrook SJ, Brooks AJ, Lape JCP. 2009 Intraguild predation in a structured habitat: distinguishing multiple-predator effects from competitor effects. *Ecology* **90**, 2434–2443. (doi:10.1890/08-1225.1)
49. Ford AT, Goheen JR, Otieno TO, Bidner L, Isbell LA, Palmer TM, Ward D, Woodroffe R, Pringle RM. 2014 Large carnivores make savanna tree communities less thorny. *Science* **346**, 346–349. (doi:10.1126/science.1252753)
50. le Roux E, Kerley GIH, Cromsigt JPGM. 2018 Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Curr. Biol.* **28**, 2493–2499. (doi:10.1016/j.cub.2018.05.088)
51. Leuthold W, Leuthold BM. 1975 Patterns of social grouping in ungulates of Tsavo National Park, Kenya. *J. Zool.* **175**, 405–420. (doi:10.1111/j.1469-7998.1975.tb01408.x)
52. Ireland HM, Ruxton GD. 2017 Zebra stripes: an interspecies signal to facilitate mixed-species herding? *Biol. J. Linn. Soc.* **121**, 947–952. (doi:10.1093/biolinnean/blx037)
53. Goodale E, Beauchamp G, Ruxton GD. 2017 *Mixed-species animal groups: behavior, community ecology and conservation*. Oxford, UK: Academic Press.
54. Rubenstein DI, Hack MA. 2004 Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates. In *Sexual selection in primates: new and comparative perspectives* (eds PM Kappeler, CP van Schaik), pp. 266–279. Cambridge, UK: Cambridge University Press.
55. Creel S, Winnie JA. 2005 Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Anim. Behav.* **69**, 1181–1189. (doi:10.1016/j.anbehav.2004.07.022)
56. Hack MA, East R, Rubenstein DI. 2002 Status and action plan for the plains zebra (*Equus burchellii*). In *Equids: zebra, asses and horses status survey and conservation action plan* (ed. PD Moehlman), pp. 43–60. Cambridge, UK: IUCN.
57. Rubenstein DI. 2010 Ecology, social behavior, and conservation in zebras. In *Advances in the study of behavior: behavioral ecology of tropical animals* (ed. R Macedo); pp. 231–258. Oxford, UK: Elsevier.
58. Martínez AE, Parra E, Muellerklein O, Vredenburg VT. 2018 Fear-based niche shifts in neotropical birds. *Ecology* **99**, 1338–1346. (doi:10.1002/ecy.2217)
59. Ford AT, Goheen JR, Augustine DJ, Kinnaid MF, O'Brien TG, Palmer TD, Pringle RM, Woodroffe R. 2015 Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. *Ecology* **96**, 2705–2714. (doi:10.1890/14-2056.1)
60. Elliot KH, Betini GS, Norris DR. 2017 Fear creates an Allee effect: experimental evidence from seasonal populations. *Proc. R. Soc. B* **284**, 20170878. (doi:10.1098/rspb.2017.0878)
61. Stears K, Schmitt MH, Wilmers CC, Shrader AM. 2020 Data from: Mixed-species herding levels the landscape of fear. Dryad Digital Repository. (doi:10.25349/D9653G)