Mixed-species herding levels the landscape of fear: Supplementary material

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1. Detailed sample sizes used in the analyses

To investigate zebra vigilance in single- and mixed-species herds across different levels of predation risk based on the presence or absence (high risk vs. low risk) of lions (*Panthera leo*), we sampled both single- and mixed-species herd types in all reserves (HiP: mixed: n = 30 herds, 84 individuals, 208 vigilance events, zebra-only: n = 58 herds, 160 individuals; 499 vigilance events, Kruger: mixed: n = 12 herds, 67 individuals, 181 vigilance events, zebra-only: n = 12 herds, 81 individuals, 296 vigilance events, Ithala: mixed: n = 15 herds, 60 individuals, 93 vigilance events, zebra-only: n = 15 herds, 35 individuals, 87 vigilance events, Isimangaliso: mixed: n = 8 herds, 40 individuals, 49 vigilance events, zebra-only: n = 8 herds, 43 individuals, 58 vigilance events). The vigilance metrics that we used included the type of each vigilance event (general versus focussed scan. See main text for the definition) as well as the amount of time devoted to general vs. focused scans. We compared both general (high risk: zebra-only: n= 199 scans, mixed-species: n= 165 scans, low risk: zebra-only: n= 59 scans, mixed-species: n= 77 scans) and focussed scans (high risk: zebra-only: n= 567 scans, mixed-species: n= 213 scans, low risk: zebra-only: n= 66 scans, mixed-species: n= 36 scans) across herd type and predation risk.

2. Calculating the percent investment cost of vigilance

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 percent investment cost of vigilance. This function represents the percentage of time lost to conduct other activities (e.g. feeding, mating) as a consequence of costly vigilance scans (see below) for each herd type and predation risk category. 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). Thus, focused scans are costly and are likely to influence the time that zebra can devote to other activities. We used the mean duration of a focused scan within a given herd type and predation risk category ($S_{duration,herd\ type,risk}$) as well as the mean number of focused scans within a given herd type and predation risk category ($S_{number,herd\ type,risk}$) to calculate the time lost to vigilance ($t_{lost,herd\ type,risk}$), which is given by

$$t_{lost,herd\ type,risk} = (S_{duration}) * (S_{number}) \quad (1)$$

Finally, we calculated the percent investment cost of vigilance (i.e. time lost for other activities; $P_{lost,herd\ type,risk}$) as a function of herd type and predation risk, using

$$P_{lost,herd\ type,risk} = \frac{t_{lost,herd\ type,risk}}{t_{total,herd\ type,risk}} * 100 \quad (2)$$

Where $t_{total,herd\ type,risk}$ is the total number of seconds (180 s) an individual was observed to assess vigilance in each herd type and risk category.

Finally, we estimated the cost of vigilance (as a percentage using *equations 1*&*2* above) as a function of herd type and predation risk. Because we statistically controlled for herd size in the analyses that generated the empirical data used in this model, our projected values reflect the costs associated with anti-predator behaviour (i.e. vigilance) and not costs associated with social behaviour (i.e. competition). The percent investment cost to vigilance was calculated using average values across herds and predation risks, thus there are no error values for the calculated costs associated with being vigilant. Additionally, we estimated how the cost of vigilance (P_{lost}; obtained from *equations 1*&*2* above) impacted the foraging behaviour of zebra as a function of herd type within each risk category.

3) Calculating the cost of vigilance on feeding behaviour as a function of herd type

We used the time lost for other activities ($P_{lost,herd\ type,risk}$, see above) to calculate how vigilance as a function of herd type impacts zebra foraging within a risk category. Specifically, to understand how herding behaviour might have a cascading effect on zebra daily bite rate within each risk category, we used empirical data on zebra foraging behaviour (i.e. bite rates) collected by Okello et al. [1]. 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 in the daily number of bites that zebra take within each herd type within a risk category. We extended this estimate to calculate the amount of additional time that zebra in a single species herd would have to devote to feeding to achieve the same number of bites as zebra in a mixed-species herd. We repeated this for both risk categories. These differences in the number of bites and feeding time, reflect the benefits of mixed-species herding.

To calculate the cost of time spent vigilant as a function of herd type and risk level on the feeding behaviour of zebra, we must first calculate the amount of time that it takes zebra to take a single bite. To do this, we can use the estimate from Okello et al. [1], who calculated that zebras take an average of 25.92 $\pm$ 0.30 bites per minute. To estimate the time it takes to make a single bite:

$$\frac{60\ s}{25.92\ bites} = 2.31\ s\ per\ bite \tag{1}$$

Using the outputs from our percent investment costs of vigilance function, we can calculate the amount of time a zebra will invest in costly, focussed scans during a one minute feeding bout. To reflect the time lost to vigilance each herd type and risk level, we subtract the average number of seconds that a zebra conducts a focussed scan per minute per herd type from 60 seconds to reflect the amount of time available to feed:

$$60\ seconds - T_{vig} = T_{avail} \tag{2}$$

Where

T_{vig}: is the average amount of time spent vigilant per 1 minute in each herd type and risk category (s/min)

T_{avail}: is the amount of time available for foraging after average time spent vigilant is accounted for (s/min)

To calculate the number of bites zebra in each herd type can achieve after we account for time lost to vigilance, we can divide T_{avail} by our estimate of the time it takes for a zebra to take (and handle) a single bite: 2.31 s per bite.

$$\frac{T_{avail}}{2.31\ s} = Bites\ per\ min \tag{3}$$

This results in zebra in:

Mixed species, low-risk herds achieving: 24.97 bites/min

Single species, low-risk herds achieving: 23.5 bites/min

Mixed species, high-risk herds achieving: 23.24 bites/min

Single species, high-risk herds achieving: 21.33 bites/min

To estimate how differences in herding behaviour might influence the number of bites achieved while foraging during a single day, we can use Rubenstein's [2] estimate that zebra spend ~16 hours per day foraging, and of that time, they spend 65% of that time feeding, which reflects ~624 min of active feeding per day. This estimate can then be used to calculate daily bite intake:

$$624\,\mathrm{min} * \frac{Bites_{single\ or\ mixed}}{min} = Bites_{total} \qquad (4)$$

Where

$Bites_{single\ or\ mixed}$: is the number of bites taken by a zebra in a given herd type (single vs. mixed) and risk (high vs. low risk) category.

$Bites_{total}$: total number of bites taken per day.

This results in zebra in:

Mixed species, low-risk herds achieving: 15,581 bites/day

Single species, low-risk herds achieving: 14,664 bites/day

Mixed species, high-risk herds achieving: 14,501 bites/day

Single species, high-risk herds achieving: 13,309 bites/day

To estimate the difference in the number of bites taken per day by zebra as a function of herd type within a risk category

$$TBites_{mixed(high\ or\ low)} - TBites_{single(high\ or\ low)} = \Delta Bites_{high\ or\ low} \qquad (5)$$

Where

$TBites_{mixed\ (high\ or\ low)}$: is the total number of bites taken in a day by a zebra in a mixed-species herd under either high or low predation risk.

$TBites_{single\ (high\ or\ low)}$: is the total number of bites taken in a day by a zebra in a single-species herd under either high or low predation risk.

$\Delta Bites_{high\ or\ low}$: the difference in the number of bites taken in a day between zebra in a single species and mixed species herd under either high or low predation risk.

This results in zebra in:

Low risk areas: differing in ~917 bites/day

High risk areas: differing in ~1192 bites/day

To estimate the amount of time that zebra would have forage to compensate for the number of bites lost to vigilance in a day, we can multiply the number of bites lost by the average time it takes for zebra to take (and handle) a single bite:

$$\Delta Bites_{high\ or\ low} * 2.31\ s = \Delta Time_{high\ or\ low} \qquad (6)$$

Where

$\Delta Bites_{high\ or\ low}$: the difference in the number of bites taken in a day between zebra in a single species and mixed species herd under either high or low predation risk.

$\Delta Time_{high\ or\ low}$: is the amount of time (in seconds) that zebra would need to forage to compensate for bites lost to vigilance under either high or low predation risk.

To compensate for time lost to vigilance as a function of herd type, zebra needing to spend:

Low risk areas: 2,118 s/day of extra feeding

High risk areas: 2,753 s/day of extra feeding

To reflect the amount of time that zebra would have feed to compensate for time lost to vigilance as a function of herd type in minutes, we divided these values by 60 seconds, which results in:

Low risk areas: ~35 min/day of extra feeding

High risk areas: ~51 min/day of extra feeding

4. Analysing zebra herd size across different seasons

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* in main text), we explored how this might vary across seasons, and thus changes in resource availability. To do this, we used data on zebra herd sizes in single- and mixed-species herds from a high-risk reserve from both the dry (July-September) and wet seasons (January-March) (dry season: zebra-only: n = 111 herds, mixed: n = 67 herds, wet season: zebra-only: n = 64 herds, mixed: n = 79 herds). We used a generalized linear model with a gamma distribution and log link function to analyse the results.

Supplementary references

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