Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds

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For many animals, a key benefit of group living is lowered predation risk. With increasing group size, individuals commonly reduce vigilance. This group size effect can arise from both dilution of risk and increased collective detection. To determine which was more important, we compared vigilance levels of plains zebra, *Equus quagga*, in areas inhabited by their main predator, lion, *Panthera leo*, as a function of herd size and composition (zebra-only versus mixed-species herds). For zebra-only herds, vigilance declined with increasing zebra numbers. In contrast, in mixed-species herds, zebra vigilance levels were significantly lower and did not vary with the total number of ungulates and/or zebra in the herd. This lower vigilance can be explained by detection benefits, since we controlled for the influence of herd size (i.e. dilution) statistically. Furthermore, we found that zebra in smaller herds were half as vigilant when they co-occurred with another preferred prey of lion, blue wildebeest, *Connochaetes taurinus*, compared with zebra-only herds. However, when zebra foraged with impala, *Aepyceros melampus*, a nonpreferred prey, there was only a slight reduction in vigilance compared with similar-sized zebra-only herds. Interestingly, the decrease in zebra vigilance when herding with wildebeest was influenced by the presence/absence, but not number, of wildebeest. In contrast, impala only reduced zebra vigilance when they comprised about 75% of the herd. Ultimately, our results indicate that for zebra in mixed-species herds, detection benefits are relatively more important than dilution over a larger range of herd sizes. However, detection only reduces vigilance when zebras herd with species that share a common predator (i.e. diluting partner). Potentially, detection by species that do not share a common predator (i.e. low-diluting partner) is not as reliable as detection by diluting species.

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Group living is a key factor in reducing predation risk (Elgar, 1989; Pulliam, Pyke, & Caraco, 1982; da Silva & Terhune, 1988). For many species, as group size increases perceived predation risk declines (Dehn, 1990; Makin, Payne, Kerley, & Shrader, 2012). This results in a reduction in individual vigilance levels as total group size increases (Berger, 1978; Dehn, 1990; Underwood, 1982). Ultimately, this enables individuals to devote more time to other behaviours such as foraging. The inverse relationship between individual vigilance and group size has been attributed to two mechanisms: (1) dilution of risk (Hamilton, 1971; Vine, 1971) and (2) greater predator detection (i.e. the 'many eyes' effect; Fairbanks & Dobson, 2007; Pulliam, 1973; Stensland, Angerbjörn, & Berggren, 2003).

The conceptual mechanism underlying detection as a cause of the inverse vigilance–group size relationship is that as the number of individuals increases, overall group detection goes up and, thus, the same overall level of risk assessment can be achieved with a reduction in individual vigilance (Elgar & Catterall, 1981; Kenward, 1978; Pulliam, 1973). However, when a predator can only attack one prey at a time, the probability that any given individual will be selected declines as the number of prey increases (i.e. dilution; Foster & Treherne, 1981). Consequently, dilution alone can reduce per capita risk even if individuals are unaware of a predator. In the classic example, Foster and Treherne (1981) showed that for water skaters, *Halobates robustus*, which are unable to detect their predators, the number of per capita attacks per unit time declined as group size increased, resulting in an inverse relationship between capture success and group size. However, in many instances, both dilution and detection contribute to altering individual vigilance, which is why Foster and Treherne's experiment is one of the few that is not confounded by the effects of detection. A long-standing

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and largely unresolved challenge has been to tease apart the beneficial contributions of these two mechanisms because both are functions of group size (Dehn, 1990).

Although a number of studies have explored dilution and detection in single-species herds (Bednekoff & Lima, 1998; Childress & Lung, 2003; Dehn, 1990; Elgar, 1989) differentiating between the benefits of these two mechanisms has remained elusive. Based on a simple analytical model developed for Rocky Mountain elk, *Cervus elaphus nelsoni*, Dehn (1990) concluded that the benefit of dilution relative to detection in lowering per capita risk increased with group size. Other studies have shown that because individuals who first detect a predator are more likely to escape than those that rely on warnings from group members (FitzGibbon, 1989), individuals should rely more heavily on vigilance in small herds in which dilution benefits are lower. The intertwining of dilution and detection has given rise to the perception that, aside from an individual that occurs by itself, detection does not operate without dilution to reduce risk (Dehn, 1990). However, this may not be the case for mixed herds of prey species. For example, in mixed-species herds, different species could potentially heighten detection via complementary senses (e.g. eyesight and hearing; Scheel, 1993) or vigilance behaviours (e.g. smaller species tend to have higher scan rates; Underwood, 1982). Yet, dilution would only operate in these herds if group members shared a common predator and thus were targeted equally (Leuthold, 1977; Metcalfe, 1984; Shrader, Post, Hagenah, & Bateman, 2013).

Mixed-species herds provide a relatively unexplored opportunity to tease apart the effects of dilution and detection on perceived predation risk. Several studies have reported a mixed-species effect (e.g. Kluever, Howery, Breck, & Bergman, 2009; van der Meer, Pays, & Fritz, 2012; Périquet et al., 2010; Scheel, 1993), whereby individuals herding with other species displayed lower vigilance than when herding only with conspecifics. However, these studies were not able to distinguish between the contributions of dilution versus detection to perceived risk. Here, we explored this issue by taking advantage of the fact that different members of a mixed group can either share the same predator and thus be similarly preferred (i.e. diluting partners) or have different predators and thus at best only act as sentinels (i.e. low-diluting partners). For example, in southern African savannahs, plains zebra, *Equus quagga*, commonly form mixed-species herds with both blue wildebeest, *Connochaetes taurinus*, and impala, *Aepyceros melampus*. The main predator of zebra is the lion, *Panthera leo*, which also strongly prefers wildebeest (Hayward & Kerley, 2005). As a result, wildebeest reduce predation risk of zebra through both dilution (sharing a common predator) and detection. However, lion usually do not prey upon impala (Hayward & Kerley, 2005), but impala are favoured by a host of other predators including leopard, *Panthera pardus*, wild dog, *Lycaon pictus*, hyaena, *Crocuta crocuta*, and cheetah, *Acinonyx jubatus* (Hayward, 2006; Hayward, Henschel, et al., 2006; Hayward, Hofmeyr, O'Brien, & Kerley, 2006; Hayward, O'Brien, Hofmeyr, & Kerley, 2006). Hence, impala could serve as sentinels (i.e. heighten detection) but are unlikely to contribute to dilution with regard to lion.

In this study, we aimed to quantify the degree to which dilution and detection influence the perception of risk (i.e. vigilance) by zebra foraging in mixed-species herds. We predicted that we would find a mixed-species effect, supporting the findings of previous studies (e.g. Kluever et al., 2009; van der Meer et al., 2012; Périquet et al., 2010; Scheel, 1993), and thus zebra would have lower vigilance levels in mixed-species herds than in similar-sized zebra-only herds (i.e. dilution is controlled for). This would probably be due to a lower perceived predation risk in mixed-species herds (Kluever et al., 2009). Alternatively, zebra may perceive social information

from conspecifics as more reliable and thus maintain lower vigilance levels when herding in zebra-only herds. However, as herd size increases, we predicted that there would be a reduction in the difference in zebra vigilance between individuals in zebra-only and mixed-species herds such that their vigilance levels would be comparable because the importance of dilution increases (e.g. Dehn, 1990). With regard to the extent to which zebra reduce their vigilance when foraging with low-diluting (i.e. impala) and diluting (i.e. wildebeest) herd partners, we predicted that detection benefits from these two partners would differ and thus the extent to which zebra reduced their vigilance would also differ. Moreover, we predicted that detection from the diluting partner, wildebeest, would result in a greater reduction of zebra vigilance than that from the low-diluting partner, impala. This is because the sharing of a common predator makes predator detection more reliable. Alternatively, impala could reduce zebra vigilance more than wildebeest because impala have more predators and, as a result, have potentially higher vigilance levels that could benefit zebra.

METHODS

We conducted our study during the end of the dry season (August–September 2011 and September 2013) in the iMfolozi portion of the Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa (28°20′S, 31°20′E) and Kruger National Park, South Africa (24.0125° S, 31.4854° E). Both universities approved all aspects of the research design (CARC Code: Wilmc1103; Ethics Code: 13/11/ Animal).

Data Collection

We recorded zebra vigilance from a stationary vehicle using binoculars. To ensure the same level of predator activity, we collected data 2 h after first light (ca. 0600 hours) and 2 h before last light (ca. 1800 hours) (as per Scheel, 1993). To minimize vigilance directed towards human disturbance, observations were made only when no other vehicles were present. In addition, only zebra herds that were more than 20 m away from the road were observed, to limit possible effects of our vehicle on their behaviour. Moreover, to control for habitat effects we limited observations to when herds were in open grasslands >50 m from woodland patches.

We determined individual vigilance by collecting focal samples. Within each herd, we observed as many individuals as possible; usually >75% of the total herd, but only recorded data from each individual once. We only sampled adult male and female zebras from mixed-sex herds (i.e. no bachelor herds) and, owing to the time of year, there were no dependent foals present during our study. To avoid pseudoreplication, we calculated a mean individual vigilance for each herd, and then used these values in the analyses (i.e. herds as replicates). Each observation began when the focal individual had its head down and was grazing. We recorded the rate and duration of each vigilance event that occurred during a 3 min foraging period. Vigilance events included any instances when the focal animal lifted its head above grazing height and scanned for potential predators, or focused its gaze and actively listened. We calculated the rate of vigilance behaviour as the number of head lifts during the 3 min observation period. We terminated an observation when the focal individual ceased foraging to engage in other, nonvigilant behaviour (e.g. grooming) or if the animal moved out of sight. We did not include observations if any individual in the herd displayed any vigilance behaviour towards us.

We defined a zebra-only herd as an aggregation of zebra that were feeding together within six adult body lengths (ca. 12 m)

from their nearest conspecific neighbour (see Scheel, 1993) which we visually estimated. A herd was considered to be mixed-species when at least one impala or wildebeest was within ca. 12 m of a zebra. In addition to frequency and duration measurements (mean seconds per 3 min), we recorded herd composition (mixed or single species) and the number of each species comprising the total herd. We made foraging observations only on adults of similar body size (i.e. no juveniles). We limited our mixed-species herds to zebra-only, zebra–wildebeest, zebra–impala and zebra–wildebeest–impala because they were the most common zebra herd types within both parks. Moreover, by using wildebeest and impala we were able to test the influence of diluting and low-diluting herd partners on zebra vigilance (see Hayward and Kerley's (2005) lion prey acceptability index).

Mixed-Species Effect

We tested whether zebra adjusted their vigilance in response to a 'mixed-species effect' (e.g. Kluever et al., 2009; Scheel, 1993). To do this, we first compared the relationships between total herd size and mean individual vigilance (herd as replicate) for zebra-only (herds: $N = 21$; focal individuals: $N = 122$) and mixed-species herds (herds: $N = 29$; focal zebra individuals: $N = 121$). This allowed us to: (1) evaluate whether overall there was a mixed-species effect, (2) determine how total herd size influenced zebra vigilance in zebra-only versus mixed-species herds, and (3) determine whether the magnitude of the mixed-species effect varied with total herd size. We also tested for a site effect by using 'site' (iMfolozi or Kruger) as a covariate, but found that it was nonsignificant. Thus, we removed it from further models.

Because our data had an overrepresentation of zero values (i.e. no vigilance behaviour observed for a focal zebra in a 3 min period), we employed a two-step procedure designed to deal with this type of non-normally distributed data. First, we used a chi-square analysis to determine whether the binominal probability (yes or no) that an individual zebra would display vigilance behaviour in a 3 min observation period differed as a function of herd composition (zebra-only versus mixed) and herd size (total number of ungulates). Second, we removed all zero values from the data set and then calculated herd vigilance means based on zebra that displayed any amount of vigilance behaviour. We tested for herd independence and found that each herd was not significantly different from the others, which allowed us to compare our herd mean data. We then used these herd means as the dependent variable in an ANCOVA to ask whether the time (mean seconds per 3 min) devoted to vigilance was related to herd composition (zebra-only versus mixed-species) and herd size. The total number of ungulates (i.e. zebra, wildebeest, impala) in a herd was the covariate. To achieve normality, we log transformed the data in JMP (v. 9). Because the full model revealed that the slopes of the relationship within zebra-only and mixed-species herds were significantly different, we did not run the reduced model (i.e. without the interaction term: herd composition∗herd size) to test for differences in the intercepts. For graphical representation, we back transformed the data.

In the analysis given above, the mixed-species effect was confounded by among-herd variation in both the number of zebra and the number of other ungulates. To isolate the mixed-species effect as a function of variation in the number of zebra in a herd, we compared vigilance in mixed and zebra-only herds for herds with similar numbers of zebra. To do this, we first assigned each zebra-only or mixed-species herd to one of three zebra herd size categories based on the number of zebra present: small (1–9 zebras: zebra-only: $N = 14$; mixed: $N = 20$), medium: (10–30 zebras: zebra-only: $N = 5$; mixed: $N = 5$) and large (>30 zebras: zebra-

only: $N = 2$; mixed: $N = 3$). These size categories were determined by natural breaks in the data. We then used a two-way ANOVA to test whether mean time (seconds per 3 min) spent vigilant (herd as replicate) was related to herd composition (zebra-only versus mixed-species) and zebra herd size category. To control for variation in the number of ungulates present within each of these size categories, we included the number of nonzebra ungulates as a covariate in the initial model. The covariate was nonsignificant and thus removed from the final model. Once again, we log transformed vigilance times and back transformed the data for graphical presentation.

Benefit of Joining a Mixed-Species Herd

To obtain an empirical estimate of the benefit to zebra in joining a mixed-species herd, we fitted separate functions to zebra vigilance. We used the vigilance trend line from mixed ($y = 30.839x^{-0.229}$, $r^2 = 0.966$) and zebra-only ($y = 0.006x^2 - 1.008x + 59.473$, $r^2 = 1$) herds based on the number of zebra within each herd. The difference between the values of these two fitted relationships yields, as a function of the number of zebra in a herd, an estimate of the time (seconds per 3 min) that an individual devoted to vigilance in a zebra-only herd that could have been devoted to other nondefensive behaviours in a mixed-species herd.

Dilution or Detection across Herd Types

To tease apart the effects of dilution and detection, we recorded the time zebra were vigilant in each of the four herd types [i.e. zebra-only (herds: $N = 22$; focal individuals: $N = 97$), zebra–wildebeest (herds: $N = 6$; focal individuals: $N = 46$), zebra–impala (herds: $N = 8$; focal individuals: $N = 21$), zebra–wildebeest–impala (herds: $N = 6$; focal individuals: $N = 24$)]. We used an ANCOVA to test whether zebra vigilance was influenced by the herd type with the total number of ungulates in a herd used as the covariate. By using this covariate, we were able to control for the total number of ungulates and were able to test directly for mixed-species detection, which is reduced individual vigilance of zebra resulting from herding with other ungulate species. Prior to analysis, we transformed the data using the best fit Box Cox Y transformation. Data were then back transformed for purposes of plotting on an arithmetic scale.

In addition, we determined whether the proportion of the herd comprising impala versus zebra and wildebeest versus zebra influenced zebra vigilance. We used a regression with the proportion of the herd comprising the nonzebra ungulates (zebra focal individuals in impala herd: $N = 28$; zebra focal individuals in wildebeest herd: $N = 34$) as the independent variable and zebra time spent vigilant as the dependent variable.

Vigilance Levels in Different Herd Types

We found significant differences in the reduction of zebra vigilance across the different herd types (see Results). In an effort to explain these differences, we compared vigilance levels of impala in impala-only herds (herds: $N = 14$; focal individuals: $N = 55$) and wildebeest in wildebeest-only herds (herds: $N = 8$; focal individuals: $N = 28$) with that of zebras in zebra-only herds (herds: $N = 12$; focal individuals: $N = 39$). To estimate differences in time spent vigilant, we used an ANCOVA with time spent vigilant as the dependent variable and species (zebra, wildebeest or impala) as the independent variable. Total herd size was the covariate to control for differences in total herd sizes.

RESULTS

Mixed-Species Effect

For a given total herd size, zebra were more vigilant when they fed with conspecifics (i.e. zebra-only herds) than when they fed in a mixed-species herd (chi square: $\chi^2 = 4.63$, $P = 0.03$). The fraction of time zebra devoted to vigilance declined sharply with increasing total herd size when they fed in zebra-only herds (Fig. 1). In contrast, in mixed-species herds, zebra spent far less time vigilant and this did not change with increasing herd size (Fig. 1, Table 1). As a result, the time devoted to vigilance for the two herd types converged at a herd size of about 65 individuals indicating where the mixed-species effect disappeared (Fig. 1).

A similar pattern was evident when time devoted to vigilance was expressed as variation in the number of zebra in a herd (Fig. 2, Table 2). For small and medium zebra herds (i.e. 1–9 and 10–30 individuals), zebra were far more vigilant when they occurred in zebra-only herds than in mixed-species herds (Fig. 2). However, vigilance levels did not differ in large herds. Overall, vigilance levels of zebra in both herd types declined with increasing total herd size, but the decline was more severe in zebra-only herds (Fig. 2, Table 2).

Our estimate of the benefit to zebra of foraging in small mixed-species herds shows that zebra devoted about 30% less time to vigilance than in zebra-only herds. This benefit decreased as the number of individuals in a herd increased (Fig. 3).

Benefit of Joining a Mixed-Species Herd

We found a significant difference in zebra vigilance across the four herd types (ANCOVA: $F_{3,38} = 8.356$, $P < 0.001$). The covariate, total number of ungulates in the herd, was not significant ($F = 0.282$, $P = 0.599$). When zebra foraged with just impala, a low-diluting partner, they did not lower their vigilance levels significantly compared with when feeding in zebra-only herds (Fig. 4). Because herd size, and thus dilution effects, were controlled for statistically, this suggests that impala did not provide a perceived detection benefit to the zebra. However, even though we aimed to control only for the effects of dilution, we accept that we most likely also controlled for some of the detection benefits associated with increasing herd size (e.g. many eyes). These benefits, however, would only comprise a proportion of the overall detection benefits because not all detection benefits are linked to herd size (e.g.
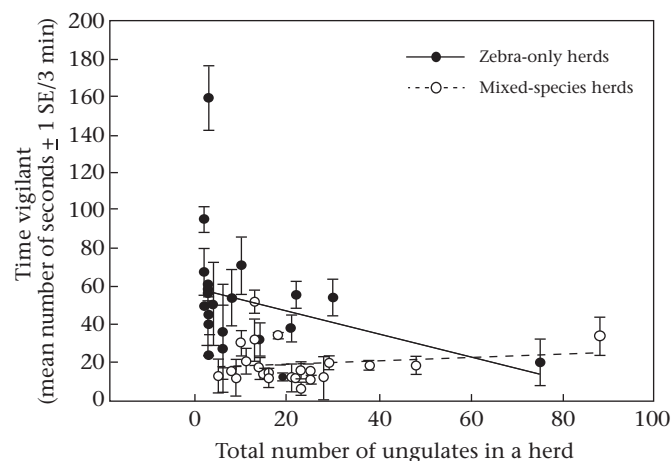
difference in vigilance behaviours and sensory modes). Moreover, if statistically we had controlled for all of the detection benefits by using herd size as a covariate, we would have found no differences in vigilance levels between the herd types (Fig. 4). Furthermore, if it were possible to statistically limit the control to dilution only, the additional detection benefits would probably only strengthen the relationships we present in Fig. 4.

In contrast to when zebra foraged with just impala, when feeding with wildebeest, a dilution partner, zebra substantially lowered their vigilance levels compared with zebra-only herds (Fig. 4). Similarly, when zebra foraged with both wildebeest and impala, they lowered their vigilance levels down to where they did not differ to those achieved when foraging in zebra–wildebeest herds (Fig. 4). The similarity in these vigilance levels indicates that the perceived antipredator benefits were driven by the zebras' association with wildebeest, and that no additional benefits were gained from herding with impala.

Zebra vigilance was not influenced by the proportion of the herd that comprised wildebeest (regression: $F = 2.00$, $P = 0.167$, $r^2 = 0.058$). However, as the proportion of impala in the herd increased, zebra significantly lowered the time they spent vigilant (regression: $F = 0.001$, $P = 0.015$, $r^2 = 0.345$). When the proportion of impala in the herd reached 75%, zebra vigilance levels approached similar levels to those of zebra herding with wildebeest.

Vigilance Levels in Different Herd Types

Zebra, wildebeest and impala all displayed significantly different levels of vigilance within their respective conspecific
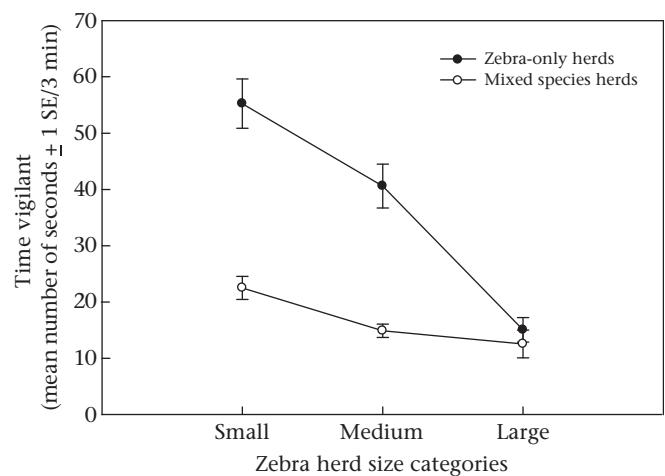
Table 1
ANCOVA results showing how vigilance levels were influenced by herd composition

Source	df	Mean square	F ratio	P
Herd type	1	1.453	27.851	**<0.001**
Total ungulates	1	0.092	1.766	0.190
Herd type∗Total ungulates	1	0.248	4.747	**0.035**
Error	46	0.052		

'Total ungulates' is the size of the foraging herd (a continuous variable) and 'Herd type' is whether the herd is a zebra-only herd or a mixed-species herd. Significant P values are shown in bold.

Figure 1. Relationship between zebra vigilance and number of ungulates in a herd for zebra-only and mixed-species herds with increasing herd size.

Figure 2. The relationship between time spent vigilant by zebra in zebra-only and mixed-species herds and size of the herd (based on number of zebra) when the total number of ungulates is controlled for. Data are the (back transformed) least squares means ± SE for small (2–9 zebra), medium (10–30) and large (31–75) herds.

Table 2
Results of an ANCOVA for time spent vigilant as a function of herd size category for zebra (small, medium and large) and herd type (single-species or mixed-species)

Source	df	Mean square	F ratio	P
Herd type	1	0.360	7.457	**0.009**
Size category	2	0.095	1.978	0.151
Herd type * Size category	2	0.155	3.218	**0.05**
Error	44	0.048		

Significant *P* values are shown in bold.

herds (ANCOVA: $F_{3,111} = 12.5$, $P < 0.001$). Impala displayed proportionally the highest vigilance (0.28), followed by zebra (0.19) and then wildebeest (0.10).

DISCUSSION

Both dilution and detection probably contribute to the well-known phenomenon where individuals reduce personal vigilance as group size increases (Roberts, 1996). However, a major challenge has been to understand the contributions of, and interactions between, these simultaneously operating mechanisms in shaping group size effects on vigilance (e.g. Bednekoff & Lima, 1998; Childress & Lung, 2003; Elgar, 1989). Based on the fit of vigilance data to models for Rocky Mountain elk, Dehn (1990) concluded that detection was more beneficial in small herds whereas dilution was more important in large herds. Similarly, our results indicate that the benefits of detection can be greatly amplified in mixed-species herds, especially in small herds in which dilution affords relatively little protection when compared with large herds. Moreover, we found that in small and medium herds, zebra herding with wildebeest, a diluting herd partner, showed lower vigilance levels than when zebra herded with impala, a low-diluting species.

Mixed-Species Effect

Several studies have reported a 'mixed-species' effect where the individual vigilance–group size relationship differed depending on whether the focal species occurred in conspecific-only herds or with other species (Kluever et al., 2009; Périquet et al., 2010; Scheel, 1993). Despite this, the mechanisms underlying this phenomenon have largely remained unexplored. In this study,

we found a substantial mixed-species effect with zebra foraging in zebra-only herds devoting more than twice the amount of time to being vigilant in small and medium herds than those in mixed herds. However, this benefit diminished with increasing total herd size to where there was no added vigilance benefit once herd size reached about 65 individuals. In mixed-species herds, individual vigilance by zebra was insensitive to variation in total herd size, which is a sharp contrast to when they foraged in zebra-only herds.

This mixed-species effect is consistent with findings reported for individual vigilance of African herbivores while drinking (Périquet et al., 2010), for several common prey species of lion (Scheel, 1993) and for a study on cattle (Kluever et al., 2009). Périquet et al. (2010) found that kudu, *Tragelaphus strepsiceros*, drinking in mixed-species herds significantly lowered their vigilance behaviour, and thus were able to drink for longer periods of time than when they drank only with conspecifics. Scheel (1993) found that the scan rates of lion prey species are reduced not only by the number of conspecifics in a herd, but also by the number of heterospecific herd mates. The results of this field study are supported by a controlled experiment performed by Kluever et al. (2009), which found that cattle exhibited a decrease in vigilance behaviour when they foraged in the presence of deer stimuli (scent and dummy deer) compared with when there were no stimuli present. These results indicate that deer reduce the perceived predation risk of cattle, but it is not clear whether dilution or detection reduced cattle vigilance.

In our study, simple dilution cannot explain the mixed-species effect we recorded. Our findings suggest that detection contributes to a greater degree than dilution, especially in small and medium herd sizes. This is characterized by greater differences in vigilance times among zebra in zebra-only versus mixed-species herds. However, the individual vigilance levels of zebra in mixed-species and zebra-only herds converged at very large herd sizes (ca. 65+ individuals). This tends to support Dehn's (1990) general prediction that as herd size increases, the detection relative to dilution benefits will diminish. In mixed-species herds, this reduction is probably due to a decrease in the benefits of complementary sensory (differences in hearing or visual abilities) and/or behavioural modes (e.g. scanning rates and frequency).

The reduction in vigilance in large herds could be a result of the overall benefit of safety in numbers that arises from dilution. One
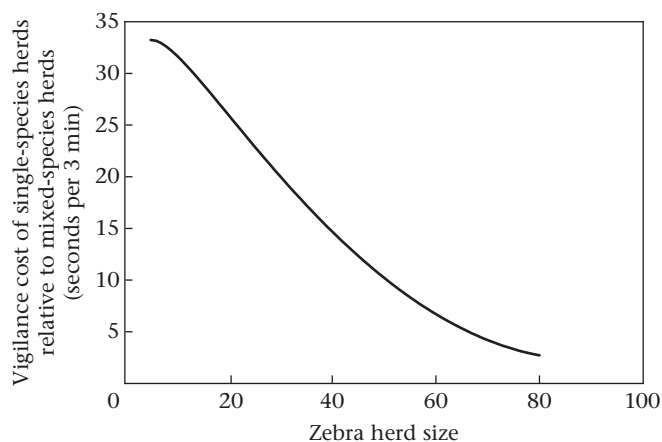
Figure 3. The estimated benefit of zebra foraging in mixed-species herds relative to zebra-only herds as a function of the number of zebra in a herd. Plotted is the number of additional seconds per 3 min observation period that individual zebra in zebra-only herds devoted to vigilance scans over that spent by individual zebra in mixed-species herds.
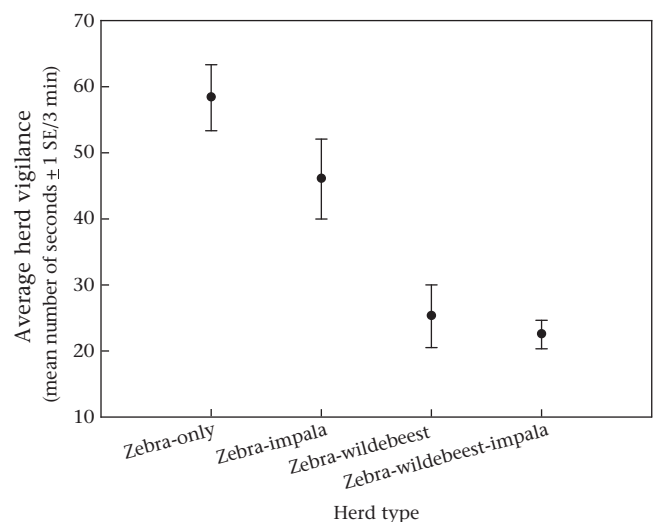
Figure 4. Vigilance time of individual zebra in various herd compositions. Impala are a low-diluting partner and wildebeest are a diluting partner.

possible reason that detection is not as powerful as dilution in large herd sizes could be that as herd size increases, individuals find it harder to collect social information (e.g. alarm call or flight response) from individuals on the other side of the herd (Lima, 1995; Lima & Zollner, 1996). This reduction in collective detection was found in shorebirds in which, beyond a certain distance away from a focal individual, the benefits of detection were lost (Metcalfe, 1984). It is possible that zebra are less likely to detect alarm calls or respond to antipredator behaviours (e.g. fleeing) of other individuals across a large herd (conspecifics or other ungulate species) as the distance is too great. However, a similar argument could be made for the effects of dilution. For individuals on the side closest to the predator, dilution benefits would not cover the whole herd, but rather be limited to nearby individuals. Nevertheless, these benefits can still be fairly large because the presence of a single other individual cuts predation risk in half. Thus, in large herds the reduction in detection benefits (e.g. not hearing alarm calls) is more severe than a reduction in dilution benefits (e.g. an increase in the probability of being attacked).

Dilution or Detection across Herd Types

Herding with other species can reduce an individual's risk via dilution, but only when the group members share the same predator (Leuthold, 1977; Metcalfe, 1984). The same can be true for different age classes of the same species that have different predators (e.g. white rhino, *Ceratotherium simum*; Shrader et al., 2013). However, an individual can potentially benefit via detection by associating with another species regardless of whether they share the same predator (a diluting partner) or not (a low-diluting partner). For a given herd size, differences in individual vigilance between zebra-only and mixed-species herds could arise from differences in (1) predator prey preference (i.e. dilution) or (2) sensory modes/vigilance behaviours between ungulate species (i.e. detection).

To further tease apart the influences of dilution and detection on zebra vigilance, we controlled for herd size (hence dilution) and compared zebra vigilance in the four herd combinations. From this analysis, we found that vigilance levels of zebra varied substantially with herd type. In an effort to explain these differences, we assessed the vigilance levels of two other plains game species. Although impala were the most vigilant species in our study, we found that zebra did not generally take advantage of this. Specifically, when the herd comprised <75% impala, zebra did not significantly reduce their vigilance. This suggests that for these herd compositions, the potential vigilance benefits gained from the relatively few (at least from a zebra's perspective) impala (i.e. <75%) were not great enough to reduce the zebras' perceived predation risk. Thus, even though in some cases >50% of the herd comprised impala, zebra continued to maintain high vigilance levels. However, once impala comprised about 75% of the mixed-species herd, zebra considered the benefits gained from the large number of highly vigilant impala great enough to reduce predation risk and thus allow the zebra to lower their vigilance.

One reason why the proportion of impala in these mixed-species herds had to be so high for zebra to consider the benefits sufficient could be that zebra may generally ignore vigilance cues from impala. This may be because several of the impala's predators (e.g. hyaena and wild dog) use different hunting tactics from lion (stalking). Ultimately, predator hunting tactics may determine the frequency and duration of vigilance behaviour needed to detect predators. Thus, the vigilance of prey species whose predators use different tactics may not be beneficial to each other. For example, Grant's gazelles, *Gazella granti*, act as sentinels for stalking predators in mixed-species herds of Thomson's,

Gazella thomsoni, and Grant's gazelles (FitzGibbon, 1990). However, despite these sentinels, Thomson's gazelles do not reduce their vigilance because the early detection benefits provided by Grant's gazelles do not reduce predation risk from cursorial predators such as wild dog and hyaena (FitzGibbon, 1990). They may, however, lower predation risk from hyaena by moving in these herds because hyaena prefer Grant's over Thomson's gazelles (Hayward, 2006). Despite this, it is possible that the mixed-species effect patterns that we recorded with zebra and wildebeest might only exist in situations in which predators shared by different prey species use the same hunting tactic (also see Bednekoff & Lima, 1998).

In contrast, zebra herding with wildebeest had substantially lower vigilance levels than those herding with conspecifics or impala. We also found that the presence of a single wildebeest resulted in a significant reduction in zebra vigilance. Furthermore, an increase in the proportion of wildebeest comprising the herd had no further effect on zebra vigilance. Additionally, when zebra, wildebeest and impala all herded together, there was no further benefit perceived by zebra.

It is possible that the dissimilarities in zebra vigilance levels in the different herds reflect the zebras' vigilance/social monitoring of other group members (i.e. both conspecifics and heterospecifics). This monitoring would allow zebra to obtain social information about the location of high-quality patches (i.e. local enhancement; Shrader, Kerley, Kotler, & Brown, 2007), assess the overall quality of an area (i.e. use public information; Valone & Templeton, 2002), and potentially limit competition (Tchabovsky, Popov, & Krasnov, 2001). Assuming that the herbivores in our study selected food patches (e.g. grass height) based on their body size (Bell, 1970, 1971) and/or the combination of body size and relative mouth dimensions (Arsenault & Owen-Smith, 2008), then we would expect that zebra would have high levels of vigilance/social monitoring when feeding with wildebeest, because they are closer in body size (zebra: 290–340 kg; wildebeest: 180–250 kg) and thus more likely to compete for food. In contrast, zebra should have lower vigilance levels when feeding with impala (40–70 kg) because they are less likely to compete for the same food (Arsenault & Owen-Smith, 2008). We did not find this, however. Rather, we found the opposite (Fig. 4).

Our results are probably explained by the work of Arsenault and Owen-Smith (2008) from the Hluhluwe-iMfolozi Park (where we conducted half our study), where they found that when feeding in the same habitats, zebra and wildebeest fed from significantly different grass heights, whereas zebra and impala utilized grass swards of the same height. In addition, Sinclair (1985) found similar foraging patterns between zebra, wildebeest and impala in the Serengeti–Mara region. Thus, the results of these studies suggest that competition for food is probably greater between zebra and impala than between zebra and wildebeest. As a result, our findings suggest that social monitoring may explain the higher vigilance levels of zebra when they fed with impala. However, the proportion explained by social monitoring is likely to be small because zebra do not maintain high vigilance levels when they feed in herds containing both impala and wildebeest. Moreover, because social monitoring tends to increase as the number of potential competitors increases (Favreau, Goldizen, & Pays, 2010), we would expect vigilance levels of zebra to increase as the proportion of impala in mixed-species herds increased. This, however, was not the case. Thus, even if social monitoring explains some of the zebras' vigilance, our results indicate that antipredator scanning was the main function behind the vigilance that we recorded. However, our experimental design does not allow us to determine the degree to which this vigilance can be divided into high- and low-cost vigilance (Hochman & Kotler, 2007).

We see two nonmutually exclusive potential explanations for our species-specific vigilance results. First, although wildebeest reduced zebra vigilance, we found that wildebeest were the least visually vigilant (lowest time spent vigilant). This suggests that they may have alternative vigilance methods based perhaps on superior senses of smell and/or hearing. Unfortunately, we were unable to quantify the use of these senses for vigilance by wildebeest. To our knowledge, the differences in sensory abilities of African plains game have not been widely studied. Thus, it is possible that wildebeest and zebra may have complementary sensory modes that enhance antipredator defence. If correct, this would help explain why zebra view wildebeest as a more reliable source of antipredator information than impala and, surprisingly, even other zebras.

It is also possible that zebra and wildebeest are not as equally preferred by lions. Hayward and Kerley (2005) categorized both zebra and wildebeest as preferred prey items of lion. However, it is plausible that when given a choice, lion may prefer to attack wildebeest. Zebra are noted as one of the few ungulate species that actively defends against predation through violent kicking (Kruuk, 1972), which could injure attacking lions. Thus, the cost of injury might be higher than the reward of a zebra kill to a lion when a second, similar-sized, less defensive prey species is present. If this is the case, zebra would then benefit by herding with the somewhat preferred/more vulnerable wildebeest, and thus they could reduce their vigilance.

Conclusions

Ultimately, our results support the findings of Dehn (1990). We found that detection was more important in small and medium herds and that dilution was more important in large herds. However, unlike previous studies (Bednekoff & Lima, 1998; Childress & Lung, 2003; Dehn, 1990; Elgar, 1989), we were able to tease apart the relative importance of detection and dilution in reducing vigilance by using mixed-species herds. For zebra, the benefit gained from detection was determined by herd partner. Interestingly, diluting species (i.e. wildebeest) provided a greater reduction in perceived predation risk (i.e. lower zebra vigilance) than when zebra foraged in zebra-only herds. In contrast, low-diluting species (i.e. impala) provided no benefit in reducing zebra vigilance. However, as the proportion of low-diluting individuals in a herd increased past a critical point, zebra considered the benefits similar to those obtained from diluting individuals. Thus, the benefits gained by herding with other species may explain why zebra predominantly move in mixed-species herds.

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