



## RESEARCH PAPER

# The Effect of Simulated African Wild Dog Presence on Anti-predator Behaviour of Kudu and Impala

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**Abstract**

In this study, we examined the behavioural, temporal and spatial effects of simulated African wild dog (*Lycaon pictus*) presence on its two main prey species: kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*). We spread African wild dog faeces around waterholes and played African wild dog sounds at different intervals to mimic immediate and non-immediate predation pressure. We looked at anti-predator behaviour at both a herd and individual level and distinguished between high-quality (detracts from all other activities), high-cost vigilance and low-quality (used to monitor the surrounding in spare time), low-cost vigilance to determine costs involved. We found that simulated African wild dog presence had little effect on anti-predator behaviour of their free-ranging prey. Only when immediate predation risk was mimicked did kudu invest in (additional) high-quality vigilance, whereas impala showed no response. Regardless of direct cues of African wild dog presence, behavioural adjustments to reduce predation risk were primarily based on environmental factors such as time of the day and broad-scale habitat structure. Predators have been shown to utilize waterholes to hunt, and prey species are therefore likely to maximize anti-predator behaviour in this high-risk environment based on environmental variables affecting predation risk, the main predator within the system, and water requirements, leaving little flexibility to respond to (simulated) African wild dog presence.

**Introduction**

For prey, the risk of predation often varies over time and space, and how prey deals with such variation has received both empirical and theoretical interest (Brown 1999; Laundré et al. 2001; Schmitz 2005). In response to an increase in predation risk, prey species have been shown to make behavioural as well as temporal and spatial adjustments by increasing the investment in vigilance behaviour (Hunter & Skinner 1998; Lung & Childress 2007; Périquet et al. 2010) and by avoiding risky areas or time frames (Valeix et al. 2009). Moreover, in spite of potential costs asso-

ciated with competition for food access (Valone 1993; Molvar & Bowyer 1994), social foragers benefit from an increased ability to detect predators (Roberts 1996; Ruxton 1996) as well as a reduction in the individual risk of being preyed upon (Wrona & Jamieson Dixon 1991). While mechanisms underlying individual responses of prey facing natural predation have received attention, experimental studies simulating the presence of a predator (via playbacks, faeces and/or urine) have provided a useful framework to investigate immediate behavioural adjustments of prey to predation risk (Parsons & Blumstein 2010; Biedenweg et al. 2011).

One of the most studied responses allowing prey to reduce predation risk is the time allocated to vigilance (Lima 1995). Even in the absence of imminent attack, prey should maintain a baseline level of vigilance because of a constant risk of predation (Ripple et al. 2001; Childress & Lung 2003). Many different factors affect the relationship between predation risk and vigilance behaviour, for example, herd size (Burger et al. 2000), presence of other herbivores (Morse 1977; Périquet et al. 2010), visibility (Burger 2001; Pays et al. 2012) and distance to cover (Underwood 1982; Burger et al. 2000). Although, even when predation risk is high, prey tends to reduce time spent vigilant when associated with conspecifics (Scheel 1993; Burger et al. 2000; Lung & Childress 2007; Périquet et al. 2010), it seems that individual predation risk is, nevertheless, related to the vigilance level of individuals; predators seem to preferentially attack non-vigilant prey as they tend to react slower upon attack than vigilant individuals, hence are more likely to be killed (Fitzgibbon 1988; Krause & Godin 1996; Hilton et al. 1999; Sirot & Touzalin 2009). Examining how the proportion of vigilant individuals varies over time with variations in the intensity of predation risk might therefore reveal the ability of an immediate behavioural adjustment of prey to limit group vulnerability.

Prey generally have to trade off time between detecting predators by being vigilant and other activities like feeding (Underwood 1982; Brown 1999; Childress & Lung 2003) and drinking (Burger & Gochfeld 1992). Vigilance then has costs, as the time spent vigilant reduces the time available for feeding and drinking. Several studies have shown that, to reduce the high costs that exclusive vigilance requires, prey can spend time vigilant while foraging, for example, birds handling seeds (Popp 1988; Baker et al. 2011) and mammals chewing with their heads up (Fortin et al. 2004; Makowska & Kramer 2007). It has therefore been suggested to distinguish between different types of vigilance behaviour: (1) high-quality vigilance (used when responding to a stimulus) that detracts from feeding and is therefore costly and (2) less costly low-quality vigilance (used to monitor the surroundings) that does not disrupt the ingestion process (Lima & Bednekoff 1999; Blanchard & Fritz 2007).

In this study, we examined the behavioural, temporal (avoidance of high-risk time frames) and spatial (avoidance of risky waterholes) responses of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*) on variations in predation risk by mimicking the presence of one of their predators, the African wild dog (*Lycaon pictus*). At both an individual and herd level, we tested for vigilance while drinking, as preda-

tors are likely to search for prey in the vicinity of waterholes (Valeix et al. 2010; Van der Meer 2011). To be able to study with more scrutiny the short-term response to (mimicked) predation risk, we discriminated between high- and low-quality vigilance. We expected that prey would make behavioural as well as temporal and spatial adjustments in response to an increase in predation risk, that is, during time periods when predators are active. We expected behavioural adjustments to be most apparent at the individual level when immediate predation risk was mimicked and temporal and spatial adjustments to be most apparent 24 h after immediate predation risk was mimicked.

## Method

### Study Area

Hwange National Park, hereafter HNP, covers 15 000 km<sup>2</sup> in the north-west of Zimbabwe (19°00'S, 26°30'E). The Hwange region is classified as semi-arid with a mean annual rainfall of 606 mm and a wet season from Oct. to Apr. Data were collected along the northern boundary of HNP covering part of HNP and its peripheral areas. The area inside HNP is a protected wildlife area. The buffer zone outside HNP is destined for trophy hunting and to a lesser extent photographic safaris.

We selected six pumped waterholes that were situated within areas frequently visited by African wild dogs, three waterholes inside HNP and three waterholes in photographic safari areas in the buffer zone outside HNP. Other predators visiting these waterholes include lion (*Panthera leo*) [density inside HNP: 2.6 ind/100 km<sup>2</sup>, outside HNP: 2.2 ind/100 km<sup>2</sup> (Elliot 2007)] and spotted hyena (*Crocuta crocuta*) [density inside HNP: 11.3 ind/100 km<sup>2</sup>, outside HNP: 5.5 ind/100 km<sup>2</sup> (Elliot 2007)]. Spoor densities indicate that leopard (*Panthera pardus*) and cheetah (*Acinonyx jubatus*) densities are relatively low, and both species are more abundant outside compared with inside HNP (Elliot 2007). All six waterholes are within commonly used photographic safari areas and are therefore regularly visited by game drive vehicles. The minimum distance between the waterholes was 10 km and the maximum distance 30 km. The waterholes were all situated in open areas with average visibility ranging between 100 and 200 m.

### Behavioural Observations

Behavioural observations were made during the dry season in Aug. and Sep., the months during which

waterhole attendance is high as natural waterholes have dried up and animals depend on artificial waterholes only. All observations were made from the car, parked at a distance from the waterhole as not to disturb the animals, from 6:00 till 18:00 h. Previous studies have shown that predation risk can be mimicked by playing the sound of a natural predator (Durant 2000; Blanchard & Fritz 2007; Blumstein et al. 2008; Webster et al. 2012). We mimicked African wild dog presence by playing sounds of African wild dogs commencing the hunt and by spreading 5 l of dissolved African wild dog faeces around the waterhole. As soon as a kudu or impala herd would come into view at a distance  $\leq 150$  m from the waterhole, the behaviour of all the individuals would be monitored every 30 s by means of a visual scan until all the individuals in the herd had finished drinking and moved away from the waterhole at a distance  $\geq 150$  m. As soon as 50% of the herd started drinking, a video was taken from which the different behaviours, sex, age, body condition (classified as low, medium or good) and position of the individuals in the herd, were determined. When analysing the video, the behaviour of the individuals within the herd was monitored during the same time span for the first 2 min or, in cases where this was not feasible, 1 min. Vigilance behaviours recorded for analysis were as follows: (1) high-quality vigilance: the animal detracts from drinking and is standing in a highly alert posture with its head up above shoulder level and ears pointed forward, and (2) low-quality vigilance: the animal is not detracted from drinking and points ears forward while drinking or lifts its head below shoulder level with ears pointed forward while it continues to swallow water.

Each waterhole was visited 3 d in a row. The first day served as a control day (C). During the second day, immediate predation risk was mimicked by spreading African wild dog faeces around the waterhole early in the morning and playing the sounds of African wild dogs each time a herd of kudu or impala came down to drink (FS). On the third day, non-immediate predation risk was mimicked by spreading African wild dog faeces around the waterhole and playing the sounds of African wild dogs early in the morning at first light when African wild dogs normally start hunting, before any of the studied prey species had come to the waterhole to drink (F). At each waterhole, this experiment was repeated 1 mo later.

The time a herd spent drinking was measured as the difference between the time when the last individual of the herd stopped drinking and the time

the first individual of the herd had started drinking. The herd size, sex and age structure, the time of visiting the waterhole and environmental factors that could affect the observed behaviour were noted. Times were divided into four categories, early morning (06:00–09:00 h), late morning (09:00–12:00 h), early afternoon (12:00–15:00 h) and late afternoon (15:00–18:00 h). The visibility around the waterhole was assessed by measuring the distance between the water's edge and the surrounding vegetation in the N, NE, E, SE, S, SW, W and NW directions. One observer was standing by the waterhole while another person walked away with the GPS to measure the distance at which the observer lost sight of this person. The average of these distances was used as a visibility index for the waterhole.

### Statistical Analysis

Controlling for species and herd size, primary analyses revealed no differences in high- or low-quality vigilance between sex ( $p \geq 0.517$ ), age ( $p \geq 0.154$ ) and sequence duration (1 vs. 2 min) ( $p \geq 0.450$ ). To avoid pseudoreplication, we therefore took the average proportion of time spent high-quality vigilant and low-quality vigilant from all individuals within a given herd. Kudu and impala were analysed separately. For the final analysis, the sample size for impala was 89 ( $\geq 24$  herds per experimental day); for kudu, the sample size was 115 ( $\geq 31$  herds per experimental day). As all animals observed were in good body condition, this variable was left out of the analysis.

For the analysis of individual anti-predator behaviour, we used a linear fixed effects model to test for differences in the proportion of time spent high-quality vigilant with experimental day, time of the day and whether there were other herbivores present as fixed factors. Whether the waterhole was located inside or outside HNP was added as a fixed factor as well to control for differences in land use and predator densities. Herd size and average visibility around the waterhole were added as covariates. We only tested for two-way interactions (experimental day  $\times$  time of day, experimental day  $\times$  visibility, experimental day  $\times$  herd size) that (1) could explain the anti-predator response to the experimental treatment, (2) could be interpreted in terms of mechanisms underlying individual decisions of prey to exhibit vigilant behaviour, (3) allow to maintain an acceptable degree of freedom in the analysis considering the large number of independent (continuous and categorical) variables and (4) fulfil the statistical requirements against

multicollinearity. However, as none of these cited interactions were significant, they were left out of the final model. To control for a possible effect of the month in which the experiment was conducted, month was added to the model as a fixed factor. In summary, the final model included experimental day, time of the day, herbivore presence, location of the waterhole, month, herd size and visibility as independent variables and the proportion of time spent high-quality vigilant as the dependent variable. The same analysis was performed for the proportion of time spent low-quality vigilant.

Visual scans of the herds were used to determine the average proportion of the herd vigilant for the entire scan duration. To meet the normality assumption, all proportions were arcsine-square-root-transformed. For the analysis of the proportion of the herd vigilant and the analysis of the time spent drinking, we used a linear fixed effects model with the same variables as described for the analysis of high- and low-quality vigilance.

A linear fixed effects model was also used to test for differences in the number of herds visiting the waterhole. Experimental day, time of day, location of the waterhole and month were added as fixed factors. Average visibility around the waterhole was added as a covariate. To test for a possible shift in time frames used to drink during the different experimental days, the two-way interaction between experimental day and time of day was added to the model.

With the lack of agreement on the best model approach to analyse behavioural data (Murtaugh 2009), we decided to present the full models rather than perform an AIC-based or stepwise model selection, as this will allow a comprehensive description of all variables tested (see Pays et al. 2012). Before entering the variables into the model, we tested for collinearity by looking at tolerance statistics and the variation inflation factor (VIF); tolerance was always  $\geq 0.63$ , and all VIF's were  $\leq 1.77$ .

All statistical analyses were performed with SPSS software version 16.0 (SPSS Inc, Chicago, IL, USA).

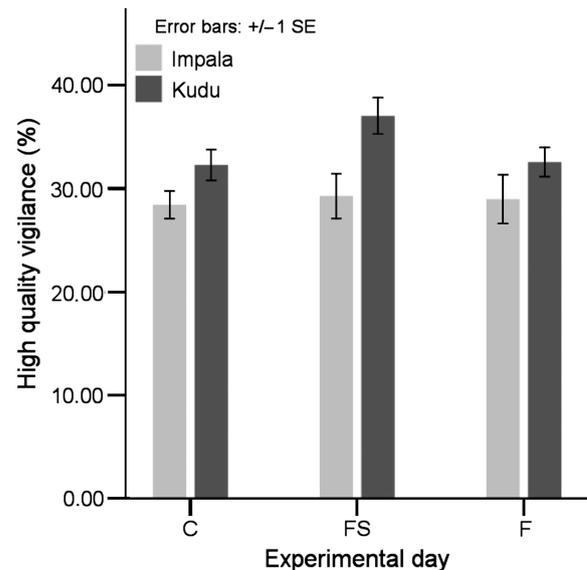
## Results

### Individual Anti-Predator Behaviour

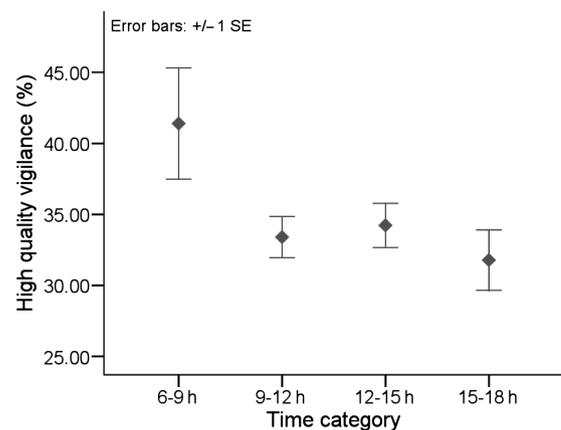
#### *High-Quality Vigilance*

The proportion of time individual kudu spent high-quality vigilant was significantly affected by the experimental treatment ( $F_{2,115} = 3.28$ ,  $p = 0.04$ ). A higher proportion of time was spent high-quality vigilant on the second experimental day (FS) compared

with the third (F) and the control day (C) (coef  $\pm$  SE =  $4.51 \pm 2.09$ ,  $p = 0.03$ ) (Fig. 1). There was no difference in proportion of time individual kudu spent high-quality vigilant between the third day (F) and the control day (C) (coef  $\pm$  SE =  $0.21 \pm 2.17$ ,  $p = 0.93$ ) (Fig. 1). Time of the day also significantly affected the proportion of time spent high-quality vigilant ( $F_{3,115} = 3.29$ ,  $p = 0.02$ ). Individual kudu spent a smaller proportion of time high-quality vigilant in the late morning, early afternoon and late afternoon compared with the early morning (coef  $\pm$  SE =  $10.39 \pm 3.37$ ,



**Fig. 1:** The proportion of time individual kudu and impala spend high-quality vigilant during the three experimental days: control day (C), African wild dog faeces and sound upon arrival (FS), African wild dog faeces and sound early in the morning (F).



**Fig. 2:** The proportion of time individual kudu spend high-quality vigilant during the early morning (6–9 h), late morning (9–12 h), early afternoon (12–15 h) and late afternoon (15–18 h).

$p < 0.01$ ) (Fig. 2). The proportion of time spent high-quality vigilant increased with visibility (coef  $\pm$  SE =  $0.06 \pm 0.03$ ,  $F_{1,115} = 4.01$ ,  $p = 0.05$ ). There was a marginally negative herd size effect on the proportion of high-quality vigilance (coef  $\pm$  SE =  $-0.41 \pm 0.22$ ,  $F_{1,115} = 3.62$ ,  $p = 0.06$ ). Whether the waterhole was placed inside or outside HNP, the presence of other herbivores or month did not significantly affect the proportion of time individual kudu spent high-quality vigilant (all  $p \geq 0.13$ ).

The experimental treatment did not affect the proportion of time individual impala spent high-quality vigilant ( $F_{2,89} = 0.01$ ,  $p = 0.99$ ) (Fig. 1) neither did herd size, visibility, time of the day, the presence of other herbivores around the waterhole, whether the waterhole was placed inside or outside HNP or month (all  $p \geq 0.07$ ).

#### Low-Quality Vigilance

The experimental treatment did not affect the proportion of time individual kudu spent low-quality vigilant ( $F_{2,115} = 0.51$ ,  $p = 0.60$ ), neither did herd size, visibility, time of the day, the presence of other herbivores around the waterhole, whether the waterhole was placed inside or outside HNP or month (all  $p \geq 0.07$ ).

The proportion of time individual impala spent low-quality vigilant was not affected by the experimental treatment ( $F_{2,89} = 0.62$ ,  $p = 0.54$ ). Low-quality vigilance of impala increased with visibility (coef  $\pm$  SE =  $0.04 \pm 0.02$ ,  $F_{1,89} = 4.41$ ,  $p = 0.04$ ). There was no effect of herd size, time of the day, the presence of other herbivores, whether the waterhole was located inside or outside HNP, or month (all  $p \geq 0.33$ ).

### Herd Anti-Predator Behaviour

#### Vigilance Behaviour

For kudu, the experimental treatment did not affect the proportion of the herd engaged in vigilance behaviour ( $F_{2,120} = 0.25$ ,  $p = 0.78$ ). The proportion of the kudu herd being vigilant increased with visibility (coef  $\pm$  SE =  $0.06 \pm 0.03$ ,  $F_{1,120} = 3.80$ ,  $p = 0.05$ ) and when there were no other herbivores present (coef  $\pm$  SE =  $6.09 \pm 2.33$ ,  $F_{1,120} = 6.84$ ,  $p = 0.01$ ). Although analyses showed a marginal effect of time of the day on the proportion of the kudu herd being vigilant ( $F_{3,120} = 2.53$ ,  $p = 0.06$ ), we did not detect any significant difference between the time categories using a *posteriori* test (all  $p \geq 0.12$ ). Herd size, location of the waterhole or month did not affect the pro-

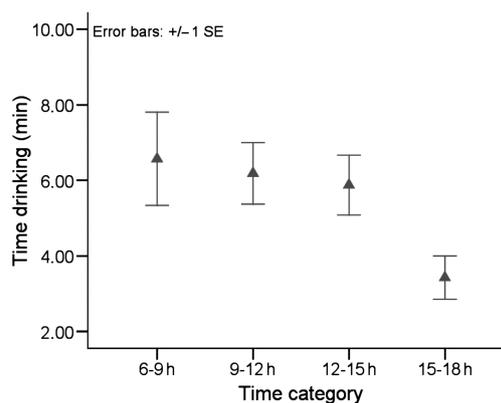
portion of the kudu herd engaged in vigilant behaviour (all  $p \geq 0.25$ ).

For impala, the experimental treatment did not affect the proportion of the herd engaged in vigilant behaviour ( $F_{2,57} = 0.42$ ,  $p = 0.66$ ), neither did herd size, visibility around the waterhole, time of the day, location of the waterhole or the presence of other herbivores (all  $p \geq 0.26$ ).

#### Time Spent Drinking

The time kudu herds spent drinking was not affected by the experimental treatment ( $F_{1,100} = 0.64$ ,  $p = 0.53$ ). Time spent drinking increased with visibility (coef  $\pm$  SE =  $0.01 \pm 0.003$ ,  $F_{1,100} = 5.77$ ,  $p = 0.02$ ) and herd size (coef  $\pm$  SE =  $0.08 \pm 0.02$ ,  $F_{1,100} = 18.72$ ,  $p < 0.001$ ). Inside HNP, kudu herds spent more time drinking compared with outside the park (coef  $\pm$  SE =  $0.56 \pm 0.18$ ,  $F_{1,100} = 9.36$ ,  $p < 0.01$ ). Time of the day affected the time kudu herds spent drinking ( $F_{1,100} = 3.45$ ,  $p = 0.02$ ). In the late afternoon, kudu herds spent less time drinking compared with the early morning (coef  $\pm$  SE =  $0.85 \pm 0.28$ ,  $p < 0.01$ ), late morning (coef  $\pm$  SE =  $0.51 \pm 0.23$ ,  $p = 0.02$ ) and early afternoon (coef  $\pm$  SE =  $0.47 \pm 0.22$ ,  $p = 0.04$ ) (Fig. 3). The presence of other herbivores or month did not affect the time a kudu herd spent drinking (all  $p \geq 0.25$ ).

The time impala herds spent drinking at the waterhole was not affected by the experimental treatment ( $F_{2,75} = 0.05$ ,  $p = 0.95$ ). The time impala herds spent drinking increased with visibility (coef  $\pm$  SE =  $0.01 \pm 0.004$ ,  $F_{1,57} = 8.01$ ,  $p = 0.01$ ) and herd size (coef  $\pm$  SE =  $0.03 \pm 0.01$ ,  $F_{1,57} = 19.19$ ,  $p < 0.001$ ). The month in which the experiment



**Fig. 3:** The time kudu herds spend drinking during the early morning (6–9 h), late morning (9–12 h), early afternoon (12–15 h) and late afternoon (15–18 h).

was conducted affected the time the impala herds spent drinking ( $F_{2,57} = 6.03$ ,  $p = 0.02$ ), herds spent more time drinking in Aug. compared with Sep. (coef  $\pm$  SE =  $0.43 \pm 0.18$ ). There was no effect of time of the day, location of the waterhole or the presence of other herbivores (all  $p \geq 0.11$ ).

#### *Spatial and Temporal Adjustments*

The number of kudu herds that came to drink at the waterhole was not affected by the experimental treatment ( $F_{2,144} = 1.16$ ,  $p = 0.32$ ). Time of the day did affect the number of herds that came to drink ( $F_{3,144} = 3.12$ ,  $p = 0.03$ ). Less herds came to drink in the early morning compared with the late morning (coef  $\pm$  SE =  $0.50 \pm 0.20$ ,  $p = 0.02$ ) and early afternoon (coef  $\pm$  SE =  $0.53 \pm 0.20$ ,  $p = 0.10$ ) (Fig. 4). There was no difference in the number of herds that came to drink in the early morning compared with the late afternoon (coef  $\pm$  SE =  $0.19 \pm 0.20$ ,  $p = 0.34$ ) (Fig. 3). The number of herds that came to drink decreased with visibility (coef  $\pm$  SE =  $-0.01 \pm 0.003$ ,  $F_{1,144} = 3.99$ ,  $p = 0.05$ ). More herds came to drink at waterholes inside HNP compared with outside the park (coef  $\pm$  SE =  $0.64 \pm 0.14$ ,  $F_{1,144} = 19.91$ ,  $p < 0.001$ ). Month did not affect the number of kudu herds that came to drink at the waterhole ( $p = 0.56$ ).

The number of impala herds that came to drink at the waterhole was not affected by the experimental treatment ( $F_{2,144} = 1.01$ ,  $p = 0.37$ ). Less herds of impala came to drink at waterholes inside HNP compared with outside the park (coef  $\pm$  SE =  $-0.60 \pm 0.15$ ,  $F_{1,144} = 15.71$ ,  $p < 0.001$ ). Time of day, visibility or month did not affect the number of

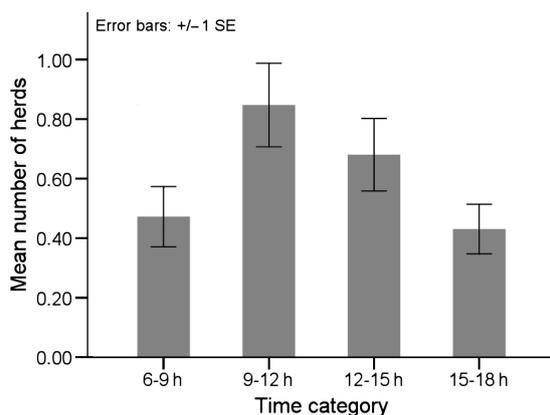
impala herds that came to drink at the waterhole (all  $p \geq 0.09$ ).

#### **Discussion**

Our results highlight the mechanism underlying short-term behavioural adjustments of the anti-predator strategies of prey under immediate predation risk by African wild dogs. Regardless of direct cues of African wild dog presence, prey seemed to primarily base their anti-predator behaviour on environmental variables such as time of the day and visibility.

For both prey species, visibility around the waterhole seemed to be a main factor determining anti-predator behaviour; an increase in visibility resulted in an increase in vigilance behaviour. In response to an increase in visibility, kudu made costly behavioural adjustments by increasing the proportion of time individuals spent high-quality vigilant and the proportion of individuals in the herd being vigilant. The decrease in the number of herds that came to drink at a waterhole with an increase in visibility suggests that kudu avoided waterholes in open areas. Impala on the other hand made low-cost behavioural adjustments by increasing the proportion of time spent low-quality vigilant. Studies that have looked at the fine-scaled effect of visibility on vigilance behaviour have generally found a decrease in vigilance with an increase in visibility (Burger 2001; Pays et al. 2012). In this study, visibility around the waterhole was measured as the distance from the waterhole to visually concealing cover and therefore gives an indication of broad-scale rather than fine-scale habitat structure.

The effect of cover on anti-predator behaviour depends on whether prey perceives cover as an obstruction or a protection (Lima 1990). Prey that spend a large amount of time in open vegetation and escape attack by predators by speed are more likely to increase vigilance when foraging in habitat with dense vegetation obstructing early detection of predators (Underwood 1982; Burger et al. 2000). Prey that spend a large amount of time in dense vegetation and escape predators by seeking cover are likely to increase vigilance when foraging further away from cover (Brown & Kotler 2004; Carrascal & Alonso 2006). Impala are selective mixed-feeding antelopes that are quick to take flight when discovering an approaching predator, using an alarm snort to signal the presence of danger (Estes 1997). Kudu are browsing antelopes that, when standing in the thicket, rely on crypsis when encountering predators and only flee when approached within their, relatively short, flight distance (Estes 1997). Although in this study both



**Fig. 4:** The number of kudu herds that came to drink during the early morning (6–9 h), the late morning (9–12 h), early afternoon (12–15 h) and late afternoon (15–18 h).

species seem to perceive an increase in distance to cover while drinking as an increase in predation risk, the level of perceived predation risk, possibly due to the difference in flight responses between kudu and impala, seems to differ resulting in different investments in anti-predator behaviour.

An increase in visibility around waterholes led to an increase in the time spent drinking. Burger (2001) found that an increase in visibility resulted in longer drinking times and a decrease in vigilance behaviour because of a lower perceived predation risk. In our study, the time spent drinking was measured as the difference between the time when the last individual of the herd stopped drinking and the time the first individual of the herd had started drinking. The longer time kudu and impala spent drinking with an increase in herd size is therefore likely to be the direct result of the method used to measure time spent drinking. It is possible that kudu needed to spend more time at waterholes with a high visibility to meet their water requirements because they spent more time vigilant and less time drinking. Low-quality vigilance does not detract from drinking, and the increase in low-quality vigilance of impala therefore does not explain the increase in time spent drinking. Possibly the increase in time spent drinking with an increase in visibility stems from a trade-off with a behaviour other than vigilance behaviour, for example moving.

Kudu seemed to try to reduce the risk of predation by utilizing waterholes during time frames when predators are less likely to be present (Fig. 4). In addition, at the predator-sensitive hours of the day, kudu adjusted their anti-predator behaviour accordingly; during the early morning when natural predation risk peaks because of an overlap of time frames at which both nocturnal (Schaller 1972; Holekamp et al. 1997) and diurnal (Creel & Creel 1995) predators hunt, kudu increase their high-quality vigilance. During the later afternoon when diurnal predators start to become active (Creel & Creel 1995), kudu seem to reduce predation risk by reducing the time spent drinking at the waterhole. The use of different anti-predator strategies during the early morning and later afternoon is possibly the result of differences in predation risk and water requirements; in the morning, predation risk peaks, but the need for water might be more urgent with the hot hours of the day ahead leaving prey no other option than to make a costly investment by increasing high-quality vigilance.

Compared with foraging, prey spend a relative high proportion of time vigilant while drinking. Kudu spend approx. 32% of their time around the waterhole high-quality vigilant, impala 28%. In compari-

son, impala in HNP have been found to only spend approx. 3% of their time high-quality vigilant while foraging (Pays et al. 2012). And although zebra in the same study area spend approx. 30% of their time vigilant while drinking (Périquet et al. 2010), they are vigilant approx. 10% of their time while foraging (O. Pays, pers. comm.). With waterholes being utilized by predators to hunt (Valeix et al. 2010; Van der Meer 2011), the predation risk while drinking might be so high that prey makes an investment in anti-predator behaviour that borders on a maximum. Compared with feeding, during which prey has time to scan the environment while chewing (Blanchard & Fritz 2007), the opportunities for low-quality vigilance while drinking are likely to be limited.

To adjust vigilance behaviour in response to predation risk, prey will therefore have to invest in high-quality vigilance. High-quality vigilance comes at a cost as it detracts prey from all other activities (Lima & Bednekoff 1999; Blanchard & Fritz 2007). In the case of drinking, high-quality vigilance is likely to either reduce the time spent drinking or, if minimum water requirements need to be met, increase the time prey spend in the high predation risk area. With the overall high level of high-quality vigilance around waterholes and the costs involved, an additional investment in high-quality vigilance is likely to only be made in cases where predation risk is perceived as exceptionally high. As all waterholes studied are frequently visited by predators, mimicking non-immediate predation risk is likely not to substantially increase the predation risk prey perceives around the waterholes on a day to day basis. Mimicking immediate predator presence on the other hand is likely to be perceived as an exceptionally high predation risk, thus resulting in a costly investment in high-quality vigilance by kudu.

Several studies have shown that stalking predators select non-vigilant prey (Fitzgibbon 1988; Krause & Godin 1996). Opportunistic predators might not have time to make this selection. It has therefore been suggested that when the most likely predator is a stalker, prey should aim to have the highest level of individual vigilance within the herd, whereas if the most likely predator is an opportunist, prey should aim to be in the largest herd and can spend less time vigilant without increasing predation risk (Cresswell et al. 2003; Cresswell & Quinn 2010). With African wild dogs (1) not being the main predator within the Hwange system (Elliot 2007) and (2) using both a stalking and an opportunistic hunting technique (Reich 1981; Fanshawe & Fitzgibbon 1993), it might be difficult for prey to show a uniform response to predation risk by this

predator. Hunting strategies of predators other than African wild dogs might partly explain the observed differences in anti-predator behaviour between kudu and impala. Average herd size of kudu ( $\bar{x} \pm SE = 5.40 \pm 0.38$ ) was smaller than that of impala ( $\bar{x} \pm SE = 11.40 \pm 1.25$ ). With kudu being a preferred prey species of the stalking lion (Loveridge et al. 2007), which apart from the predominantly scavenging spotted hyena (80% of the diet) (Drouet-Hoguet 2007) is the main predator within the Hwange system (Elliot 2007), kudu might mainly rely on high levels of individual vigilance to reduce predation risk rather than large herds. In addition, browsers such as kudu are less dependent on surface water than grazers and mixed feeders such as impala (Western 1975) which results in additional differences in the trade-off between drinking and vigilance. With predators utilizing waterholes to hunt (Valeix et al. 2010; Van der Meer 2011), both species are likely to perceive waterholes as environments with an extremely high predation risk. Prey is therefore likely to maximize their anti-predator behaviour around waterholes based on environmental variables affecting predation risk, the main predator within the system and water requirements, leaving little flexibility to respond to direct cues of African wild dogs' presence.

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