



Anti-predator behaviour of kudu and impala in response to mimicked African wild dog presence: do age and sex matter?

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Abstract

Predators not only prey upon certain prey species, but also on certain age–sex classes within species. Predation risk and an individual's response to this risk might therefore vary with an individual's characteristics. We examined the proportion of time different age–sex classes of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*) spent high quality vigilant (costly vigilance that detracts from all other activities) in response to mimicked predation risk by African wild dogs (*Lycaon pictus*). For both species predation risk was the main factor determining the investment in high quality vigilance behaviour. Age–sex class-specific responses were not related to age–sex class specific lethality risk presented by African wild dogs. For impala, regardless of predation risk, age seemed to have some effect on the investment in high quality vigilance with sub-adult impala spending more time high quality vigilant than adult impala, which is possibly why African wild dogs predominantly preyed upon adult impala.

Keywords

vigilance, predation risk, African wild dog, prey preference, age, gender, impala, kudu.

1. Introduction

In an environment with predators, prey behaviour is mainly shaped by predation risk (Lima, 1998). Prey uses behavioural adjustments to reduce preda-

tion risk and respond to temporal variations in this risk (Hunter & Skinner, 1998; Lung & Childress, 2007; Valeix et al., 2009; Périquet et al., 2010; Favreau et al., 2013). One of the most studied behavioural adjustments is group formation and vigilance behaviour (Krause & Ruxton, 2002; Barta et al., 2004). Group foragers benefit from an increased ability to detect predators (Ruxton, 1996; Pays et al., 2013) and a reduction of their individual risk of being preyed upon (Foster & Treherne, 1981; Wrona & Jamieson Dixon, 1991). Therefore, an individual's investment in vigilance behaviour generally decreases with an increase in herd size (Burger et al., 2000; Pays et al., 2012a). Other behavioural responses to predation risk include changes in habitat use (Creel et al., 2005; Hebblewhite et al., 2005) and variations in time allocated to vigilance (Lima, 1995).

Several studies show that alterations of behaviour in response to predation risk can result in fitness costs (Creel & Christianson, 2008), e.g., by limiting drinking or feeding time (Burger & Gochfeld, 1992), and by decreasing feeding rates (Ruckstuhl et al., 2003; Cowlshaw et al., 2004). However, various species of birds (Baker et al., 2011) and mammals (Fortin et al., 2004; Makowska & Kramer, 2007) are able to continue food ingestion during vigilance periods (Fortin et al., 2004; Pays et al., 2012b). Especially herbivores (Spalinger & Hobbs, 1992) are able to be vigilant while chewing food, here-with minimizing the reduction of food intake (Illius & FitzGibbon, 1994). To investigate ecological mechanisms underlying vigilance costs, recent studies have therefore stressed the necessity to distinguish between vigilance during which the animal is standing in an alert position without chewing food (hereafter called high quality vigilance) or vigilance while the animal is chewing food (hereafter called low quality vigilance) (Blanchard & Fritz, 2007). Such distinction is particularly important when investigating vigilance in response to predation risk because high quality vigilance should maximize predator detection but is expected to incur foraging costs as it does not allow vigilance/feeding multitasking.

Predation risk varies over time and space (Hunter & Skinner, 1998; Lung & Childress, 2007; Valeix et al., 2009), but can also vary per individual. Diet composition of carnivores show that predators not only preferentially prey on certain species (Hayward & Kerley, 2005; Hayward et al., 2006a, b), but also more heavily prey upon specific age–sex classes within these species (FitzGibbon, 1990; Owen-Smith, 1993; Van der Meer et al., 2013). Several studies have focussed on differences in anti-predator behaviour between age–sex classes (San José et al., 1996; Burger et al., 2000; Matson et al., 2005),

especially in relation to reproduction and maternal care (San José et al., 1996; Lung & Childress, 2007). In the presence of predation risk, an individual's investment in vigilance behaviour varies per age and sex class (Childress & Lung, 2003; Lung & Childress, 2007; Winnie & Creel, 2007; Lea & Blumstein, 2011). However, this investment does not necessarily reflect age and sex class specific variations in predation risk, e.g., despite elk bulls being over selected by wolves, bulls did not increase vigilance in response to wolf presence whereas cows did (Winnie & Creel, 2007).

Although in gregarious species males and females have functional reasons to differ in their time allocated to vigilance (Pays & Jarman, 2008), contrasting results have been reported for several prey species (Burger & Gochfeld, 1994; Childress & Lung, 2003; Lung & Childress, 2007; Rieucou et al., 2012; Benoist et al., 2013). Direct interference between males (e.g., for territoriality or access to females) requires them to continuously monitor the presence and activity of potential rivals (Baldellou & Henzi, 1992). Females are constrained in their time allocation, as their nutrient requirements and food intake may increase strongly during pregnancy and lactation (Speakman, 2008), herewith limiting their time available for vigilance. Males and females may thus take different decisions when trading off food or water access with vigilance, especially in the presence of increased predation risk. In addition to sex-effects on the vigilance response of prey, Arenz & Leger (2000) proposed three main reasons to explain why (as reported in several studies including Lung & Childress, 2007; Pays et al., 2012a; Benoist et al., 2013) juveniles should be less vigilant than adults: (1) juveniles need time to learn certain aspects of behaviour, (2) because of their small size, juveniles may be harder for predators to detect, so they may not need to be as vigilant as adults and (3) nutritional and energetic requirements differ between juveniles and adults, with juveniles being constrained by their need to invest in feeding for growth. In this context, individual traits such as age and sex are expected to affect individual investment in (costly) high quality vigilance under varying predation risk, for example when predators predominantly prey upon specific age–sex classes. However, the question whether age affects high quality vigilance independently of sex, or vice versa, remains largely unanswered.

Simulating the presence of a predator (via playbacks, faeces and/or urine) has proven to be a useful method to investigate immediate behavioural adjustments to predation risk (Parsons & Blumstein, 2010; Biedenweg et al.,

2011; Hettena et al., 2014). In this study we determined African wild dog preference for specific age–sex classes of their main prey species kudu and impala (Van der Meer et al., 2013), and mimicked immediate predation risk by this predator to investigate the relationship between predator preference and the investment of kudu and impala in high quality vigilance. We predicted that, in the presence of immediate predation risk by African wild dogs, the different age–sex classes of kudu and impala adjusted their investment in high quality vigilance in accordance with this predator’s preference for specific age–sex classes.

2. Method

2.1. Study area

Hwange National Park (HNP) covers ca. 15 000 km² in northwest Zimbabwe (19°00’S, 26°30’E). The region is classified as semi-arid with a mean annual rainfall of 606 mm and a wet season from October to April. Vegetation consists of scattered woodland scrub mixed with grassland. For this study, we selected six pumped waterholes along the northern boundary of HNP in areas frequently visited by African wild dogs. The selected waterholes were situated 10–30 km apart, in open areas (visibility ranging between 100–200 m) that were commonly used for photographic safaris and therefore regularly visited by game drive vehicles.

2.2. Prey preference

African wild dog predominantly predate on kudu and impala (Van der Meer et al., 2013). African wild dog selection for age–sex classes of these species was analysed using a Jacobs index (Jacobs, 1974; see also Hayward et al., 2006a, b) according to the formula: $D = (r - p)/(r + p - 2rp)$, where r is the proportion of age–sex classes killed and p the proportion of age–sex classes available for a certain prey species. D ranges between -1 (strong avoidance) and $+1$ (strong preference), values close to zero indicate that prey is killed in proportion to its availability. Data on age–sex classes of prey killed were obtained from 22 radio-collared African wild dog packs (for a detailed description of the method see Van der Meer et al., 2013). Data on available age–sex classes of kudu and impala were obtained from 2007 and 2008 12 h waterhole census in the study area.

2.3. *Prey vigilance*

Observations were made in August and September, the months during which natural water sources have dried up and waterhole attendance is high. Behavioural observations were made between 6:00 and 18:00 h from a vehicle parked at a distance from the waterhole. Playing the sounds of a natural predator can be used to mimic predation risk (Blanchard & Fritz, 2007; Blumstein et al., 2008; Hettena et al., 2014). In this study we mimicked predation risk by playing sounds of an African wild dog pack commencing a hunt, in addition we spread 5 l of dissolved African wild dog faeces around the waterhole. Prior to visiting each waterhole, the faeces solution was prepared by filling 2/3 of a 5 l water bottle with crushed dried African wild dog faeces, after which the bottle was topped up with warm water and shaken till the faeces dissolved. Each waterhole was visited during two subsequent days. The first day served as a control day, during the second day immediate predation risk was mimicked by spreading African wild dog faeces solution around the waterhole in the early morning and playing African wild dog sounds when a herd of kudu or impala came down to drink. The length of the sound fragment was 30 s, the fragment was played at an intensity similar to the intensity experienced under natural conditions. At each waterhole we repeated this experiment one month later. As soon as 50% of the herd started drinking, a video was taken from which high quality vigilance behaviour and age (adults, sub-adult, juvenile), sex and body condition (low, medium or good) of individual kudu and impala 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. For our analyses we recorded the proportion of time each individual spent high quality vigilant. High quality vigilance was defined as vigilance which detracts from drinking and all other activities, and during which the animal is standing in a highly alert posture with its head up above shoulder level and its ears pointed forward. Herd size, whether or not other herbivores were present and the time of visiting the waterhole 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).

2.4. *Data analysis*

Kudu and impala were analysed separately. In total we observed 333 individual impala (control day: 176, experimental day: 157) and 352 individual

kudu (control day: 183, experimental day: 169). For both the control and experimental day, sample size for each age–sex class was ≥ 14 . To meet the normality assumption, the proportion of time spent high quality vigilant was arcsine-square-root-transformed. We fitted mixed linear models to relate high quality vigilance to the explanatory variables. Predation risk varies over time and space, e.g., African wild dog hunts are most common during dusk and dawn (Estes & Goddard, 1967) predation risk by this predator is therefore likely to peak in the early morning and late afternoon. Consequently, variables like time of day (Matson et al., 2005; Valeix et al., 2009; Van der Meer et al., 2012), distance from cover (Burger et al., 2000; Matson et al., 2005), visibility (Pays et al., 2012b; Van der Meer et al., 2012) and presence of other herbivores (Morse, 1977; Périquet et al., 2010) have been found to affect vigilance behaviour of prey. We therefore controlled for the time of visiting the waterhole and herbivore presence, and added waterhole as a random variable to control for potential differences in environmental characteristics, e.g., visibility. Predation risk, age, sex, or age–sex were added as fixed factors, herd size as a covariate (Herd size (mean \pm SE), kudu 8.20 ± 0.31 , impala 15.92 ± 0.74). As all animals observed were in good body condition, this variable was left out of the analysis. While a debate in ecology exists about methods for appropriate model selection (see the special issue of *Ecology*, *Ecology* 95(3) 2014), we used Akaike's Information Criterion corrected for small sample size (AIC_c) as selection criterion for the most appropriate model (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). Comparable AIC_c values were calculated using maximum likelihood estimation. We considered models to be competing if the difference in AIC_c value compared to the model with the lowest AIC_c value (ΔAIC_c) was ≤ 2 (Burnham & Anderson, 2002). We used Akaike weights (ω_i) as an indication of support for each model and contrasted the likelihood of the best model with competing models by calculating the evidence ratio (Burnham & Anderson, 2002, pp. 75–79). Because several models had similar levels of support from the data we applied model averaging (following Buckland et al., 1997) to make robust parameter estimates and predictions for the predictor variables in the best candidate models. In models with and without interaction terms the main effect parameters do not have the same meaning (Brambor et al., 2006), we therefore only applied model averaging on the models without interaction terms. Statistical analyses were performed using SPSS software release 20.0 (SPSS, Chicago, IL, USA).

3. Results

3.1. Prey preference

African wild dogs predominantly selected adult impala, sub-adults were avoided. For kudu the opposite seemed to be the case, sub-adults were selected over adults, adult females were avoided. For an overview of the Jacobs index for the various age and sex classes of kudu and impala see Table 1.

3.2. Prey vigilance

For kudu the three best candidate models (M6, M7, M10) were competitive ($\Delta AIC_c \leq 2$). The evidence ratio showed that the model including predation risk (M6) was 2.63-times more likely than the model including predation risk and herd size (M7) and 1.84-times more likely than the model including predation risk and age–sex class (M10). Akaike weights and parsimony dictates that the model including predation risk (M6) was the best model to explain the proportion of time kudu spent high quality vigilant (Table 2). Thus predation risk was the key variable explaining the investment in high quality vigilance for kudu (Table 3). High quality vigilance increased in the presence of immediate predation risk (Figure 1), for an overview of model averaged parameter estimates for the best candidate model see Table 3. Cal-

Table 1.

Jacobs index of African wild dog prey selection in relation to age–sex classes of kudu and impala.

| | | | | |
|---------------|--------------|----------------|------------------|----------|
| Kudu | | | | |
| Adult male | Adult female | Sub-adult male | Sub-adult female | Juvenile |
| 0.12 | −0.44 | 0.49 | 0.39 | −0.04 |
| Adult | Sub-adult | Juvenile | | |
| −0.37 | 0.41 | −0.04 | | |
| Male | Female | Juvenile | | |
| −0.09 | 0.09 | −0.04 | | |
| Impala | | | | |
| Adult male | Adult female | Sub-adult male | Sub-adult female | Juvenile |
| 0.66 | 0.35 | −0.76 | −0.09 | −* |
| Adult | Sub-adult | Juvenile | | |
| 0.76 | −0.85 | −* | | |
| Male | Female | Juvenile | | |
| 0.17 | −0.29 | −* | | |

* Not available during the time of the year this study took place.

Table 2. Number of parameters (K), AIC_c , ΔAIC_c , model weights (ω_i) and log likelihood (LL) for models of arcsin-sqrt-transformed high quality vigilance of kudu as a function of predation risk, herd size and age and sex class plus the parameters estimates for the variables in the best candidate models for high quality vigilance of kudu.

| ID | Model | K | AIC_c | ΔAIC_c | ω_i | LL |
|-----|---|-----|----------------|----------------|-------------|-----------------|
| M1 | Control | 7 | 2811.68 | 9.99 | 0.00 | -1398.68 |
| M2 | Control + Herdsize | 8 | 2813.42 | 11.73 | 0.00 | -1398.50 |
| M3 | Control + Age | 9 | 2814.05 | 12.36 | 0.00 | -1397.76 |
| M4 | Control + Sex | 9 | 2815.73 | 14.04 | 0.00 | -1398.61 |
| M5 | Control + AgeSex | 11 | 2811.74 | 10.05 | 0.00 | -1394.48 |
| M6 | <i>Control + PredRisk</i> | 8 | <i>2801.69</i> | <i>0.00</i> | <i>0.38</i> | <i>-1392.64</i> |
| M7 | Control + Herdsize + PredRisk | 9 | 2803.63 | 1.94 | 0.15 | -1392.56 |
| M8 | Control + Age + PredRisk | 10 | 2804.79 | 3.10 | 0.08 | -1392.08 |
| M9 | Control + Sex + PredRisk | 10 | 2805.65 | 3.96 | 0.05 | -1392.50 |
| M10 | Control + AgeSex + PredRisk | 12 | 2802.92 | 1.23 | 0.21 | -1389.00 |
| M11 | Control + Herdsize + PredRisk + AgeSex × PredRisk | 10 | 2805.74 | 4.05 | 0.05 | -1392.55 |
| M12 | Control + Age + PredRisk + Age × PredRisk | 12 | 2806.84 | 5.15 | 0.03 | -1390.96 |
| M13 | Control + Sex + PredRisk + Sex × PredRisk | 12 | 2806.78 | 5.09 | 0.03 | -1390.93 |
| M14 | Control + AgeSex + PredRisk + AgeSex × PredRisk | 16 | 2808.92 | 7.23 | 0.01 | -1387.65 |

Waterhole was included in all models as a random variable. Control indicates that presence of other herbivores and time of day were included in all models. The best model is indicated by italics.

Table 3.

Model averaged parameter estimates for the parameters in the best candidate model (M6) for arcsinsqrt-transformed high quality vigilance of kudu.

| Parameter | β | SE | 95% CI | |
|--|---------|------|--------|-------|
| | | | Upper | Lower |
| Intercept | 26.59 | 2.48 | 31.43 | 21.75 |
| Predation risk (no risk used as the reference) | | | | |
| Yes | 5.04 | 1.47 | 7.90 | 2.18 |
| Herbivore presence (present used as the reference) | | | | |
| Not present | 1.61 | 1.69 | 4.90 | −1.68 |
| Time of day (15:00–18:00 h used as the reference) | | | | |
| 6:00–9:00 h | 7.30 | 2.59 | 12.35 | 2.24 |
| 9:00–12:00 h | 0.71 | 2.06 | 4.73 | −3.31 |
| 12:00–15:00 h | 2.75 | 2.10 | 6.85 | −1.35 |

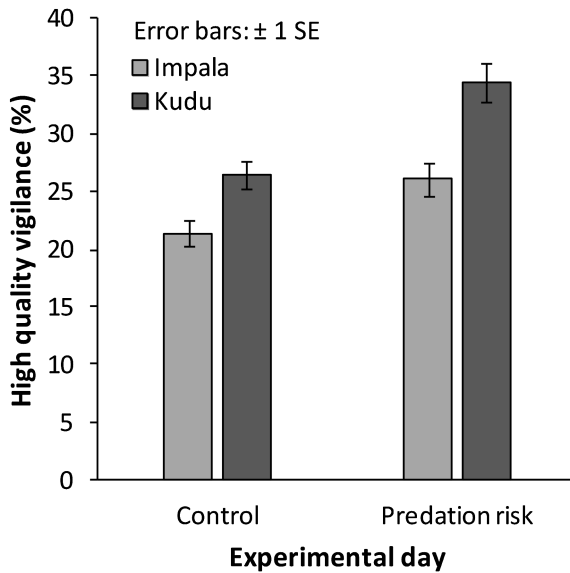


Figure 1. Proportion of high quality vigilance of kudu and impala in relation to predation risk by African wild dogs.

culated as the mean over the different models, the variance explained by the random variable waterhole was 4.02 ± 0.10 (mean \pm SE).

For impala three candidate models (M21, M22, M26) had close and low AIC_c values ($\Delta AIC_c \leq 2$) (Table 4). The two models including age and predation risk and the two-way interaction age \times predation risk were nested (M22, M26) (Table 4), therefore the parsimony principle suggests to retain the candidate model without the interaction (M22). However, another candidate model including herd size and predation risk was competitive (M22) (Table 4). Based on the evidence ratio the model including predation risk and age (M22) was 1.49-times more likely than the model including predation risk and herd size (M21). The model averaged parameter estimates show that predation risk is the main predictor of the proportion of time impala spent high quality vigilant (Table 5). Although age and herd size seem to play a role, taking into consideration that predation risk is in all best candidate models and the model with predation risk only (M20) had an AIC_c value of 2.36, this role seems to be relatively little. This is supported by the evidence ratio's which show that the model including predation risk and herd size (M21) was only 1.33-times more likely than the model containing predation risk only (M20), and the model including predation risk and age (M22) was 1.98-times more likely than this simpler model (M20). Overall, the proportion of time impala spent high quality vigilant increased in the presence of immediate predation risk (Figure 1), adult impala spent less time high quality vigilant than sub-adult impala and an individual's investment in high quality vigilance decreased with an increase in herd size. See Table 5 for an overview of model averaged parameter estimates for the best candidate models. Calculated over the different models, the mean variance explained by the random variable waterhole was 4.26 ± 0.32 (mean \pm SE).

4. Discussion

Vigilance allows individuals to escape from predators, consequently predation risk has been found to determine an individual's investment in vigilance behaviour (Hunter & Skinner, 1998; Matson et al., 2005; Lung & Childress, 2007; Périquet et al., 2010). In accordance with other prey species (Hunter & Skinner, 1998), both kudu (Périquet et al., 2010) and impala (Hunter & Skinner, 1998; Matson et al., 2005) increase their investment in vigilance behaviour when predators are in the vicinity. However, in order to accurately

Table 4. Number of parameters (K), AIC_c , ΔAIC_c , model weights (ω_i) and log likelihood (LL) for models of arcsin-sqrt-transformed high quality vigilance of impala as a function of predation risk, herd size and age and sex class plus the parameters estimates for the variables in the best candidate models for high quality vigilance of impala.

| ID | Model | K | AIC_c | ΔAIC_c | ω_i | LL |
|-----|--|-----|----------------|----------------|-------------|-----------------|
| M15 | Control | 7 | 2601.53 | 7.09 | 0.01 | -1293.60 |
| M16 | Control + Herdsize | 8 | 2600.23 | 5.79 | 0.02 | -1291.89 |
| M17 | Control + Age | 8 | 2599.91 | 5.47 | 0.02 | -1291.73 |
| M18 | Control + Sex | 8 | 2602.79 | 8.35 | 0.00 | -1293.17 |
| M19 | Control + AgeSex | 10 | 2604.06 | 9.62 | 0.00 | -1291.69 |
| M20 | Control + PredRisk | 8 | 2596.80 | 2.36 | 0.10 | -1290.18 |
| M21 | <i>Control + Herdsize + PredRisk</i> | 9 | <i>2596.23</i> | <i>1.79</i> | <i>0.13</i> | <i>-1288.84</i> |
| M22 | <i>Control + Age + PredRisk</i> | 9 | <i>2595.43</i> | <i>0.99</i> | <i>0.20</i> | <i>-1288.44</i> |
| M23 | Control + Sex + PredRisk | 9 | 2597.93 | 3.49 | 0.06 | -1289.69 |
| M24 | Control + AgeSex + PredRisk | 11 | 2599.51 | 5.07 | 0.03 | -1288.35 |
| M25 | Control + Herdsize + PredRisk + Herdsize \times PredRisk | 10 | 2597.25 | 2.81 | 0.08 | -1288.29 |
| M26 | Control + Age + PredRisk + Age \times PredRisk | 10 | 2594.44 | 0.00 | 0.32 | -1286.88 |
| M27 | Control + Sex + PredRisk + Sex \times PredRisk | 10 | 2600.06 | 5.62 | 0.02 | -1289.69 |
| M28 | Control + AgeSex + PredRisk + AgeSex \times PredRisk | 14 | 2601.00 | 6.56 | 0.01 | -1285.84 |

Waterhole was included in all models as a random variable. Control indicates that presence of other herbivores and time of day were included in all models. The two best models are indicated by italics.

Table 5.

Model averaged parameter estimates for the parameters in the best candidate models (M21, M22) for arcsin $\sqrt{\text{rt}}$ -transformed high quality vigilance of impala.

| Parameter | β | SE | 95% CI | |
|--|---------|------|--------|-------|
| | | | Upper | Lower |
| Intercept | 23.16 | 2.42 | 27.88 | 18.45 |
| Predation risk (no risk used as the reference) | | | | |
| Yes | 3.39 | 1.32 | 5.96 | 0.82 |
| Age class (sub-adult used as the reference) | | | | |
| Adult | -2.42 | 1.29 | 0.10 | -4.94 |
| Herd size | -0.08 | 0.05 | 0.02 | -0.18 |
| Herbivore presence (present used as the reference) | | | | |
| Not present | -1.74 | 1.64 | 1.45 | -4.94 |
| Time of day (15:00–18:00 h used as the reference) | | | | |
| 6:00–9:00 h | 7.78 | 2.65 | 12.95 | 2.61 |
| 9:00–12:00 h | 4.68 | 2.12 | 8.80 | 0.55 |
| 12:00–15:00 h | 4.87 | 2.25 | 9.26 | 0.49 |

determine an individual's investment in vigilance behaviour it is important to distinguish between low quality vigilance and costly high quality vigilance which does not allow for vigilance/feeding multitasking (Blanchard & Fritz, 2007). In this study we made this distinction and found that immediate predation risk was the primary influence on the proportion of time individual kudu and impala spent high quality (costly) vigilant.

An individual's investment in vigilance behaviour varies per age and sex class (Burger & Gochfeld, 1994; Lung & Childress, 2007; Lark & Slade, 2008; Lashely et al., 2014), but its relationship remains unclear. Some studies report males to be more vigilant than females (Burger & Gochfeld, 1994; Matson et al., 2005; Tadesse & Kotler, 2014), others demonstrate the contrary (Winnie & Creel, 2007; Lashely et al., 2014), whereas some find no difference (Lark & Slade, 2008). The same counts for age related differences in vigilance behaviour; some studies report sub-adults to be less vigilant than adults, while others find the opposite or no effect (for an overview see Arenz & Leger, 2000). Most of these studies did not examine age and sex class specific investment in vigilance behaviour in the presence of predation risk. In the presence of predation risk, adult females increase their investment in vigilance behaviour (Laundré et al., 2001; Childress & Lung, 2003; Lung & Childress, 2007; Winnie & Creel, 2007), especially when with calve

(Hunter & Skinner, 1998; Laundré et al., 2001; Childress & Lung, 2003; Lung & Childress, 2007). Vigilance behaviour of adult males does not seem to be affected by predation risk (Laundré et al., 2001; Childress & Lung, 2003; Lung & Childress, 2007; Winnie & Creel, 2007), whereas sub-adult males and females either showed no response (Childress & Lung, 2003) or an increased investment in vigilance behaviour in response to predation risk (Lung & Childress, 2007). Although some of these studies find an age and sex class specific investment in vigilance behaviour that seems to correspond with age and sex class specific predation risk (Laundré et al., 2001; Childress & Lung, 2003; Lung & Childress, 2007), others find the opposite (Winnie & Creel, 2007).

In this study we found no difference in the investment in high quality vigilance for the different age–sex classes of kudu, while, regardless of predation risk, adult impala spent less time vigilant than sub-adult impala. Even in the presence of immediate predation risk, a reduced body condition has been found to limit an individual's investment in vigilance behaviour (Bachman, 1993; Winnie & Creel, 2007; Lea & Blumstein, 2011). This study was carried out outside the breeding season, during a period of the year when adult male and female impala are generally in good condition (Gallivan et al., 1995; Marshal et al., 2012). With all observed individuals being in good condition and this study examining the trade-off between vigilance and drinking rather than foraging, it seems unlikely that body condition explains the found differences in investment in vigilance behaviour of adult and sub-adult impala. In the presence of predators, older experienced females are more successful in rearing young than younger females (Mech & McRoberts, 1990), indicating that anti predator behaviour is affected by experience. Several studies indeed show habituation to brief direct and indirect encounters with predators (Dacier et al., 2006; Rouco et al., 2011), and a stronger anti predator response to predation risk of naive individuals compared to experienced individuals (Jachner, 2001; Rouco et al., 2011). Possibly, the higher investment of sub-adult impala in high quality vigilance is related to experience. Young growing animals need more food than adults to complete body growth, and therefore generally spent less time vigilant and more time foraging (San José et al., 1996; Burger et al., 2000). A stronger anti predator response of young, less experienced, individuals might therefore not become apparent when studying the trade-off between foraging and

vigilance, but might show when studying the trade-off between drinking and vigilance which is less affected by quality and limitation of resources.

When a predator attacks prey, non-vigilant individuals are slower to detect the attack than vigilant individuals, hence non-vigilant individuals are less quick to take flight (Hilton et al., 1999) and therefore more likely to be targeted by the predator (FitzGibbon, 1988; Krause & Godin, 1996; Sirot & Touzalin, 2009). The lower level of high quality vigilance of adult impala might explain why African wild dogs predominantly prey upon this age class. Although African wild dogs predominantly prey upon certain age–sex classes (Table 1), like most other predators (Cronje et al., 2002), they do prey on kudu and impala throughout the whole range of classes (Van der Meer et al., 2013). Therefore, even when an individual is not from a preferred age–sex class, it is still subjected to a lethality risk. In addition, predators seem to target non vigilant prey (FitzGibbon, 1988; Krause & Godin, 1996; Sirot & Touzalin, 2009). Regardless of age–sex class, prey is thus likely to reduce the chance of being preyed upon by increasing the time they spent high quality vigilant when presented with immediate predation risk by a predator. Factors other than age–sex class related differences in predation risk are likely to affect this individual investment in high quality vigilance, e.g., herd size (Burger et al., 2000; Pays et al., 2012a). In accordance with other studies on the species (Hunter & Skinner, 1998; Matson et al., 2005; Pays et al., 2012b), impala decreased their investment in high quality vigilance with an increase in herd size. It also has to be kept in mind that African wild dog densities are relatively low and lion (*Panthera leo*), the predominantly scavenging spotted hyena (*Crocuta crocuta*) and to a lesser extent, leopard (*Panthera pardus*), are the main predators in the system (Fritz et al., 2011). It is therefore possible that the observed anti predator behaviour is affected by predation pressure of predators other than African wild dogs.

Several studies have shown that playing sounds of a natural predator can be used to mimic predation risk (Blanchard & Fritz, 2007; Blumstein et al., 2008; Hettena et al., 2014). With our acoustic and olfactory simulation we therefore expected to evoke anti-predator behaviour, especially while prey in the study area will have both ecological and evolutionary experience with African wild dogs. In this study we did not use (heterospecific) control vocalizations (e.g., white noise, silence), we therefore cannot exclude the possibility that the recorded behaviour includes responses related to noise intensity or novelty. However, especially when prey has ecological and/or

evolutionary experience with a predator, prey has been shown to correctly associate, discriminate and respond to playbacks of vocalizations of their predators (Hettena et al., 2014). We therefore feel that the observed anti predatory behaviour in this study was primarily associated to the mimicked predation risk. This is supported by the difference in response between the species, suggesting that kudu and impala were capable to correctly associate African wild dog faeces and playbacks to predation risk and perceived this risk differently.

This study shows that age–sex class specific investment in high quality vigilance of prey is not necessarily related to age–sex class related predation pressure. However, for both kudu and impala, predation risk shaped the time individuals invested in high quality vigilance. Favreau et al. (2013) showed that impala experimentally alarmed by lion playbacks increased time spent high quality vigilant and decreased their feeding rate with 23% in the 3-min post playback period. Blanchard & Fritz (2007) found that, compared to low quality vigilance, impala delayed their first chew and chewed considerably less when engaged in high quality vigilance. Pays et al. (2012b) showed that individual impala foraging on poor quality patches spent more time high quality vigilant compared to those feeding on high quality patches. These results suggest that high quality vigilance incurs costs. Our study highlights how, despite these costs, animals used high quality vigilance to improve predator detection and underlines the importance to distinguish between high and low quality vigilance when investigating anti predator behaviour of prey.

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