

Flight behavioural responses to sport hunting by two African herbivores

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Sport hunting may have severe behavioural consequences, and possibly conservation implications for wildlife populations. We used flight initiation distances by two herbivores, impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*) to assess the impacts of sport hunting on their flight behaviour. We compared Gwaai, a designated hunting area adjacent to Hwange National Park, a protected area in Zimbabwe. We aimed to estimate flight initiation distances (FIDs) for impala and kudu as this can be a good measure of hunting effect on behaviour. Our results suggest that impala and kudu are more flight prone in hunting areas than in non-hunting areas. We propose habituation to explain the shorter FIDs in the protected area, and the risk of being shot by hunters the higher FIDs in the hunting area. We concede that more field observations are needed to estimate the distance at which animals will always trigger an immediate flight response from approaching predators (D_{\min}) and the distance above which prey will not move away from an approaching predator as it is not perceived to be dangerous (D_{\max}) in our study area. However, we suggest that D_{\min} is a useful index for wildlife managers to assess predation risk.

Key words: sport hunting, flight initiation distance, habituation, index of insecurity.

INTRODUCTION

Flight initiation distance (FID), the distance at which an animal flees from an approaching predator, has been a primary metric in the study of optimal escape theory and risk assessment (Cooper & Frederick 2010). FID is a useful tool for wildlife managers in developing buffer and setback distances between animal nesting/feeding areas and human visitors (e.g. Fernandez-Juricic *et al.* 2005), and their use in the assessment of animal welfare states as an indicator of fear or distress (e.g. Dwyer 2004).

Animals show decreased flight responses in areas with high, non-lethal human activities (Stankowich & Blumstein 2005), and variation in disturbance typically is correlated with the intent of activity. Hunting and nature-viewing individuals seek out direct interactions with wildlife, as opposed to hiking, biking, or snowmobiling individuals whose chief intent is not necessarily to interact directly with wildlife. From a functional perspective, animals

incur time costs, in the form of lost feeding and mating opportunities (e.g. Stankowich 2008), in order to sustain high rates of anti-predator vigilance and maintaining a zone of awareness within which they will treat any predator detected as a potential threat (Stankowich & Coss 2007). It is important to know whether individuals therefore habituate or sensitize (i.e. perceive greater risk) to regular exposure to non-lethal human disturbance (e.g. Rodriguez-Prieto *et al.* 2009) or hunting activity. Further, wildlife conservation and management would benefit from a better understanding of how hunting pressure is accounted for by animals in considering the costs and benefits of alternative responses to flight (Cooper & Frederick 2007).

The distance to cover or safe refuge has been shown to influence FID in fish (e.g. Dill 1990), birds (e.g. Rodriguez-Prieto *et al.* 2008) and mammals (e.g. Blumstein *et al.* 2005). The review and meta-analysis of important factors influencing FID by Stankowich & Blumstein (2005) showed that species' perceived risk increased by 43% when prey is far from rather than near a potential refuge.

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Considering that the hunting strategies of sport hunters, e.g. hiding and shooting from a certain distance, may differ from those of natural predators, e.g. stalking and chasing down (Sinclair *et al.* 2003), it is unclear whether or not animals subject to human hunting pressure make similar adjustments in their flight behaviour compared to those only chased by natural predators.

Sport hunting is a disturbance stimulus that can indirectly affect fitness and population dynamics *via* the energetic costs and feeding opportunities lost during risk avoidance (Sutherland 1998; Frid & Dill 2002; Crosmary *et al.* 2012). As predatory encounters escalate, prey must make a series of assessments and decisions regarding the level of threat posed by the predator, when to flee considering distance to the predator and access to closed/safe habitats (e.g. Blumstein 2003) and the optimal escape strategy based on predator's mode of attack and prey's physiological or morphological limitations (e.g. Stankowich & Coss 2007). FIDs can therefore be used as an indirect assessment of exploitation levels, as the degree of hunting that the population has experienced may affect flightiness (Frid & Dill 2002).

Benefits of increasing group size include shared vigilance, dilution of risk, predator swamping, confusion of predators, and an increased ability to mob predators (e.g. Curio 1978; Foster & Treherne 1981; Stankowich & Blumstein 2005). Two hypotheses are used to explain group size effect: 1) the 'many eyes' hypothesis proposes that the chances of a predator being detected by any individual increases with herd size (e.g. Tammie *et al.* 2005), and 2) the 'dilution effect' hypothesis which proposes that the animal's probability of being preyed upon in a large group is small hence it needs to be less vigilant and can feed more (e.g. Lima 1990; Tammie *et al.* 2005). Although these hypotheses have been used in explaining vigilance under natural predation, flight response (through FIDs) can be related to vigilance levels and we expect that groups that can detect the presence of hunters will flee early especially if the population is under hunting pressure.

Models of the relationship between FIDs and initial distance from an approaching threat to the animal group (starting distance) by Blumstein (2003) suggested two critical distances: a minimum distance (D_{\min}) and a maximum distance (D_{\max}). The D_{\min} is the distance at which prey are constantly aware of other animals nearby, and they will always trigger an immediate flight response, not showing

differences between other factors affecting FIDs such as group sizes and habitats. When testing for FID, if the starting distance is below D_{\min} , then FID will always equal the starting distance, (a straight regression line $y = x$ with slope of 1). The D_{\max} is the distance above which prey will not move away from an approaching predator due to lack of perceptual capabilities, simply not being attentive to activities beyond this distance, or that they perceive the predator but do not treat it as dangerous. Beyond D_{\max} , the slope of FID against starting distance should therefore be close to 0, but D_{\max} may be influenced by habitat or group size. Between D_{\min} and D_{\max} , prey should take into consideration other factors affecting FID besides starting distance, e.g. group size, habitat and distance to cover (Blumstein 2003). When FID is plotted against starting distance, we expect to get changes in slopes, from 1 moving towards 0. In this study, slopes close to 1 are associated with high levels of 'insecurity' while those closer to 0 with 'security'.

We used two ungulates (impala, *Aepyceros melampus*, and greater kudu, *Tragelaphus strepsiceros*) that are common and widely distributed throughout African savannas and woodlands (Jarman & Sinclair 1979) to investigate impacts of trophy hunting on FIDs, by comparing FIDs in a hunting area (Gwaai) to a strictly protected area (Hwange National Park, HNP). Both areas lie in northern Zimbabwe. We also attempted to determine the distances beyond which humans can be said to minimally disturb foraging impala and kudu, and compared these between the two areas. The smaller bodied impala (40–80 kg) uses grassland–woodland open associations, while the larger bodied kudu (120–315 kg) is a savanna woodland species that avoids open grasslands. The estimated per capita hunting risk based on the ratio of hunting quotas over population size estimates for the two species were similar though slightly higher in kudu than impala (1.7% and 1.4%, respectively) (Crosmary *et al.* 2012).

We hypothesized that impala and kudu show greater FID in hunting area compared to protected areas due to perceived hunting risk. We also hypothesized that starting distance, habitat and group size interact to determine FID. At similar starting distance, greater FIDs were predicted in open than closed habitats because animals can detect approaching humans from longer distances and they are likely to be further away from refuge, hence increased vigilance behaviour. The distance

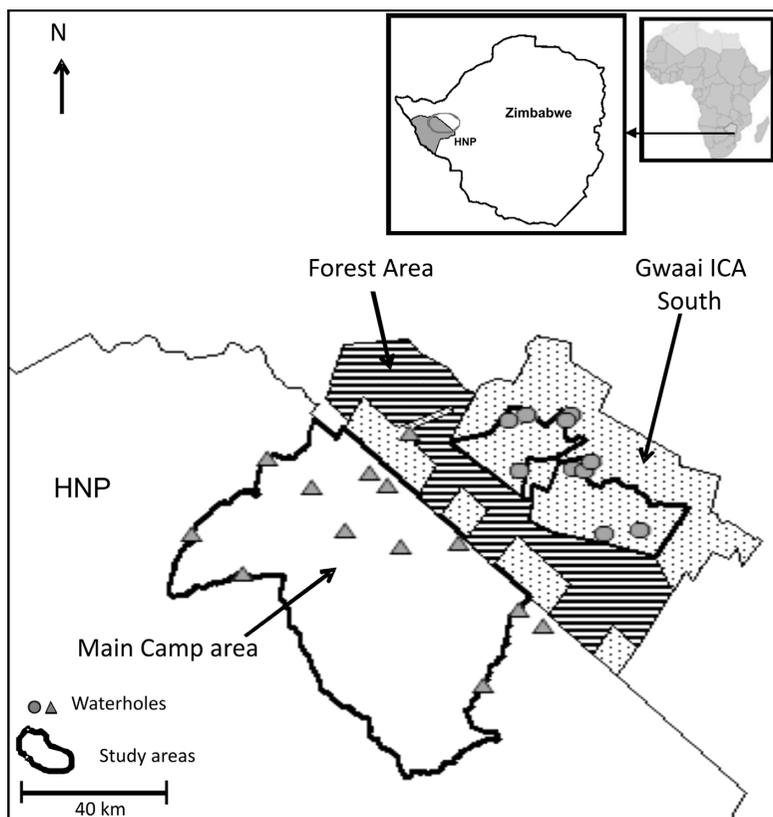


Fig. 1. Study area in Main Camp (part of HNP) and Gwaai hunting area in northwest Zimbabwe.

moved by the approacher is expected to decrease with decreasing starting distance (animals have less time to assess risk in short starting distances) and with increasing distance to cover (Cooper & Frederick 2010).

STUDY AREA AND METHODS

The study was conducted in Main Camp block of HNP, and in the hunting areas of Gwaai Intensive Conservation Area (ICA). HNP is 14 651 km², located on northwestern border of Zimbabwe (19°00'S, 26°30'E), and Main Camp block covers an area of about 1260 km² (Fig. 1). In Gwaai ICA, our study area was located to the south of the Bulawayo–Victoria Falls road (Gwaai ICA South, c. 880 km²). Both areas are characterized by an average annual rainfall of 600 mm normally received between November and April. Poaching activities are very low in the Main Camp block in comparison to Gwaai where surrounding villagers sometimes encroach into the hunting area for meat.

Vegetation is typical of southern African dystrophic wooded and bushed savannas with patches of

grasslands, dominated mainly by *Colophospermum mopane*, *Combretum* and *Acacia* species, *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). Main Camp has a high concentration of artificially pumped waterholes (Valeix *et al.* 2007), high levels of human activity and high prey density (Loveridge *et al.* 2007). Lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) are present as principal predators in Gwaai ICA at comparable densities to those in HNP but wild dogs (*Lycan pictus*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*) exist at relatively lower densities (Elliot 2007). Densities (per km²) for impala and kudu in Main Camp were 1.43 ± 0.47 and 1.59 ± 0.24 , respectively (Crosmar *et al.* 2012). Sizes of encountered herds were slightly higher in Main Camp than in Gwaai ICA for impala (mean 8.8 ± 0.9 and 5.4 ± 0.85 , respectively) and for kudu (mean 4.4 ± 0.63 and 3.6 ± 0.7 , respectively).

Behavioural observations

Following the procedure of Setsaas (2007), we drove a Landrover 110 along accessible roads

Table 1. Summary of starting distance measurements done in open and closed habitats of Main Camp and Gwaai ICA. Distance measurements are given in metres.

Species	Parameter	Main Camp		Gwaai ICA	
		Open habitats	Closed habitats	Open habitats	Closed habitats
Impala	Total observations	11	12	18	20
	Starting dist range	40–70	58–105	32–120	22–125
	Mean starting dist (\pm S.D.)	59.2 \pm 11.1	74.3 \pm 16.2	99.8 \pm 19.1	83.3 \pm 29
Kudu	Total observations	11	6	14	17
	Starting dist range	18–103	44–104	20–109	15–97
	Mean starting dist (\pm S.D.)	62.8 \pm 26.9	75.2 \pm 23.3	77.9 \pm 28.3	59.8 \pm 26.6

or fireguards at 25–30 km/h at the onset of the hunting season (May to July) in 2008 with two observers on top. When a herd/singleton of impala or kudu was seen, the vehicle was immediately stopped and the engine switched off. A range-finder (Bushnell Yardage Pro Sport 450, Bushnell Performance Optics, Netherlands) was used to take the starting distance – measured as distance from the vehicle to the animal(s). One person walked (in an upright posture) straight towards the herd, until the group or one member of the group, started moving away (flight), the distance from the person to the original position of animals was defined as the FID. Flight ranged from walking to trotting, sprinting or bounding. When a group of animals took flight while parking the vehicle or while the experimenter was getting out of the vehicle we took the distance from the vehicle to the group as the FID. There were a few observations where a group/singleton initiated flight before we stopped the vehicle (1.1% for kudu and 0.6% for impala observations mainly in the hunted area for both species). In these cases, starting distance could not be measured hence we excluded them from our analysis. Distance to cover was measured as the distance from original position of animals to the nearest bush/woodland cover. The size, composition and geographic location of each herd/singleton was recorded which helped us to avoid repeated FID measurements. Habitats were visually categorized, with open habitat was defined as having approximately less than 40% tree/bush cover, and more than that was defined as a closed habitat. In total, 288.4 km of road transects were driven in HNP and 198 km were driven in Gwaai.

Data analysis and model selection

The FIDs were analyzed using linear models taking (1) area – with two levels: hunted (Gwaai)

and protected (HNP), (2) habitat – with two levels: open and closed, (3) starting distance (4) distance to cover and (5) herd size as explanatory variables. The distance measurements were square root transformed to meet normality of residuals after running the linear models. Only the FID measurements for which we had confidence that observed flight responses and disturbance was strictly by the experimenter were retained for analysis. In the model selection process we generated all possible models (with single effects and all possible interactions among the above mentioned variables). Using the ‘AICcmodavg’ R package (Mazerolle, 2013) we selected the best models using the lowest Akaike Information Criteria (AICc) modified for small sample sizes (Burnham and Anderson, 2002). Table 1 shows the number of starting distance measurements in the different areas. We plotted the relationship between FID and significant predictor variables both for impala and kudu in the protected and hunting areas. There were no FID measurements done less than starting distances of 22 m and 18 m (for impala and kudu, respectively), and beyond 125 m for both species (see Table 1) and this restricted us from estimating D_{\min} and D_{\max} using piecewise regression.

RESULTS

For both impala and kudu, the best AICc models explaining variation in FIDs retained area (hunting and protected), starting distance and the interaction term area \times starting distance as explanatory variables (Table 2).

Impala

Impala FIDs in hunting area (mean 82.1 \pm 4.6m) were longer in comparison to the protected area (mean 50 \pm 2.5 m), and FIDs increased less with increasing starting distance in the protected area

Table 2. Akaike Information Criteria (AICc) for the top candidate models for impala and kudu. The chosen models are denoted by an asterisk (*).

Model	K	AICc	Δ AICc	W_i
Impala models				
*Area + starting distance + area \times starting distance	5	-4984.37	0.00	0.77
Area + starting distance + habitat + area \times starting distance	6	-4981.98	2.38	0.23
Area + starting distance + habitat + area \times habitat	6	-4966.33	18.03	0.00
Kudu models				
*Area + starting distance + area \times starting distance	5	-3429.43	0.00	0.77
Area + starting distance + habitat + area \times starting distance	6	-3427.01	2.42	0.23
Area + starting distance + habitat + area \times habitat	6	-3417.07	12.36	0.00

compared to the hunting area (area by FID interaction: $\beta = 0.698$, $t = 11.579$, $P = 0.006$). Slopes for each area are given by equations in Fig. 2a.

Kudu

Kudu FIDs in the hunting area (mean 64.1 ± 4.6 m) were also longer compared to protected area (mean 42.9 ± 3.4 m). Similar to impala, FIDs increased less with increasing starting distance in the protected area compared to the hunting area (area by FID interaction $\beta = 0.876$, $t = 15.986$, $P < 0.001$). Slopes for each area are given in Fig. 2b.

DISCUSSION

Our results suggest that both impala and kudu in the hunting area were more wary which is consistent with other findings, for example impala in Serengeti (Setsaas *et al.* 2007) and other large mammals in Tanzania (Caro *et al.* 1998).

Our attempts to go beyond a simple estimate of FID and to try to define D_{\min} and D_{\max} in the two areas were unfruitful given the paucity of data. In particular, there were no observations made at short starting distances (i.e. less than 22 m and 50 m for impala and kudu, respectively) so that D_{\min} could not be determined since the slopes had already departed from 1 at the shortest starting distances. However, in the hunting area, the slopes that were close to 1 (i.e. 0.85 and 0.92 for impala and kudu, respectively), which suggest that the D_{\min} was likely to be very close to the minimum starting distances. Basing on Chamaillé-Jammes & Blumstein's (2012) arguments, we suggest that the slopes in protected area that are far below 1 for impala and kudu hints that these animals are less wary (have low index of insecurity compared to those in hunting areas (with high index of insecurity). There were also few observations made beyond

125 m in both hunted and protected areas to properly determine D_{\max} .

It has been shown that through habituation, animals can allow closer approaches by potential predators (like humans when they exist in high densities (e.g. Dunham 1979; Blumstein *et al.* 2003). However, in our case, although all the animals experience some form of interaction with humans, one is normally lethal (being shot in the hunting area) and the other is not lethal (e.g. game viewing and photographing in the protected area). Thus, we suggest that animals in the hunting area show a lower acceptance to humans (caused by the high frequency of lethal encounters) while those animals in protected area show a higher acceptance to humans (habituation) caused by a low frequency of lethal encounters. Poaching activities and hunting for food rations, particularly in the hunting area, may also have increased the perceived risks of being killed on encounter with humans.

The effects of herd size and habitat type were probably overshadowed by the effect of hunting in our study. Animals were expected to be more wary and avoid open habitats that are exposed to hunters, as was the case outside Serengeti National Park (Caro 1999). However, generally reduced FIDs in closed habitats may be due to limited ability to detect threats at longer distances (Stankowich & Blumstein 2005). The influence of herd sizes on impala and kudu FIDs were not selected for in the best models. This could possibly be due to the small ranges in the herd sizes in the protected and hunting areas (impala: mean 8.8 ± 0.9 and 5.4 ± 0.85 , and kudu: mean 4.4 ± 0.63 and 3.6 ± 0.7 , respectively). Stankowich (2008) noted that the herd size effect might be confounded by the fact that as the herd size increases, it is more likely to contain a target animal for hunters and therefore the group is disturbed more in com-

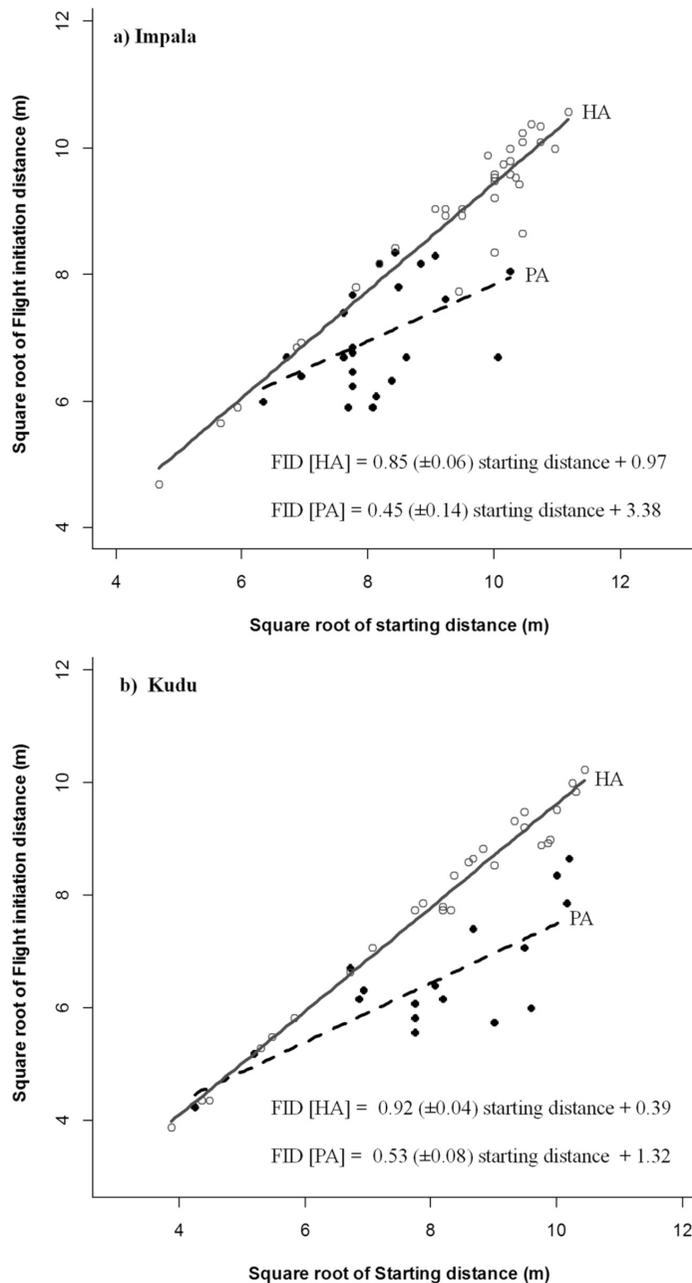


Fig. 2. Plots of square root of FID against starting distance for (a) impala and (b) kudu in Gwaai hunting area (HA) and HNP, a protected area (PA).

parison to smaller ones. Also, if disturbance stimuli such as approaching humans and gunshots are usually followed by death of a group member, then animals are likely to increase their FIDs (Stankowich 2008) and may not necessarily feel secure in larger groups.

Although we did not make an inter-species comparison of FID due to data paucity, kudu which usually form smaller herds generally had higher levels of insecurity in comparison to impala that form larger herds. Kudu is also one of the main prey species for most large predators in the study

area (Elliot 2007), and it is therefore expected to react quickly to any disturbance stimuli. In addition, animals rarely have perfect information and are generally expected to maximize fitness by over-estimating rather than under-estimating risk. Over-estimation costs, such as lost feeding opportunities, have milder fitness consequences than the cost of underestimating danger, which might be immediate death (Cooper & Frederick 2007). This can also explain the non-inclusion of distance to cover effect in our best models for the two species.

Our study revealed that slopes of the relationship between starting distance and FID were greater in hunted than in protected populations of kudu and impala. This suggests that impala and kudu in hunting areas were more flight prone than in non-hunting areas. We further suggest that the relative effect of hunting overshadowed the effect of habitat type and herd size, and that habituation to humans may have occurred in the protected area. Although the slopes of the relationship between starting distance and FID suggest that hunted animals were more 'insecure', further experimental observations at shorter starting distances (for protected areas) and longer starting distances (for both protected and hunting areas) are required to determine D_{min} and D_{max} for the two herbivores. However, we believe that applying a simple approach focusing singly on determining D_{min} , i.e. when the slope of FID against starting distance departs from 1, could be a useful index of general flight tendencies or habituation to humans, which can be applied in assessing predation risk by wildlife managers.

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REFERENCES

- BLUMSTEIN, D.T. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manage.* 67: 852–857.
- BLUMSTEIN, D.T., ANTHONY, L.L., HARCOURT, R. & ROSS, G. 2003. Testing a key assumption of wildlife buffer zones: Is flight initiation distance a species-specific trait? *Biol. Conserv.* 110: 97–100.
- BLUMSTEIN, D.T., FERNANDEZ-JURICIC, E., ZOLLNER, P.A. & GARITY, S.C. 2005. Interspecific variation in anti-predator behaviour and human-wildlife coexistence. *J. Appl. Ecol.* 42: 943–953.
- BURNHAM, K.P. & ANDERSON, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, Berlin.
- CARO, T.M., PELKEY, N., BORNER, M., SEVERRE, M., CAMPBELL, K.L.I., HUIH, S.A., KUWAI, J.O. & WOODWORTH, B.L. 1998. The impact of tourist hunting on large mammals in Tanzania; an initial assessment. *Afr. J. Ecol.* 36: 321–346.
- CARO, T.M. 1999. Densities of mammals in partially protected areas: the Katavi ecosystem of western Tanzania. *J. Appl. Ecol.* 36: 205–217.
- CHAMAILLÉ-JAMMES, S. & BLUMSTEIN, D.T. 2012. A case for quantile regression in behavioral ecology: getting more out of flight initiation distance data. *Behav. Ecol. Sociobiol.* 66: 985–992.
- COOPER, W.E. & FREDERICK, W.G. 2007. Optimal flight initiation distance. *J. Theor. Biol.* 244: 59–67.
- COOPER, W.E. & FREDERICK, W.G. 2010. Predator lethality, optimal escape behavior, and autotomy. *Behav. Ecol.* 21: 91–96.
- COOPER, W.E., HAWLENA, D. & PÉREZ-MELLADO, V. 2009. Interactive effect of starting distance and approach speed on escape behavior challenges theory. *Behav. Ecol.* 20: 542–546.
- CROSMARY, W., MAKUMBE, P., CÔTÉ, S.D. & FRITZ, H. 2012. Vulnerability to predation and water constraints limit behavioural adjustments of ungulates in response to hunting risk. *Anim. Behav.* 83: 1367–1376.
- CURIO, E. 1978. The adaptive significance of avian mobbing. *Z. Tierpsychol.* 48: 175–183.
- DILL, L. 1990. Distance-to-cover and the escape decisions of an African cichlid fish, *Melanochromis chipokae*. *Environ. Biol. Fishes.* 27: 147–152.
- DUNHAM, K.M. 1979. The feeding ecology of impala in the Sengwa Wildlife Research Area. M.Sc. thesis, University of Rhodesia, Salisbury.
- DWYER, C.M. 2004. How has the risk of predation shaped the behavioural responses of sheep to fear distress? *Anim. Welfare.* 13: 269–281.
- ELLIOT, N. 2007. A comparison of two methods for estimating population densities of lion (*Panthera leo*) and other large carnivores using spoor transects and call-up stations. M.Sc. thesis, Oxford University, Oxford.
- FERNÁNDEZ-JURICIC, E., VENIER, M.P., RENISON, D. & BLUMSTEIN, D.T. 2005. Sensitivity of wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum approaching distances and buffer areas for grassland birds. *Biol. Conserv.* 125: 225–235.
- FOSTER, W.A. & TREHERNE, J.E. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature.* 293: 466–467.
- FRID, A. & DILL, L.M. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Eco.* 6: 11–16.

- JARMAN, P.J. & SINCLAIR, A.R.E. 1979. Feeding strategy and the pattern of resource-partitioning in ungulates, in Serengeti. In: A.R.E. Sinclair & M. Norton-Griffiths (Eds), *Dynamics of an ecosystem* (pp. 130–163). University of Chicago Press, Chicago.
- LIMA, S.L. 1990. The influence of models on the interpretation of vigilance. In: M. Bekoff and D. Jamieson (Eds), *Interpretation and explanation in the study of animal behaviour: explanation, evolution and adaptation* (pp. 246–267). Westview Press, Boulder, CO.
- LOVERIDGE, A.J., SEARLE, A.W., MURINDAGOMO, F. & MACDONALD, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biol. Conserv.* 134: 548–558.
- MATSON, T., GOLDIZEN, A. & PUTLAND, D. 2005. Factors affecting the vigilance and flight behaviour of impalas. *S. Afr. J. Wildl. Res.* 35: 1–11.
- MAZEROLLE, M.J. 2013. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.32.
- RODRIGUEZ-PRIETO, I., FERNANDEZ-JURICIC, E. & MARTIN, J. 2008. To run or to fly: low cost versus low risk escape strategies in blackbirds. *Behaviour.* 145: 1125–1138.
- RODRIGUEZ-PRIETO, I., FERNÁNDEZ-JURICIC, E., MARTÍN, J. & REGIS, Y. 2009. Antipredator behavior in blackbirds: habituation complements risk allocation. *Behav. Ecol.* 20: 371–377.
- ROGERS, C.M.L. 1993. A woody vegetation survey of Hwange National Park. Department of National Parks and Wildlife Management, Harare.
- SETSAAS, T.H., HOLMERN, T., MWAKALEBE, G., STOKKE, S. & RØSKAFT, E. 2007. How does human exploitation affect impala populations in protected and partially protected areas? A case study from the Serengeti Ecosystem, Tanzania. *Biol. Conserv.* 136: 563–570.
- SINCLAIR, A.R.E., MDUMA, S. & BRASHARES, J.S. 2003. Patterns of predation in a diverse predator-prey system. *Nature.* 425: 288–290.
- STANKOWICH, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. *Biol. Conserv.* 141: 2159–2173.
- STANKOWICH, T. & BLUMSTEIN, D.T. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proc. R. Soc., B.* 272: 2627–2634.
- STANKOWICH, T. & COSS, R.G. 2007. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behav. Ecol.* 18: 358–367.
- SUTHERLAND, W.J. 1998. The importance of behavioural studies in conservation biology. *Anim. Behav.* 56: 801–809.
- TAMMIE, M.A., ANNE, W.G. & DAVID, A. P. 2005. Factors affecting the vigilance and flight behaviour of Impalas. *S. Afr. J. Wildl. Res.* 35: 1–11.
- VALEIX, M., CHAMAILLE-JAMMES, S. & FRITZ, H. 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia.* 153: 739–748.

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