African ungulates recognize a locally extinct native predator

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Abstract

Large carnivores are important ecosystem components but frequently suffer local extinctions. However, re-introductions and shifting conservation attitudes have lead to some population repatriations. Since the ecological consequences of predation may relate to indirect effects of predation risk, reconstruction of carnivore ecosystem function could depend on adequate predator recognition by prey. We evaluated behavioural responses in naïve and lion exposed impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*) and warthogs (*Phacochoerus africanus*) to audio calls of a native (African lion *Panthera leo*) and an alien (grey wolf *Canis lupus*) predator as well as to unfamiliar (music) and familiar (running water) neutral controls. Our results demonstrated stronger behavioural responses to lions than to any of the other calls, even in naïve populations, and suggest that retained predator recognition may enable rapid reconstruction of carnivore ecosystem function throughout Africa. However, since recognition may be lost in large increments we urge that carnivore repatriations should be a prioritized component of African ecosystem conservation.

INTRODUCTION

Compelling evidence suggests that large mammalian carnivores have important roles in terrestrial ecosystems (Ray et al. 2005; Estes et al. 2011). It has also been recognized that a large part of such ecosystem function is caused by indirect effects unrelated to the demographic consequences of prey being killed, such as alterations in prey foraging behaviour, habitat use, and physiological responses to environmental variation in response to predation risk (Sih et al. 1985; Creel and Christianson 2008). Therefore, appropriate recognition of predators and subsequent behavioural

responses to predation risk exhibited by prey may be a prerequisite for carnivores to supply their full suite of ecosystem functions (Berger 2007).

Large carnivores are typically extinction prone and most continents have suffered dramatic declines in their terrestrial large carnivore fauna (Dalerum et al. 2009). However, some populations have repatriated parts of their historical range, either through natural dispersal or human re-introductions (Wabakken et al 2001; Hayward and Somers 2009). Although there is a great geographic and taxonomic variation in the retention of predator recognition (Blumstein 2006), studies on ungulates in the northern hemisphere have shown a loss in behavioural responsiveness to predators and predation related species (Berger 1999; Berger et al. 2001), including subtle behaviours (Berger 2007), which has lead to higher predator sensitivity in naïve populations (Sand et al. 2006). These results coincide with a broader taxonomic context, where loss of predator recognition appears to be common across a wide range of taxa (Hettena et al. 2014). Such loss of appropriate response to predation risk could seriously impede the ecological effects of predator re-introductions or recoveries. However, some prey may recover their anti-predator behaviour swiftly after predator re-colonization (Hunter and Skinner 1996; Berger et al. 2001; Laundre′ et al. 2001; Berger 2007) and rapidly evolve anti-predator responses to introduced alien species (McLean et al. 1996; Anson and Dickman 2012).

Loss of predator recognition and antipredatory behaviour may be caused by a large social component in proximate regulation of transmission of recognition patterns (Brown and Laland 2001; Griffin 2004). However, some form of genetic inheritance is typically intimated (McLean et al. 1996; Blumstein 2006), and retention is predicted to be high if there is little fitness costs associated with recognition (Lahti et al. 2009). Although some species appear to respond to predators they have been evolutionary isolated from (Hettena et al. 2014), retention of recognition of a locally extinct predator as a potential threat may not necessarily be linked to ecologically relevant responses. Furthermore, the specificity in predator recognition can substantially influence the response (Griffin et al. 2001), and the severity of the response is predicted to correlate with the severity of the risk derived from perceived cues (Shettleworth 1998). Therefore, loss of predator exposure could lead to a loss of predator specific responses to cues normally associated with that predator, even if appropriate antipredatory behaviour has remained within the behavioural repertoire of the prey species (Curio 1993).

Africa contains one of the most diverse assemblages of large carnivores on Earth (Dalerum et a. 2009; Dalerum 2013). However, despite widespread carnivore range contractions (Dalerum et al. 2008), we currently have limited knowledge of how local extinctions of apex predators in Africa have influenced the capability of prey to recognize them, and subsequently to express appropriate antipredatory behaviour under renewed predation risk. Such knowledge is not only important for the ecological consequences of predator recovery, but also for our understanding of maintenance of predator recognition in environments with both diverse predator and prey communities (Dobson 2009). In addition, studies on predator recognition in ungulates are underrepresented among predator discrimination studies, and studies on how mammals respond to extinct or alien predators are rare (Hettena et al. 2014).

In this study we evaluated predator recognition measured as both immediate and short-term behavioural responses to audio calls of African lion (*Panthera leo*, a native predator) and grey wolves (*Canis lupus*, an alien predator) as well as neutral control sounds in three species of African ungulates, impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*, hereafter referred to as wildebeest), and common warthog (*Phacochoerus africanu*s, hereafter referred to as warthog), and contrasted the responses of populations naïve to recent lion predation to those that have experienced re-introduced lions over the past 15 years. We hypothesized that the

responses of naïve populations to calls of a lions would be of comparable magnitude to those of an wolves, as a consequence of a loss of specific predator recognition, and also that naïve populations would respond less strongly to calls of lions compared to lion exposed populations, caused by a recovery of predator response behaviour in areas were lions have been reintroduced.

MATERIALS AND METHODS

Study areas

We conducted experiments on naïve populations of impala, wildebeest and warthog in Lapalala Wilderness (23°51S, 28°16E), a privately owned game reserve within the Waterberg Biosphere, Limpopo Province, South Africa. It was formed in 1981 and consists of sequentially purchased pieces of previously commercial farmland, and encompasses 36,000ha. It is currently not open to the public, although occasional guided hunts are allowed. These hunts take place on foot. It also contains a wilderness school and management related activities such as bush clearing and burning occurs frequently (Isaacs et al. 2013). Lapalala hosts healthy populations of a range of large and medium sized herbivores, with impala, wildebeest, greater kudu (*Tragelaphus strepsiceros*) and warthog being the most numerous (Isaacs et al. 2013). It also contains a range of predators, including resident populations of leopards (*Panther pardus*) and brown hyaenas (*Hyaena brunnea*), and transient individuals of African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*). The reserve has, since its initiation, never hosted any populations of lions. Although no detailed historical records exist for central Limpopo, lions were probably exterminated from north-central South Africa in the early 20th century (Skead 2011). We therefore regard populations of antelope in Lapalala wilderness to be naïve in terms of their exposure to lion predation. However, a neighbouring reserve has held lions, and ungulates in Lapalala my occasionally have heard lion roars. Since we did not hear lions on any occasion in Lapalala during 4 years of field work, and since ungulates in Lapalala were naïve to lion predation, we regard the potential influence of this neighbouring reserve on our results to be limited in terms of habituating the ungulates to the sound of this predator.

To enable comparisons with prey that experience current lion predation we also conducted experiments on Welgevonden Game Reserve (24°18S**,** 27°80E), another privately owned reserve that is similar in size (37,500 ha), topography, vegetation and fauna to Lapalala. It is situated approximately 50 km away. Welgevonden is a commercially operating game reserve and has hosted a population of lions since they were re-introduced 1998. Welgevonden is a syndicated reserve consisting of over 50 land-owners. It contains 15 commercial game lodges and several private ones. Hunting is not allowed but game-viewing vehicles are frequently occurring throughout the reserve. Similar to Lapalala, there are also frequent management related activities such as bush clearing and burning. The number of lions at the time of the experiments ranged from 8-14 adults distributed across two prides and occasionally one coalition of males. Although the study areas lie in relatively close proximity, they are both heavily fenced, and the lion population in Welgevonden strictly monitored. Furthermore, most of the areas between the two reserved consist of equally heavily fenced game reserves or commercial cattle farms that are closely monitored. Therefore, no lions were able to disperse out of Welgevonden to potentially confound the results, and similarly it is exceptionally unlikely that any prey species had dispersed between the two study areas.

Experimental design

Between May 2009 and June 2012 we opportunistically identified foraging groups of impala, wildebeest and warthog by driving roads during field periods that lasted from 1-2 weeks. We restricted our experiments to groups where at least half of the individuals were engaged in foraging to avoid potential bias (Dalerum et al. 2008). Once a group was located, we turned off the engine and waited 5-20 minutes until there were no signs of the animals being aware of the vehicle. We recorded the number and age composition of animals as well as the observation distance and the closest distance of any group member to nearest vegetation cover (Table 1). Only adult and sub-adult individuals were included in group size estimates.

To enable later recording of behaviour, we filmed each group using a handheld digital video camera. We recorded 3 minutes of base-line behaviour, after which we broadcasted a 45 second audio clip of one of the four experimental categories (see below) using two synchronized speakers connected to a 350 Watt amplifier powered by a 12 V battery. We then continued the video recording until 10 minutes after the end of the call, or until all members of the group had moved out of sight. Throughout the study we broadcasted four different sounds; a native predator (lion roar), an alien predator (grey wolf howls), a neutral unfamiliar control (popular music; a 45 second clip containing the crescendo of the song 'My heart will go on' performed by Celine Dion), and a neutral familiar control (running water). We only broadcasted one sound to each group to avoid conditioning. We only broadcasted music to naïve impala, as we did not encounter the other species frequently enough in Lapalala to enable sufficient sample sizes within the time frame of the study. In order to not disturb the game viewing experience for visitors in Welgevonden, we did not broadcast music to any groups in this reserve. The selection of which call to give to a group was based on a pseudo-random design, in which we made a sequential list of the call order for each species at the initiation of each field day. We did not do another call within 5 km of a previous call to avoid habituation, and only one call of each call category within this distance the same day. The speakers were mounted close (< 1 meter) together on the observation vehicle, and the distance from the study animals to the broadcast speakers were therefore the same as the observation distance (Table 1).

We scored three types of behavioural responses to calls; immediate response, proportion of time foraging and being vigilant after the calls, and the time it took for individuals or groups to resume pre-call behaviour. Immediate behavioural responses were recorded at the time of the call. We scored it as a categorical variable with 5 classes of increasing severity; "no response", "look up", "warn", "aggregate" and "abandon". We used one score for the whole group, and used the most severe behaviour exhibited by the majority of the group members: "No response" - less than half of the individuals raised their head; "Look up" - at least half of the individuals temporarily lifted their heads; "Warn" - at least half of the individuals were giving warning calls; "Aggregate" - at least half of the individuals abandoned their foraging behaviour and aggregated in close association to one another; "Abandon" - at least half of the individuals abandoned the foraging location. The behaviours were scored during the duration of the call, and the "Abandon" class was scored if the initiation of moving out of the foraging location was initiated before the end of the call.

The effect of calls on proportion of time spent foraging and being vigilant was quantified using focal observations scored from the recorded videos. We used the video recordings since we simultaneously recorded data on several individuals. These observations were by necessity done on groups that did not abandon their foraging sites. We timed the duration of behaviours by recording them onto a portable digital assistant device (PDA) or onto a laptop computer. An animal was defined as foraging if it was standing up with its head distinctly below its shoulders, or if it was standing up and foraging feeding from a bush. An animal was defined as vigilant if it was

standing up with its head clearly raised above its shoulders and scanning its surroundings. We were not able to distinguish between social and anti-predatory vigilance. We conducted a focal observation of 180 seconds prior to and another of 180 seconds immediately after the end of a call. If we could not determine the behaviour of an animal, because it had its head obscured or it was out of sight, we did not include that time in the total observation time for subsequent analyses. However, in no case did we include focal data beyond 180 seconds after the end of the call. If possible we used the same animals for the pre- and post call observations. However, this was not possible in 15 % of the focal observations (55 out of a total of 359 observations). In these cases different animals were used for pre- and post observations to not loose behavioural information. The focal animals were chosen at random, but we selected a new animal if we could not observe the selected one for at least 60 seconds. We aimed to record focal observations on 5 individuals each in 5 groups of every call category, although this was not always possible (Table 1). We recorded focal data on 104 individual impala in Lapalala and 97 in Welgevonden, on 75 wildebeest in Lapalala and 71 in Welgevonden, and on 56 warthogs in Lapalala and 51 in Welgevonden. The number of impala observed per group ranged from 3 to 6, and the number of wildebeest and warthogs ranged from 2 to 5 for both species.

We measured recovery time after a call either as the time it took for an individual to return to foraging or as the time it took for the proportion of animals within a group to return to the pre-call baseline. Time until foraging was derived directly from the focal data, and from the same individuals. However, this time was capped at the end of the focal period (i.e. 180 seconds after the end of a call). It hence represents a conservative measure of recovery time. We also conducted scan observations of the group with 1 min. intervals for 5 minutes prior to and for 10 minutes after a call. As with the focal data, scan data were recorded from the recorded videos, and the behaviours were classified in the same manner. For each scan event, we only used the total number of observable individuals to calculate the binomial proportions in subsequent analyses. We collected scan data on the same groups as we collected data on focal observations.

The research was approved by the University of Pretoria Animal Care and Ethics Committee (ec017-12). The owners of Lapala Wilderness and Welgevonden Private Game Reserve kindly gave permission to carry out the work on each respective reserve.

Data analyses

We used cumulative link models with a logit link function and a multinomial error to evaluate the effects of the different calls on immediate behavioural responses. We used generalized linear mixed models with a logit link function and binomial error to evaluate the effect of the calls on proportion of time animals were engaged in foraging or vigilance pre- and post calls as well as on the proportion of animals that were engaged in foraging and vigilance. We used generalized linear mixed models with a log link function and Poisson error to evaluate the effect of calls on time until return to foraging behaviour.

In all analyses, we first evaluated the effect of calls on naïve ungulates by only using data from Lapalala. In these analyses on naïve populations, we used call type as a fixed experimental effect in the models on immediate response and time until return to foraging, the interaction (as well as main effects) of call type and time period (i.e. pre- or post call for focal data and a categorized time sequence since end of call for scan data) on the models on focal and scan data. Secondly, we evaluated if any contrasts in the responses to the varying stimuli differed between naïve and lion exposed populations by creating a second set of models that also included data from Welgevonden. When we also included data from Welgevonden, we fitted reserve and its interaction with the experimental terms described above as additional fixed effects. For the models

on focal data we fitted observation animal nested within observation group as random terms, for the models on scan data we fitted the sequential observation event grouped across observation groups as random terms, and for the models on time until foraging we fitted observation group as a random term. We also included the fixed effects of age and sex of the observation animal (only for models using data from focal observations), group size, the presence of juveniles (not for naïve impala, since we did not observe juveniles in those groups), observation distance and distance to cover if these terms contributed to the model fit was assessed by Akaike's Information Criterion (Akaike 1974; see Table S1-S6 for a full set of model contributions by these variables). We additionally added a random term for each observation to account for over-dispersion in the generalized linear mixed models (Elston et al. 2001). Fixed effects were evaluated with sequential likelihood ratio tests and parameter estimates with associated Wald tests. Statistical analyses were carried out using the software R version 2.15.1 for Linux (http://www.r-project.org) and the contributed packages ordinal (Christensen 2012) and lme4 (Bates et al. 2013).

RESULTS

Naïve impala and wildebeest showed more severe immediate responses to calls of lion compared to wolf (Figure 1). In all three species there were more severe immediate responses to calls of both predator species compared to a familiar control, although the difference for warthog was non-significant because of infinite parameter estimates and associated inflated standard errors (Table 2). Naïve impala responded less strongly to an unfamiliar control than to lion but more strongly to an unfamiliar than to a familiar control. Immediate responses did, however, not differ between an unfamiliar control and wolf. The effect of call on immediate responses did not differ between naïve and lion exposed populations (Figure 1b; impala $\chi^2 = 0.54$, df = 2, $P = 0.764$; wildebeest $\chi^2 = 0.91$, df = 2, $P = 0.633$; warthog $\chi^2 = 0.97$, df = 2, $P = 0.617$).

Naïve impala and warthog foraged significantly less after calls of lion compared to wolf, and warthog were significantly more vigilant (Figure 2a; Table 3). Individuals of all three species decreased foraging and increased vigilance more after hearing lion compared to a familiar control. Only naïve impala and wildebeest foraged less after calls of wolf compared to a familiar control, and impala and warthog showed a trend for increasing vigilance. Naïve impala foraged less in response to lions compared to an unfamiliar control, but did not differ in vigilance. Impala did not differ in response between wolf and an unfamiliar control, nor between an unfamiliar and a familiar control. Lion exposed and naïve populations exhibited similar responses (foraging: impala $\chi^2 = 7.02$, df = 2, $P = 0.030$, wildebeest $\chi^2 = 4.65$, df = 2, $P = 0.098$, warthog $\chi^2 = 0.27$, df = 2, $P = 0.874$; vigilance: impala $\chi^2 = 0.49$, df = 2, $P = 0.782$, wildebeest $\chi^2 = 1.21$, df = 2, $P = 0.545$, warthog $\chi2 = 3.80$, df = 2, $P = 0.149$), although the foraging responses of predator exposed impala were weaker than in naïve animals (Figure 2b).

Naïve impala, wildebeest and warthog took longer time to return to foraging behaviour after hearing lion compared to both wolf and a familiar and unfamiliar control (Figure 3a). Naïve wildebeest and warthog took longer until they returned to foraging after hearing wolf compared to a familiar control, and there was a similar trend for impala (Figure 3a; Table 4). Naïve impala did not take longer to return to foraging after hearing wolf compared to an unfamiliar control, nor after hearing an unfamiliar compared to a familiar control (Table 4). It took longer for the percent of animals engaged in foraging and vigilance to return to pre-call baseline after calls from lions compared to both wolf and a familiar control (Figure 3b; Table S7-S12). There were no differences between naïve and lion exposed populations either in the effect of call on time until foraging (Figure 3c; impala $\chi^2 = 0.97$, df = 2, $P = 0.615$; wildebeest $\chi^2 = 1.70$, df = 2, $P = 0.428$; warthog $\chi^2 = 0.32$, df = 2, $P = 0.854$) or on the effect of call on the percent of groups engaged in

foraging (Figure 3d; impala $\chi^2 = 12.37$, df = 22, $P = 0.949$; wildebeest $\chi^2 = 24.21$, df = 22, $P = 0.336$; warthog $\chi^2 = 9.99$, df = 22, $P = 0.986$) and vigilance (Figure 3d; impala $\chi^2 = 19.67$, df = 22, $P = 0.603$; wildebeest $\chi^2 = 32.60$, df = 22, $P = 0.068$; warthog $\chi^2 = 2.80$, df = 22, $P > 0.999$).

DISCUSSION

Although the observed responses differed in detail between the three species, overall our results demonstrated stronger behavioral responses to lions than to any of the other calls in naïve populations. Naïve populations also showed remarkable similarity in all response types compared to populations exposed to recent and current lion predation. The results suggest that these African ungulates have retained the ability to recognize lions as a potential threat, and concur with a recent study that similarly highlight that mule deer (*Odocoileus hemionus*) appear to have retained the ability to recognize locally extinct wolves (Hettena et al. 2014). These findings contrast suggestions from some studies showing that prey species have lost their ability to recognize locally extinct predators (Blumstein et al. 2000; Berger 2007; Berger et al. 2011), but are consistent with others showing that predator recognition have been retained (Hunter and Skinner 1996; Byers 1997; Coss 1999).

We suggest that our results could have been caused by a genetic inheritance of lion recognition in these ungulate species, potentially enhanced by the continued predation pressure imposed by other non-extinct large carnivore species (e.g., Blumstein and Daniel 2002). Retention of traits after relaxed selection is expected if the cost of retaining the trait is low, and there is no active selection on the trait itself (Lahti et al. 2009). The detected ability to recognized lions may represent such an evolutionary 'relict', especially since the time for evolution to have acted on eroding recognition has been short (probably in the time frame of less than 20 generations). However, since alterations of traits after relaxed selection can appear rapidly and in large increments (Lahti et al. 2009), we suggest that the retention of predator recognition and specific anti-predatory behaviour may rapidly be lost.

While generalizations of predator stimuli may be evolutionary beneficial (Tinbergen 1951), it can also carry costs associated with reduced time for feeding or reproduction (Ydenberg and Dill 1986; Blumstein and Daniel 2005). We suggest that the observed responses represent a trade-off in stimuli generalization, which includes recognition mechanisms for the specific predators that prey have co-evolved with and a generalized response to novel sounds as a potential but less severe threat. In impala, we found no significant differences in the responses to an alien predator compared to a novel neutral control, which suggests that novel stimuli may be generalized as a potential threat irrespective of their structure. However, we highlight that our experiments did not allow us to fully resolve how these ungulate species generalize novel stimuli, since we only introduced audio stimuli and had insufficient samples of novel but neutral sounds.

We found remarkable similarities in responses between naïve and lion exposed populations, with the only detected differences being that responses to native predators in some instances were more severe in naïve compared to exposed populations. Many predators do not make sounds while hunting. Subsequently, audio cues of predators can be regarded as an indication of general presence, but not necessarily of an immediate threat (Blumstein et al. 2000). We suggest that the observed differences may represent a habituation to the constant presence of lions in exposed populations, and subsequently that predator exposure may result in a more efficient time allocation under different threat scenarios (Lima and Bednekoff 1999). However, we point out that any differences between the reserves could have been confounded by several variables that we did not directly quantify, for instance the frequent occurrence of tourist vehicles in Welgevonden, and the occasional hunting parties in Lapalala. In addition, social factors may

substantially influence vigilance rates in gregarious antelope facing predation risk (Favreux et al. 2013), which further could have influenced our results.

To conclude, our experiments suggested that some populations of African ungulates have retained the ability to recognize a native but locally extinct apex predator, the lion, as a potential threat. We argue that this recognition may have been genetically inherited. We suggest that re-introduction and re-colonization of lions have the potential for rapid restoration of ecological processes related to indirect effects of predation, but since recognition may be lost in large increments we recommend that utilization of this retained predator recognition for ecological restoration should be prioritized to enable rapid reconstruction of predation effects in ecosystems.

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Table 1
Number of groups, group sizes and observation distances (meters) for call-back experiments in naïve and lion exposed populations of impala, blue wildebeest and warthog.

		Impala			Blue wildebeest			Warthog		
		N[a]	Group size[b]	Obs. distance[b, c]	N[a]	Group size[b]	Obs. distance[b, c]	N[a]	Group size[b]	Obs. distance[b, c]
Naïve groups	Familiar control	15 (5)	11.9 ± 9.4	122.7 ± 45.7	10 (5)	18.2 ± 12.5	127.7 ± 58.8	11 (8)	3.8 ± 1.8	95.6 ± 44.3
	Unfam. control	14 (5)	14.2 ± 13.1	141.1 ± 65.5						
	Wolf	11 (5)	12.9 ± 8.8	111.8 ± 40.1	10 (5)	21.7 ± 13.5	137.5 ± 62.4	8 (5)	2.7 ± 1.3	97.3 ± 36.8
	Lion	11 (4)	12.2 ± 6.4	105.0 ± 56.2	10 (6)	16.2 ± 9.4	130.9 ± 62.3	9 (5)	3.3 ± 1.6	110.8 ± 48.0
Lion exposed groups	Familiar control	9 (6)	19.7 ± 14.6	106.6 ± 43.5	13 (4)	15.3 ± 5.8	95.6 ± 44.3	13 (5)	3.5 ± 1.3	106.3 ± 53.3
	Wolf	7 (5)	14.9 ± 10.8	115.6 ± 45.0	14 (4)	21.8 ± 12.9	122.1 ± 62.0	12 (7)	4.0 ± 2.5	101.9 ± 45.9
	Lion	7 (5)	20.9 ± 13.9	129.9 ± 80.3	17 (6)	23.2 ± 14.6	125.1 ± 47.6	12 (3)	3.0 ± 1.1	92.8 ± 54.4

a Numbers in brackets reflect number of groups where focal and scan data were collected from recorded videos

b Mean ± 1 sd

c Distance to loud-speakers during calls were the same as observation distance

Table 2
Coefficients from cumulative link models describing the difference in the severity of the immediate behavioral response of audio calls of lion (a native predator), wolf (an alien predator), a familiar control (FC, running water) and an unfamiliar control (UC, popular music) in naïve impala, wildebeest and warthog. Each coefficient describes the relative difference between each pair of calls in terms of the severity of the behavioral response. Behavioral responses were coded by as an ordinal variable with increasing severity; no response, look up, warn, aggregate, and abandon foraging site.

	Impala			**Wildebeest**			**Warthog**		
	β	**Z**	**P**	**β**	**Z**	**P**	**β**	**Z**	**P**
lion vs. wolf	-3.10	3.01	0.002	-1.77	1.89	0.058	-1.06	0.96	0.335
lion vs. FC.	-5.82	2.91	< 0.001	-5.97	5.05	< 0.001	-23.26	< 0.01	0.998
wolf vs. FC	-2.86	1.07	0.007	-5.13	3.29	0.001	-21.19	< 0.01	0.998
lion vs. UC	-4.08	3.77	< 0.001						
wolf vs. UC	0.97	0.95	0.340						
UC vs. FC	-1.89	2.22	0.027						

Table 3
Coefficients from generalized linear mixed models describing the difference in proportion of time spent foraging or being vigilant during 180 seconds immediately after audio calls of lion (a native predator), wolf (an alien predator), a familiar control (FC, running water) and an unfamiliar control (UC, popular music) compared to 180 seconds prior to the call in naïve impala, wildebeest and warthog. Each coefficient describe the relative difference between each pair of calls in terms of the difference in the proportion of time spent foraging and being vigilant post- and pre-call.

	Impala			**Wildebeest**			**Warthog**		
	β	**Z**	**P**	**β**	**Z**	**P**	**β**	**Z**	**P**
Foraging									
lion vs. wolf	1.51	5.30	< 0.001	0.32	1.42	0.155	0.97	8.89	< 0.001
lion vs. FC.	2.04	6.70	< 0.001	0.80	11.24	< 0.001	1.16	11.24	< 0.001
wolf vs. FC	0.62	2.25	0.024	0.47	2.18	0.029	0.18	1.79	0.072
lion vs. UC	1.75	5.88	< 0.001						
wolf vs. UC	0.24	0.95	0.344						
UC vs. FC	0.29	1.06	0.290						
Vigilance									
lion vs. wolf	-0.24	0.47	0.638	-0.92	1.70	0.088	3.11	3.41	< 0.001
lion vs. FC.	-1.17	2.10	0.036	-1.46	2.84	0.005	-3.90	4.65	< 0.001
wolf vs. FC	-0.95	1.87	0.061	0.54	0.94	0.347	-1.51	1.81	0.070
lion vs. UC	-0.25	0.46	0.648						
wolf vs. UC	-0.06	0.13	0.897						
UC vs. FC	-0.89	1.65	0.098						

Table 4
Coefficients from generalized linear mixed models describing time until animals return to foraging after broadcasts of lion (a native predator), wolf (an alien predator), a familiar control (FC, running water) and an unfamiliar control (UC, popular music) in naïve impala, wildebeest and warthog. Each coefficient describes the relative difference in terms of time until animals returned to foraging between each pairs of calls.

	Impala			**Wildebeest**			**Warthog**		
	B	**Z**	**P**	**β**	**Z**	**P**	**β**	**Z**	**P**
lion vs. wolf	-2.07	2.11	0.034	-2.23	2.03	0.042	-3.49	3.03	0.002
lion vs. FC.	-3.81	3.66	< 0.001	-5.79	4.70	< 0.001	-7.00	5.21	< 0.001
wolf vs. FC	-1.73	1.63	0.103	-3.78	2.50	0.012	-3.62	2.57	0.010
lion vs. UC	-3.68	3.61	< 0.001						
wolf vs. UC	-1.60	1.54	0.122						
UC vs. FC	-0.13	0.12	0.902						

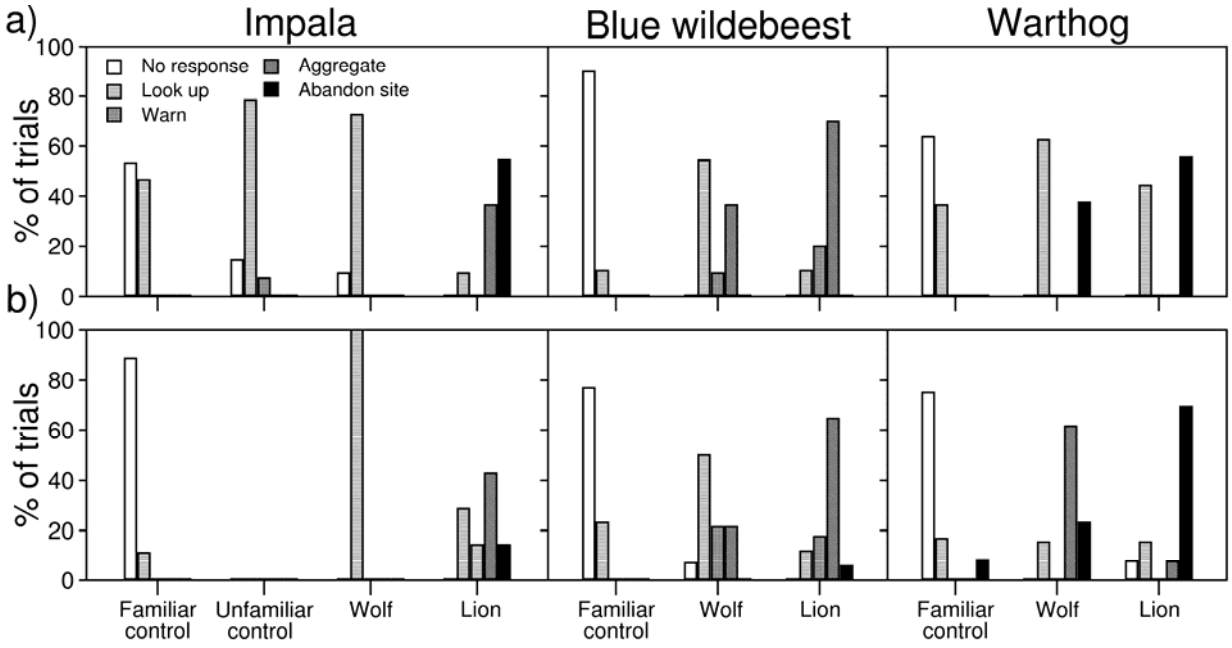

Figure 1
Immediate behavioural responses of naïve (a) and lion exposed (b) foraging groups of impala, blue wildebeest and warthog to audio calls of a familiar control (running water), an unfamiliar control (popular music, only for naïve impala), grey wolf (an alien predator) and lion (a native predator). Behavioural responses were categorized as an ordinal response variable with escalating response severity; no response, look up, warn, aggregate and abandon foraging site.

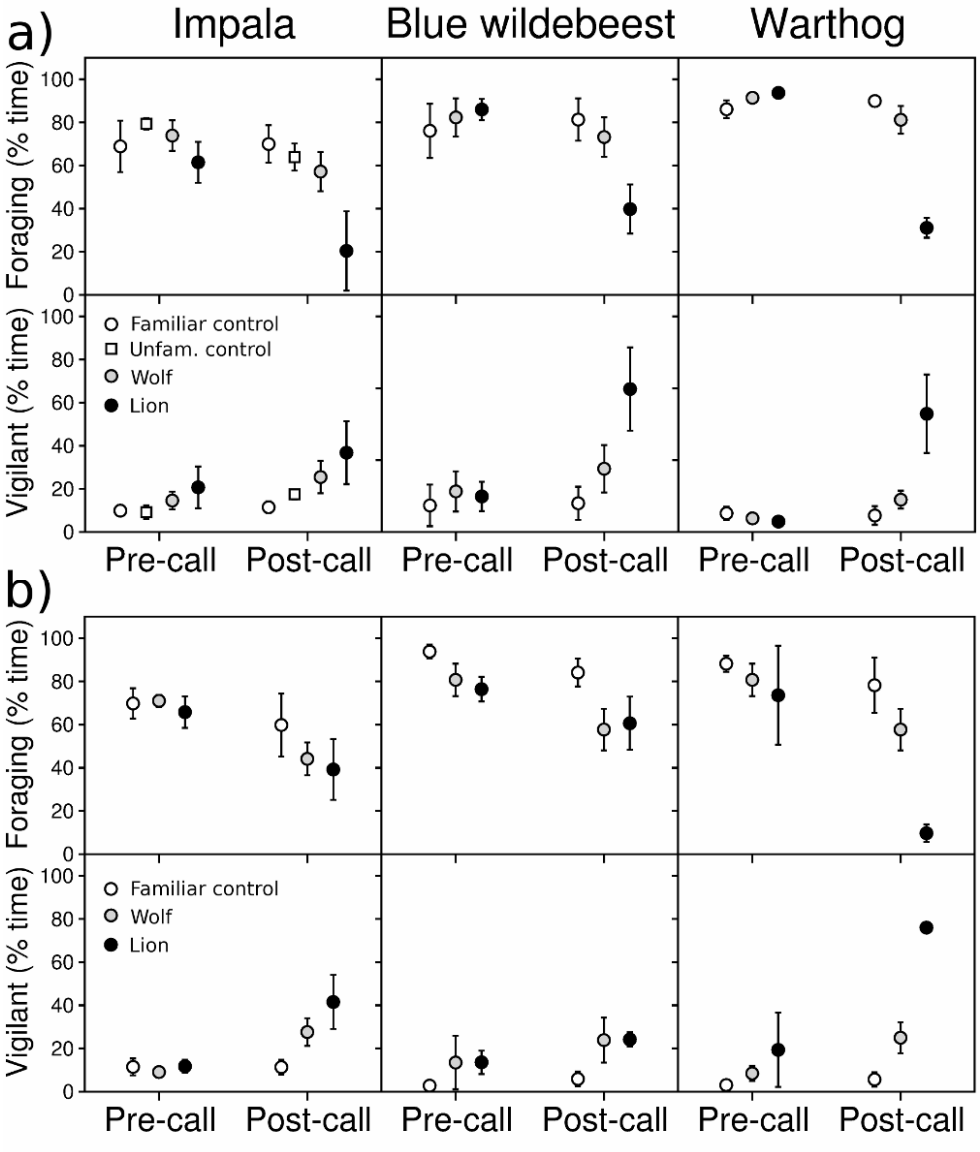

Figure 2
Time spent foraging and being vigilant during 180 second observations of naïve (a) and lion exposed (b) individuals of impala, wildebeest and warthog prior to and after audio calls of a familiar control (running water), an unfamiliar control (popular music; only for naïve impala), grey wolf (an alien predator) and lion (a native predator). Figure presents mean ± SE of group means.

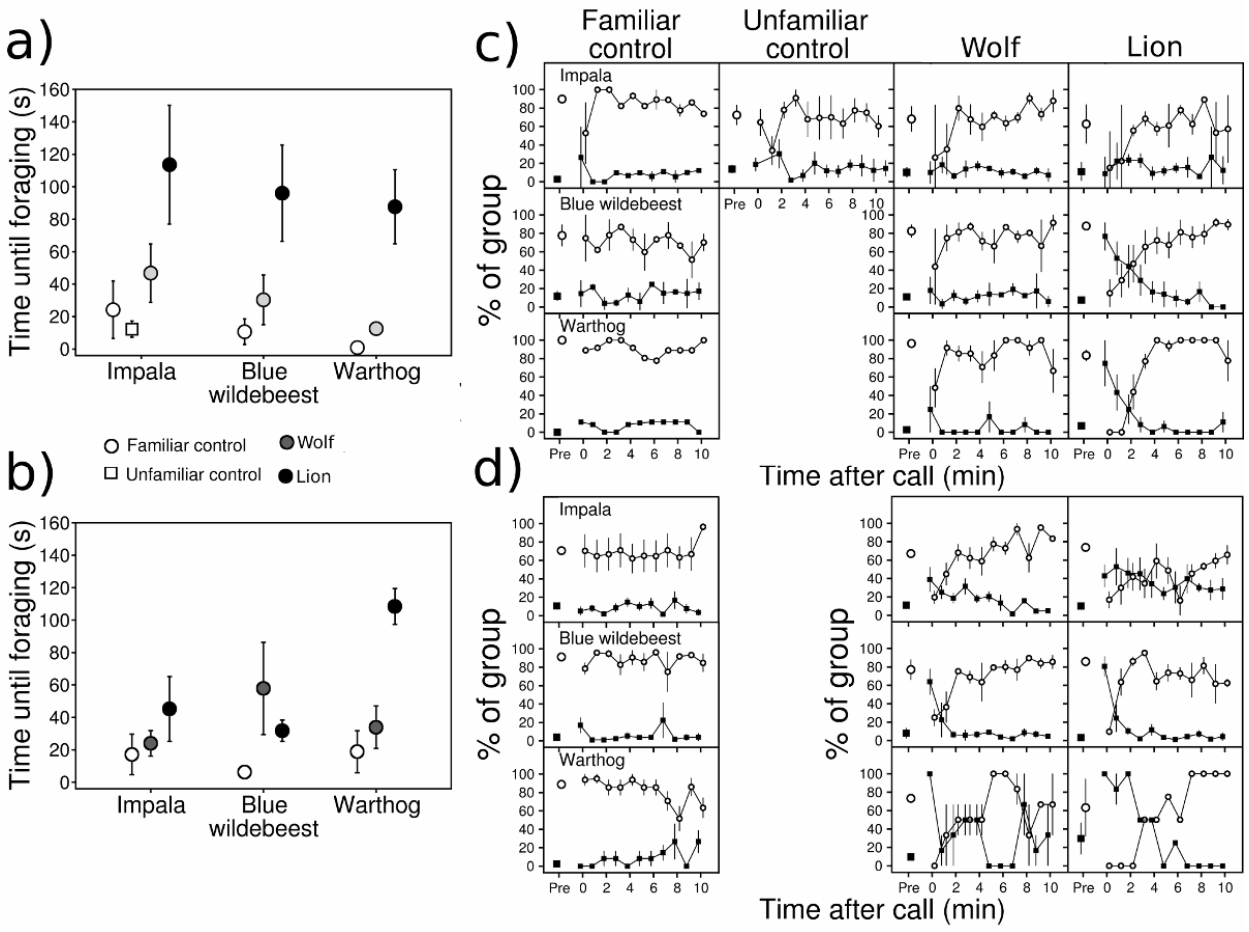

Figure 3
Time until resuming foraging after exposure to audio calls of a familiar control (running water), an unfamiliar control (popular music, only for naïve impala), grey wolf (an alien predator) and lion (a native predator) for naïve (a) and lion exposed (c) impala, blue wildebeest and warthog, and the proportion of animals in naïve (b) and lion exposed (d) groups engaged in foraging and vigilance after calls. Figures present mean ± SE of group means.