



## Original Article

# African ungulates recognize a locally extinct native predator

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Large carnivores are important ecosystem components but frequently suffer local extinctions. However, reintroductions and shifting conservation attitudes have led 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 behavioral responses in naive 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 behavioral responses to lions than to any of the other calls, even in naive 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.

**Key words:** African ungulates, antipredatory behavior, large carnivores, predation, predator recognition, reintroduction.

## 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 behavior, 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 behavioral 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 reintroductions (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 behavioral responsiveness to predators and predation-related species (Berger 1999; Berger et al. 2001), including subtle behaviors (Berger 2007), which has led to higher predator sensitivity in naive 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 reintroductions or recoveries. However, some prey may recover their antipredator behavior swiftly after predator recolonization (Hunter and Skinner 1998; Berger et al. 2001; Laundré et al. 2001; Berger 2007) and rapidly evolve antipredator responses to introduced alien species (McLean et al. 1996; Anson and Dickman 2013).

Loss of predator recognition and antipredatory behavior 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 cost associated with recognition (Lahti et al. 2009). Although some species appear to respond to predators they have been evolutionarily 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

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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 behavior has remained within the behavioral repertoire of the prey species (Curio 1993).

Africa contains one of the most diverse assemblages of large carnivores on Earth (Dalerum et al. 2009; Dalerum 2013). However, despite widespread carnivore range contractions (Dalerum, Somers, 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 behavior 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 behavioral 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 3 species of African ungulates, impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*, hereafter referred to as wildebeest), and common warthog (*Phacochoerus africanus*, hereafter referred to as warthog), and contrasted the responses of populations naive to recent lion predation to those that have experienced reintroduced lions over the past 15 years. We hypothesized that the responses of naive populations to calls of lions would be of comparable magnitude to those of wolves, as a consequence of a loss of specific predator recognition. We also hypothesized that naive populations would respond less strongly to calls of lions compared to lion exposed populations, caused by a recovery of predator response behavior in areas where lions have been reintroduced.

## MATERIALS AND METHODS

### Study areas

We conducted experiments on naive 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 36 000 ha. 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 (*Lycan 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 naive in terms of their exposure to lion predation. However, a neighboring reserve has contained lions, and ungulates in Lapalala may 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 naive to lion predation, we regard the potential influence of this neighboring 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 reintroduced 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 to 14 adults distributed across 2 prides and occasionally 1 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 2 reserves 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 2 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 to 2 weeks. We restricted our experiments to groups where at least half of the individuals were engaged in foraging to avoid potential bias (Dalerum, Lange, et al. 2008). Once a group was located, we turned off the engine and waited 5–20 min 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 subadult individuals were included in group size estimates.

To enable later recording of behavior, we filmed each group using a handheld digital video camera. We recorded 3 min of baseline behavior, after which we broadcasted a 45-s audio clip of one of the 4 experimental categories (see below) using 2 synchronized speakers connected to a 350-W amplifier powered by a 12-V battery. We then continued the video recording until 10 min after the end of the call or until all members of the group had moved out of sight. Throughout the study, we broadcasted 4 different sounds: a native predator (lion roar), an alien predator (grey wolf howls), a neutral unfamiliar control (popular music; a 45-s 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 naive impala, as we did not encounter

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

	Impala			Blue wildebeest			Warthog		
	N <sup>a</sup>	Group size <sup>b</sup>	Obs. distance <sup>b,c</sup>	N <sup>a</sup>	Group size <sup>b</sup>	Obs. distance <sup>b,c</sup>	N <sup>a</sup>	Group size <sup>b</sup>	Obs. distance <sup>b,c</sup>
Naive 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
Unfamiliar 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

<sup>a</sup>Numbers in brackets reflect number of groups where focal and scan data were collected from recorded videos.<sup>b</sup>Mean ± 1 SD.<sup>c</sup>Distance to loud-speakers during calls were the same as observation distance.

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 m) 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 3 types of behavioral 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 behavior. Immediate behavioral 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 behavior 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 behavior and aggregated in close association to one another; “Abandon”—at least half of the individuals abandoned the foraging location. The behaviors 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 behaviors by recording them onto a portable digital assistant device 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 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 antipredatory vigilance. We conducted a focal observation of 180 s prior to and another of 180 s immediately after the end of a call. If we could not determine the behavior 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 s after the end of the call. If possible, we used the same animals for the pre- and postcall 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 postobservations to not lose behavioral 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 s. 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 precall 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 s 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 min prior to and for 10 min after a call. As with the focal data, scan data were recorded from the recorded videos, and the behaviors 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 Lapalala 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 behavioral 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 postcalls 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 behavior.

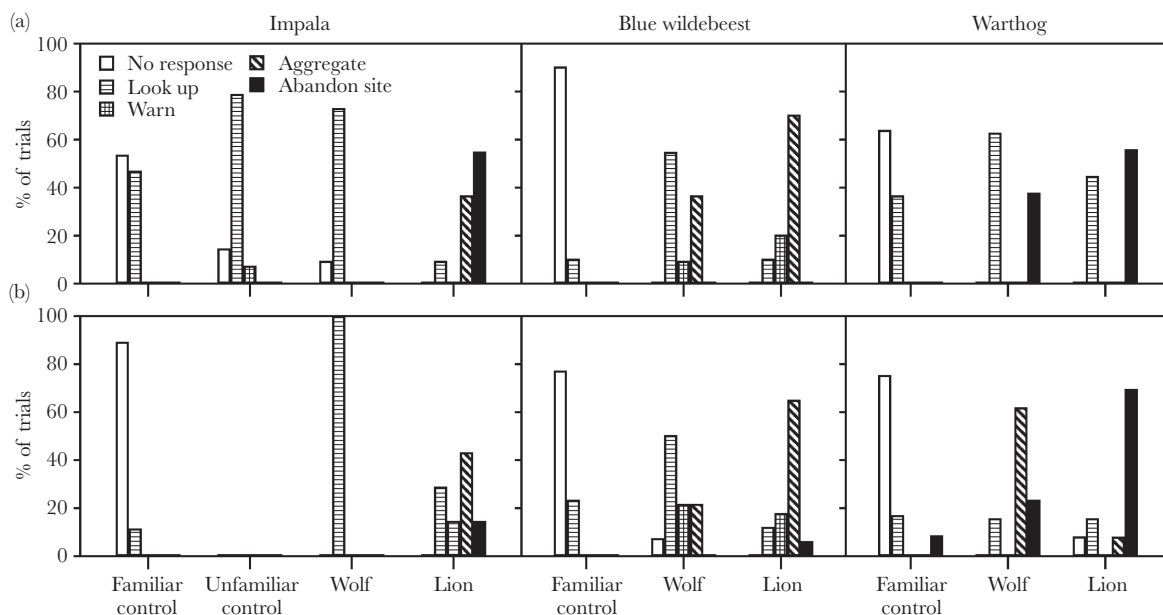
In all analyses, we first evaluated the effect of calls on naive ungulates by only using data from Lapalala. In these analyses on naive populations, we used call type as a fixed experimental effect in the models on immediate response and time until return to foraging, the interaction (as well as main effects) of call type and time period (i.e., pre- or postcall 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 naive 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 naive 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 [Supplementary Tables S1–S6](#) for a full set of model contributions by these variables). We additionally added a random term for each observation to account for overdispersion 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

Naive impala and wildebeest showed more severe immediate responses to calls of lion compared to wolf (Figure 1). In all 3 species, there were more severe immediate responses to calls of both predator species compared to a familiar control, although the difference for warthog was nonsignificant because of infinite parameter estimates and associated inflated standard errors (Table 2). Naive 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 naive 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  $\chi^2 = 0.97$ ,  $df = 2$ ,  $P = 0.617$ ).

Naive 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 3 species decreased foraging and increased vigilance more after hearing lion compared to a familiar control. Only naive impala and wildebeest foraged less after calls of wolf compared to a familiar control, and impala and



**Figure 1**

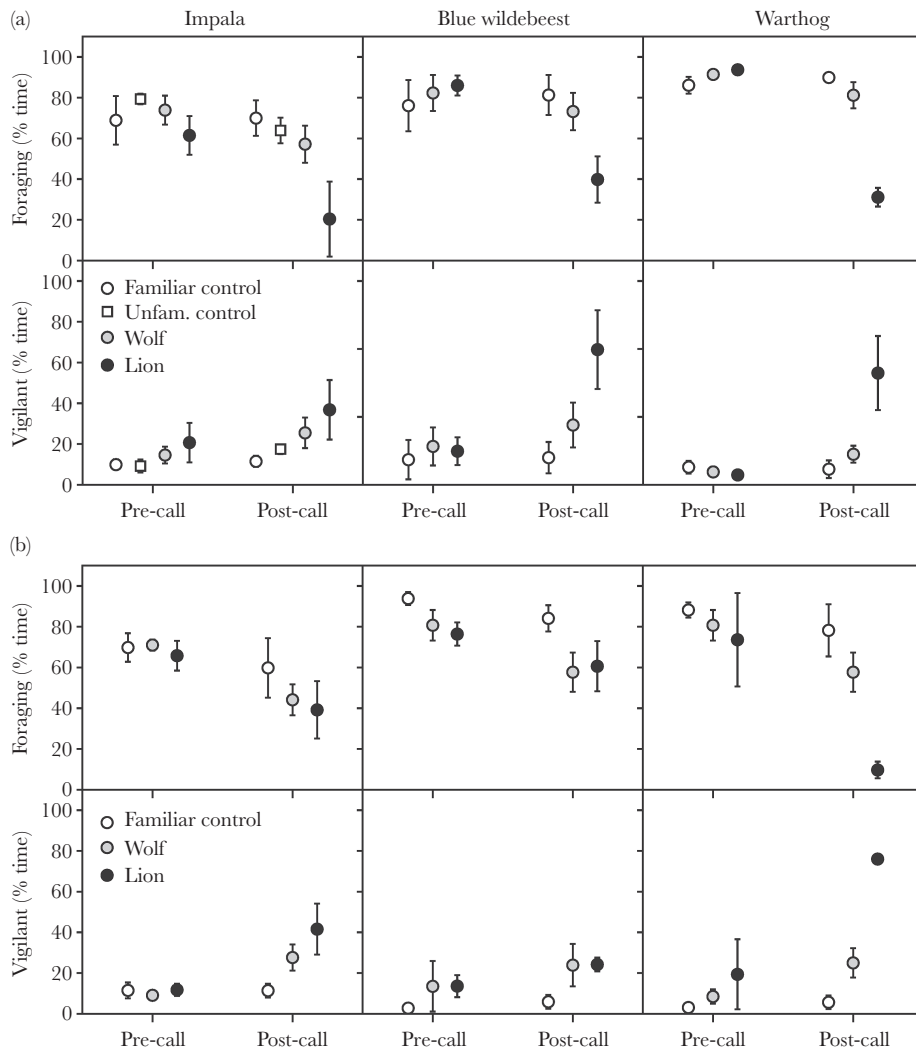
Immediate behavioral responses of naive (a) and lion exposed (b) foraging groups of impala, blue wildebeest, and warthog to audio calls of a familiar control (running water), an unfamiliar control (popular music, only for naive impala), grey wolf (an alien predator), and lion (a native predator). Behavioral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

**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 naive impala, blue wildebeest, and warthog**

	Impala			Blue wildebeest			Warthog		
	$\beta$	$\zeta$	<i>P</i>	$\beta$	$\zeta$	<i>P</i>	$\beta$	$\zeta$	<i>P</i>
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						

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.



**Figure 2**

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

warthog showed a trend for increasing vigilance. Naive 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 naive populations exhibited similar responses (foraging: impala  $\chi^2 = 7.02$ , *df* = 2, *P* = 0.030;

**Table 3**

**Coefficients from generalized linear mixed models describing the difference in proportion of time spent foraging or being vigilant during 180 s 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 s prior to the call in naive impala, blue wildebeest, and warthog**

	Impala			Blue wildebeest			Warthog		
	$\beta$	$\zeta$	<i>P</i>	$\beta$	$\zeta$	<i>P</i>	$\beta$	$\zeta$	<i>P</i>
<b>Foraging</b>									
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						
<b>Vigilance</b>									
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						

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 precall.

wildebeest  $\chi^2 = 4.65$ , *df* = 2, *P* = 0.098; warthog  $\chi^2 = 0.27$ , *df* = 2, *P* = 0.874 and vigilance: impala  $\chi^2 = 0.49$ , *df* = 2, *P* = 0.782; wildebeest  $\chi^2 = 1.21$ , *df* = 2, *P* = 0.545; warthog  $\chi^2 = 3.80$ , *df* = 2, *P* = 0.149), although the foraging responses of predator exposed impala were weaker than in naive animals (Figure 2b).

Naive impala, wildebeest, and warthog took longer time to return to foraging behavior after hearing lion compared to both wolf and a familiar and unfamiliar control (Figure 3a). Naive 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). Naive 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 precall baseline after calls from lions compared to both wolf and a familiar control (Figure 3b; Supplementary Tables S7–S12). There were no differences between naive 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

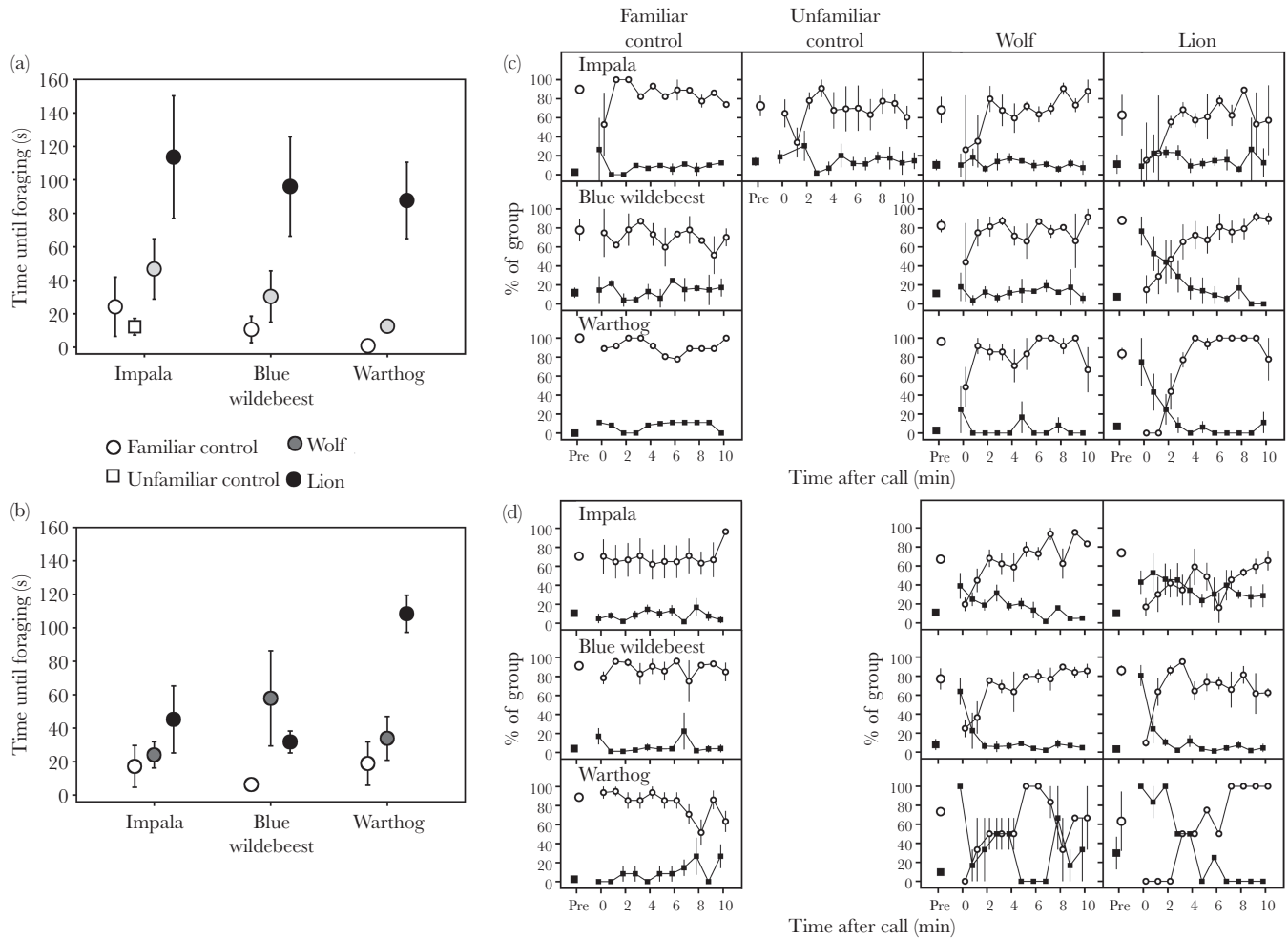
Although the observed responses differed in detail between the 3 species, overall our results demonstrated stronger behavioral responses to lions than to any of the other calls in naive populations. Naive populations also showed remarkable similarity in all response types compared to populations exposed 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 et al. 2001; Berger 2007) but are consistent with others showing that predator recognition have been retained (Byers 1997; Hunter and Skinner 1998; 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 nonextinct 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 recognize 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 behavior 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 coevolved 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 naive and lion exposed populations, with the only detected differences being



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

**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 naive impala, blue wildebeest, and warthog

	Impala			Blue wildebeest			Warthog		
	$\beta$	$\zeta$	<i>P</i>	$\beta$	$\zeta$	<i>P</i>	$\beta$	$\zeta$	<i>P</i>
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						

Each coefficient describes the relative difference in terms of time until animals returned to foraging between each pairs of calls.

that responses to native predators in some instances were more severe in naive 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 reintroduction and recolonization 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.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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