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Wildlife in a Premier African Protected Area do not Perceive Ecotourists as Predators

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Abstract

Researchers have reported that the presence of ecotourists may displace or disturb wildlife with potentially adverse effects, and may be a more serious problem if wildlife perceive ecotourists as predators. I used a playback experiment to test if wildlife at Bwindi Impenetrable National Park, Uganda, perceive ecotourists as predators. I contrasted wildlife behavioural responses to vocalizations that simulate those of ecotourists to those of local predators (positive controls; dogs and the extirpated native apex predator, leopard) and a non-predator (negative control; insects). Using responses from 14 mammal species, I show that wildlife do not perceive ecotourists as predators, responding no more fearfully to ecotourist vocalizations than to insects, but demonstrating persistent aversive reactions to local predators. My results suggest limited impacts of ecotourism, but negative impacts of dogs and leopard extirpation on the Bwindi wildlife community. Future research should test the response of individual species of conservation concern to ecotourism.

Keywords

Anti-predator behaviour, ecotourism, fear, perceived predation risk, poaching, predator-prey interaction, protected areas, playback experiment

Co-Authorship Statement

Dr. Michael Clinchy will be the second co-author on the manuscript that will be published from this thesis. Mike provided a great deal of guidance on the overall experimental design, experimental site set-up, statistical analysis and the writing of this thesis.

Dr. David Macdonald will be the third co-author on the manuscript that will be published from this thesis. David provided the University of Oxford Turner-Kirk research scholarship to me which supported this research.

Dr. Liana Zanette will be the fourth co-author on the manuscript that will be published from this thesis. Liana provided feedback and guidance in the development of my experimental design and set-up, data analysis and the writing of this thesis. Further, Liana provided the NSERC funding that supported this research.

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Chapter 1

1 Introduction

1.1 Ecotourism in protected areas

Ecotourism is the responsible travel to natural areas that conserves the environment, sustains the well-being of the local people, and involves education and learning (Bateman & Fleming 2017). Because it is non-consumptive of wildlife, ecotourism has been widely adopted by protected area agencies as a strategy, not only to ensure the long-term survival of wildlife populations but also to generate incentives for conservation (Balmford et al. 2009; Sandbrook 2010). Ecotourism provides an opportunity for the public to connect with nature and the ecosystem services it provides, especially in developing countries because of their reliance on international ecotourism. Ecotourism worldwide generates millions of dollars annually, much of it from wildlife watching in protected areas (Balmford et al. 2009). In my country, Uganda, international ecotourism is 9% of GDP, with Bwindi Impenetrable National Park (hereafter "Bwindi"), my study site, being the country's principal ecotourist destination because of its half of the world's remaining 880 critically endangered mountain gorilla (*Gorilla beringei*), which visitors each pay 600 US$ to see (Sandbrook & Semple 2006; Sandbrook 2010; Ahebwa et al. 2012).

The number of ecotourists visiting terrestrial protected areas has grown over the years, estimated at a staggering 8 billion visits per year worldwide (Balmford et al. 2015). The expansion of ecotourism in protected areas has not gone unchallenged. Researchers have often raised concerns that ecotourism may not be completely benign, as it has been frequently assumed (Knight 2009; Geffroy et al. 2015; Reilly et al. 2017). Ecotourists may potentially induce changes in wildlife behaviour, disturb or displace wildlife, all of which are likely to have negative impacts on wildlife (Blom et al. 2004; Mullner et al. 2004; Shutt et al. 2014; Geffroy et al. 2015; Bateman & Fleming 2017). Research shows that ecotourists in protected areas induce anti-predator behaviour in wildlife including increased vigilance, reduced foraging and increased flight responses (Duchesne et al. 2000; Cuiti et al. 2012a). Ecotourism may, therefore, be a serious problem and can have

effects on wildlife populations and long-term survival, if wildlife perceive ecotourists as predators (Blom et al. 2004; Geffroy et al. 2015; Trimmer et al. 2017).

1.2 The presence of predators and the fear of predation it induces in wildlife

Broadly, fear is as the amount of perceived danger. In the context of this study, I define fear as the amount of predation risk animals perceive, often exhibited in the form of specific anti-predator responses. Responses to predation risk may be innate acquired through an evolutionary process, or learned through experience, either by observing conspecifics and heterospecifics or surviving a predation attack (Blumstein 2002). Researchers have documented fear responses in animals on everything ranging from water fleas (*Daphnia*) to elephants (Preisser et al. 2005). Some prey, for instance, *Daphnia*, develop morphological features such as spines against predatory fish (Dodson 1988; Tollrian 1995), while some prey may exhibit physiological (e.g. elevated glucocorticoid concentrations (Sheriff et al. 2009) and behavioural (Zanette et al. 2011) changes. The predator-induced changes in morphology, physiology or behaviour are costly and can have direct consequences on prey reproduction, growth and survival (Preisser et al. 2005).

The literature from both correlative and experimental studies on predator-prey interactions demonstrates that the fear of predators in wildlife is strong enough to affect prey demography, long-term survival, and ecological communities. For example, in a correlational study, Creel et al. (2007) studied the reproduction of female elk (*Cervus elaphus*) under different levels of wolf (*Canis lupus*) predation risk at Yellowstone National Park. Elk occupying areas of heightened predation risk had lower oestrogen levels and lower reproduction than female elk in low predation risk areas. Another correlative study that addressed the relationship between coyote (*Canis latrans*) density and white-tailed deer (*Odocoileus virginianus*) fecundity and reproductive success suggested that the fear of being killed by coyotes reduced ovulation and lactation in white-tailed deer (Cherry et al. 2016).

Experiments have reported similar effects of fear on wildlife population and demography. A manipulation by Zanette et al. (2011) broadcast predator calls to song sparrows (*Melospiza melodia*) to test the effects of perceived predation risk on free-ranging wildlife. This experiment showed that the change in behaviour: habitat use, vigilance, nest attendance and foraging, solely induced by the fear of being killed by a predator reduced the number of offspring produced per year. Females exposed to predator playbacks laid fewer eggs, of which a greater proportion failed to hatch, and even for those that hatched, a greater proportion of their nestlings died. In another manipulation (Eggers et al. 2006), perceived nest predation risk, simulated by broadcasting playbacks of nest predators near nest sites, induced a reduction in egg clutch size in the Siberian jay (*Perisoreus infaustus*). In response to heightened predation risk, birds chose nest sites that provided more protective cover from predators, but reduced temperature and light levels, impacting the parent's ability to maintain the desired incubation temperature, consequently reducing egg hatchability (Eggers et al. 2006). LaManna & Martin (2016) showed that hearing vocalizations of nest predators in a playback experiment, and the fear of being killed that came with it, increased attentiveness and reduced nest mortality in Swainson's thrush (*Catharus ustulatus*). However, increased attentiveness resulted in a reduced reproductive output of the birds, through reductions in hatch success, number of hatchlings and nestling survival, caused by reduced incubation periods and parental nest attendance.

Fear of predators in wildlife may have important consequences on ecological communities. Suraci et al. (2016) demonstrated that after hearing large carnivore playbacks, raccoons (*Procyon lotor*) on the Gulf Islands of British Columbia reduced their foraging. This caused changes in the abundance of species at lower trophic levels throughout the whole inter-tidal community. Fear effects in wildlife are not limited to prey but also predators. For instance, recent experimental work has shown that a mesopredator (European badger, *Meles meles*) and an apex predator (cougar, *Puma concolor*) perceive humans as frightening (Clinchy et al. 2016; Smith et al. 2017). In response to hearing vocalizations of humans in conversation, both badgers and cougars traded-off foraging time for anti-predator behaviour, either by fleeing from the experimental site or increasing the amount of time spent vigilant. In the case of apex

predators, the fear of humans is so great that they may choose to forego a cache in response to hearing a human voice. This may affect prey abundance, if apex predators spend less time at kill sites and compensate for the reduced foraging with increased kill rates (Smith et al. 2015; Smith et al. 2017). These studies show that the presence of humans in general, including non-threatening humans, and the amount of fear human presence induces, elicits anti-predator behaviour in wildlife. The anti-predator behaviour often comes at the cost of fitness-enhancing behaviours such as foraging with potentially long-term effects on wildlife populations (Trimmer et al. 2017).

1.3 Ecotourists as sources of fear in wildlife

Ecotourists may be a source of predator-induced fear if hunting or wildlife persecution is a prevalent human activity in the protected area, and humans are a significant cause of mortality to wildlife (Dorresteijn et al. 2015; Kuijper et al. 2016). Correlative work has shown that the fear of humans may induce changes in both the spatial and temporal habitat use of wildlife (Rogala et al. 2011; Rasmussen & Macdonald 2012) or by inducing increased flight response (Stankowich 2008; Ciuti et al. 2012a). In protected areas where hunting by humans is permitted, wildlife often flee at greater distances (i.e., flight initiation distance, the distance at which an animal begins to flee while being approached by a predator) when approached by ecotourists, than areas where hunting is not permitted (Stankowich 2008). Likewise, where hunting intensity varies temporally, wildlife often exhibit greater flight initiation distances to the presence of ecotourists during peak than low hunting seasons (Stankowich & Blumstein 2005). Ciuti et al. (2012a) also reported that elk exhibited high levels of vigilance to ecotourist presence in public areas where hunting was permitted, but not in the national park where hunting was prohibited. A few studies have correlated the fear induced by the presence of ecotourists with reduced reproductive success and survival in wildlife. For example, hoatzins (*Opisthocomus hoazin*) at ecotourist exposed nests had significantly lower chick survival than birds at nests without ecotourists (Mullner et al. 2004). Yellow-eyed penguins (*Megadyptes antipodes*) in areas with high levels of ecotourist visitation had fledglings with lower weights than penguins in infrequently visited areas, causing reduced juvenile survival, recruitment and overall breeding success (Ellenberg et al. 2007).

Although frequently considered benign (Knight 2009; Geffroy et al. 2015; Reilly et al. 2017), the literature presented in the preceding paragraph suggests that wildlife in protected areas may perceive ecotourists as a source of predation. Fear responses of wildlife to human cues, therefore, provide a reliable means of testing the impacts of ecotourism on wildlife in protected areas (Duchesne et al. 2000; Frid and Dill 2002; Caro 2005; Stankowich and Blumstein 2005; Stankowich 2008; Ciuti et al. 2012). Only five studies available have used fear responses of wildlife to human cues to experimentally test the impacts of human activity on wildlife in protected areas. One of these studies used both visual (colour) and olfactory cues to show that African elephants (*Loxodonta africana*) can distinguish between the Maasai men who kill elephants and the Kamba agriculturalists who pose no harm (Bates et al. 2007). The elephants showed increased anti-predator behaviour when they detected the scent of garments previously worn by Maasai than Kamba men, and reacted aggressively to red colour garments which are traditionally worn by the Maasai and not other humans in the protected area.

Four studies have used human vocalizations to test the fear humans induce in wildlife. These studies have established that wildlife including pig-tailed langur (*Simias concolor*, Yorzinski & Ziegler 2007), African elephant (McComb et al. 2014), European badger and cougar, often respond to human vocalizations just as wildlife would respond to any other predator vocalization (Hettena et al. 2014). These experiments also suggest that wildlife can accurately identify humans as predators based on vocalizations, and consequently demonstrate appropriate anti-predator behaviour. European badgers, which humans heavily hunt in Britain (Tuyttens et al. 2000; Cassidy 2012), responded more fearfully to human vocalizations than to their non-predator (sheep) and local native predators bears (*Ursus arctos*) and dogs (*Canis familiaris*). African elephants accurately discerned between the vocalizations of two types of humans which pose different levels of threat, responding fearfully to vocalizations of the Maasai men who kill elephants, and not to vocalizations of Maasai boys or women or Kamba language speakers who do not hunt the elephants, clearly distinguishing human predators from human non-predators. The cougars Smith et al. (2017) studied also responded significantly more fearfully to human vocalizations than to the negative control sounds of the non-predator Pacific tree frog (*Pseudacris regilla*).

Such studies highlight the essential impacts of humans as predators on wildlife behaviour which may have potential consequences on populations and ecological communities. It is by acting through behaviour that the fear of predators affects reproduction, i.e., fecundity (Eggers et al. 2006; LaManna & Martin 2016) and offspring survival (Zanette et al. 2011; Dudeck et al. 2017). If wildlife fear all humans in general as predators, not just the human predators (hunters, persecutors, poachers), but the human non-predators (ecotourists) as well, then we would expect the presence of ecotourists in protected areas to induce fear in wildlife. This heightened perceived predation risk may be accordingly matched by wildlife in the form of increased anti-predator behaviour such as increased fleeing, vigilance, and reduced foraging, at the cost of reproduction and long-term survival. In such cases, protected areas should prevent ecotourism because the mere presence of ecotourists and the fear of death ecotourists may induce can kill wildlife causing fewer wildlife numbers in protected areas, as the fear of death can indeed reduce the number of offspring produced (Zanette et al. 2011; Dudeck et al. 2017; Trimmer et al. 2017). If ecotourism reduces wildlife numbers, then ecotourism may contradict the management goals of protected areas —to conserve wildlife for the enjoyment of the current and future generations, by eliminating or regulating human activities that may reduce wildlife abundance and threaten long-term survival (Parsons et al. 2016).

1.4 Testing if wildlife perceive ecotourists as predators

Testing if wildlife perceive ecotourists as predators necessitates comparing wildlife behavioural response to cues of ecotourists with cues of known local predators and non-predators. In protected areas worldwide, dogs are common, either as hunting dogs (Grignolio et al. 2011; Lindsey et al. 2013) or just accompanying humans (Parsons et al. 2016). African protected areas are particularly interesting in that dogs are not only used as hunting or poaching dogs (Lindsey et al. 2013; Mugerwa et al. 2013), but are also ubiquitous as free roaming "village" dogs (Boyko et al. 2009). Regardless of whether hunting or accompanying or village dogs, dogs interact with wildlife as predators (Vanak & Gompper 2009; Hughes & Macdonald 2013). Cues that simulate dog presence may, therefore, represent a reliable signal of mortality to wildlife in protected areas, and may

be expected to induce anti-predator behaviour in wildlife (Vanak et al. 2009; Parsons et al. 2016).

Besides dogs, wildlife in protected areas coexist with their coevolved native non-human predators, mostly large carnivore apex predators, which are the most important sources of mortality to wildlife, and wildlife accordingly demonstrate anti-predator reactions to cues of these native non-human predators (Thuppil & Coss 2013; Hettena et al. 2014). Throughout the tropical rainforest biome, large carnivores of the genus *Panthera* which includes: tigers (*P. tigris*), jaguars (*P. onca*) and leopards (*P. pardus*) are the apex predators in these systems. Previous studies have reported strong fear responses by wildlife to the vocalizations of these apex predators (Durant 2000; Schel & Zuberbuhler 2009; Thuppil & Coss 2013), with wildlife (e.g., Guereza colobus monkey (*Colobus guereza*) and European badger) reported to retain recognition and anti-predator behaviour against apex predators, decades following their local extirpation (Schel & Zuberbuhler 2009; Hettena et al. 2014).

Many animals use predator auditory cues (vocalizations) to assess their risk of predation and respond accordingly by engaging in anti-predator behaviour. A predator vocalization is a signal to prey that a predator is present at that particular point in time and in close proximity, making acoustic playback experiments powerful means to directly test wildlife fear of its predators (Hettena et al. 2014; Suraci et al. 2017). A total of over 180 experiments have used vocalizations of predators in playback experiments to test fear of predators in wildlife, on animals ranging from wolf spiders (*Cyanocitta cristata*) to elephants (Hettena et al. 2014). Visual cues in comparison to auditory cues are often impractical, as animals will quickly habituate if the cut-out (a common visual cue) is immobile for extended periods of time. Visual cues may also be impractical in dense habitats such as tropical rainforests. The effectiveness of visual cues relies on their ability to be seen by wildlife, yet vision in tropical rainforests is often limited due to the dense vegetation. Olfactory cues, on the other hand, may not signal the presence of a predator at the site, and the stimuli may deteriorate fast under moist, humid conditions, like those in tropical rainforests.

1.5 **Ecotourism in a premier African protected area: Bwindi Impenetrable National Park**

Bwindi Impenetrable National Park is a premier African protected area, a principal destination for ecotourism primarily because of its mountain gorillas and numerous other rare or endemic species of mammals and birds. The government of Uganda designated Bwindi a forest reserve in 1932, and later an animal sanctuary in 1964. Following extensive surveys for biodiversity and illegal human exploitation of the forest in the late 1980s, Bwindi was identified as the most important forest in Uganda for biodiversity conservation, triggering its upgrade to national park status in 1991. The upgraded status of Bwindi was not positively received by local people, causing substantial resentment and conflict between local communities and park agency (Hamilton et al. 2000). To ease these tensions and attract local support for conservation of Bwindi, the park agency devised strategies to link conservation and local livelihoods, and central to this strategy was the development of ecotourism (Sandbrook 2010).

In 1991, habituation of gorillas started, involving daily visits to the gorillas by small groups of people. Unlike some protected areas in other parts of the world where wildlife is provisioned with attractants to increase tolerance of ecotourists, Bwindi strictly prohibits food provisioning for wildlife by ecotourists. Ecotourism has been ongoing in Bwindi since 1993 and has been rapidly growing with over 20,000 ecotourists currently visiting Bwindi annually, mainly from North America and Europe. Ecotourism at Bwindi is a high value activity that generates enough revenue to support park management costs and contribute greatly to the national budget of the Uganda Wildlife Authority (Archabald & Treves 2001). As noted in the first paragraph of the introduction, Bwindi is one of Africa's prime ecotourist destinations, where ecotourists each pay 600 US$ to see mountain gorillas. Today, there are 13 groups of habituated gorillas for ecotourism in Bwindi ranging throughout the park (Seiler & Robbins 2016), each visited by a maximum of eight ecotourists per day, spending 1 hour viewing the animals. More gorilla groups have been earmarked for future habituation and subsequent ecotourism.

As in other protected areas around the world, the expansion of ecotourism in Bwindi has often received resistance from researchers who suggest that the presence of

ecotourists may not be completely safe for wildlife in the park (Butynski & Kalina 1998; Sandbrook & Semple 2006; Seiler & Robbins 2016). Ecotourism in Bwindi involves hiking on foot for long distances, through dense forest vegetation or along narrow temporary game trails, either for purposes of finding and viewing gorillas or enjoying the landscape during a forest walk. The rugged undulating hills covered in a mix of dense herbaceous and woody tropical forest vegetation, in a very remote part of the country, means that transit is only possible on foot. A team of two to four Uganda Wildlife Authority (UWA) tourism guides, rangers, and porters accompany small groups of ecotourists. Speaking in English (the common language for ecotourists), the tourist guide and rangers often interact with ecotourists. Loud conversation within the national park is discouraged, but ecotourists and guides often chat loudly during forest walks, and even during gorilla watching.

Although ecotourism is now flourishing at Bwindi, the park suffered from past armed conflict and lack of order (Hamilton et al. 2000). The intensive poaching often with dogs that succeeded the armed conflict led to the extirpation of several mammal species in Bwindi during the 1970s including the buffalo (*Syncerus caffer*), giant forest hog (*Hyloxhoerus meinertzhageni*) and the only large apex native predator, leopard (Butynski 1984). Stability and order were restored in the mid-1980s, facilitating the establishment of ecotourism (McNeilage et al. 2006; Ahebwa et al. 2012). But poaching for bush-meat and village dogs are present (McNeilage et al. 2006; Millan et al. 2013; Mugerwa et al. 2013; Proboste et al. 2015), and the leopard, which once roamed the park is still locally absent (Butynski 1984; Kingdon et al. 2013). These conditions thus make Bwindi a model protected area for an experiment to test the response of wildlife to ecotourism, insofar that I can contrast wildlife's behaviour response to cues simulating the presence of ecotourists (potential predators) with those of local predators: introduced (dogs) and native (leopards).

1.6 Research objective and hypothesis

My objective was to test the impacts of ecotourism on wildlife at Bwindi, by testing if wildlife at Bwindi perceive ecotourists as predators. I tested the hypothesis that the fearful response of wildlife to vocalizations simulating ecotourist presence would reflect

the predatory threat ecotourists may pose to wildlife. To test this hypothesis, I experimentally simulated the presence of ecotourists by broadcasting playbacks of human vocalizations. I contrasted wildlife fear behavioural responses to vocalizations simulating the presence of ecotourists as potential predators, and vocalizations of local predators, consistent with the fact that animals recognize and respond to vocalizations of their predators. I wish to highlight that my interest was not to investigate the mechanism (s) driving wildlife fear responses of ecotourists, but rather to better understand the conservation implications and potential effects of ecotourism on wildlife.

To accomplish this research, I tested the efficacy of a newly developed research tool, the Automated Behavioural Response (ABR) system. The ABR is a motion-triggered, camera trap-based system for conducting playback experiments on free-ranging wildlife without the need of observer presence (Suraci et al. 2017). The ABR is set up in an area where wildlife is likely to be present, for instance, along a game trail. When an animal arrives in the area, its motion activates the ABR to broadcast playbacks, to which the animal responds with a behavioural response. The behavioural response is then recorded by the camera trap in a short 30 second video. I participated in testing the efficacy of the ABR, and together with my colleagues, I have published details on the functioning of the ABR (Suraci et al. 2017). I here describe a fear behavioural response metric, which, combined with the ABR, can be used to quantify wildlife responses to threatening and non-threatening stimuli.

Chapter 2

2   Methods

2.1   Study system

My study site, Bwindi, is a tropical rainforest system. Tropical rainforests are biomes found in the equatorial zone between the Tropic of Cancer and Tropic of Capricorn, latitudes that are warm with an average temperature of 20°C year-round, with over 1,500 mm of rain every year with no marked cold or dry spells (Ghazoul & Sheil 2010). Tropical rainforests cover about 7-10% of the global land area, spanning majorly three continents: Africa, Asia, and Central and South America. Tropical rainforests provide habitat for an estimated 50% of terrestrial biodiversity– the highest of all terrestrial ecosystems, and a fascinating array of ecological processes (Gentry 1992).

Tropical rainforests provide important ecological services including carbon storage, habitat for wildlife, buffer the rate of global warming and support local livelihoods of a substantial proportion of the World's population and national economies (Malhi & Phillips 2004; Lewis et al. 2009; Ghazoul & Sheil 2010). In tropical rainforests, medium-to-large mammals comprise rich communities of species from a variety of diverse trophic groups and body sizes (Ghazoul & Sheil 2010; Ahumada et al. 2011). This diversity plays a significant role in ecosystem functioning ranging from seed dispersal, ecotourism attractions to regulating forest carbon storage and climate (Brodie & Gibbs 2009; Bello et al. 2015; Peres et al. 2016). Yet, medium-to-large mammals are often most vulnerable to human impacts because of their conspicuous size and wide-ranging requirements (Ripple et al. 2016). Understanding their response to human impacts is both of scientific and management interest.

2.2   Study area and species

This study was conducted on a free-living wildlife community at Bwindi Impenetrable National Park, Uganda, from 17 February to 3 April 2015, during the peak ecotourism season. Bwindi is located in south-western Uganda at 0°53′ to 1° 08′S, 29° 35′ to 29° 50′E (Appendix A). The 321 km^2 forest was recognized as a UNESCO world heritage

site in 1994 (Hamilton et al. 2000). Bwindi lies on the edge of the Albertine Rift, a region containing more endemic species of vertebrates than any other region of mainland Africa, and therefore a high priority area for conservation. Bwindi is a home to an estimated 28 species of medium to large mammals and numerous rare and endemic species. The terrain at Bwindi is rugged with steep ridges and narrow valleys. Elevation ranges from 1190 m to 2607 m above sea level, and the vegetation is of medium-altitude moist evergreen forest and high altitude sub-montane forest (Mugerwa et al. 2013). Bwindi is immediately surrounded by a high human population density of up to 500 people per km^2, which legally and illegally enter the forest to access resources. Bwindi protects mountain gorillas for Uganda's international ecotourism, and actively prohibits the presence of dogs inside the national park. Yet, poaching of wildlife, often with dogs and wire snares, remains a major threat to wildlife and management of the park (Mugerwa et al. 2013; Harrison et al. 2015).

2.3 Overview of experimental design

To test the impacts of ecotourism on wildlife, I experimentally compared the behavioural responses of wildlife to playbacks of vocalizations meant to simulate the presence of an ecotourist to those of two known local predators (extant introduced large predator used for poaching, dog and extirpated native apex predator, leopard) and an extant non-predator (insects: cicadas and common crickets). The two local predators (dog and leopard) were the positive controls, and the local non-predator (insects) was the negative control for the experiment. Behavioural responses to playbacks were recorded using motion-activated video cameras that also recorded sound. If wildlife responded no more aversively to the ecotourist than to the non-predator (insect) vocalizations, but more aversively to the local predator (dog and leopard) vocalizations, this would suggest that wildlife in Bwindi do not recognize ecotourists as predators, and that ecotourists are indeed benign.

Previous research has documented anti-predator behavioural responses of mammals to human playbacks. I used vocalizations of English speakers and not local languages because English is the used language during ecotourism tours, both by ecotourists and tour guides. Although local people in villages immediately neighbouring

the park speak local languages (Rukiiga, Rufumbira, and Swahili), local people are prohibited from entering the park, and only do so illegally as poachers, or occasionally, legally to collect non-timber forest resources. When they do enter the park illegally or otherwise, local people speak local languages. Wildlife may indeed be expected to respond significantly to local languages, if local people are sources of mortality to wildlife at Bwindi, as was demonstrated on elephants by McComb et al. (2015). However, this was not the question I endeavoured to address for my study, as my interest was to test for potential impacts of ecotourists (who speak English). Recent experiments have also shown that dog playbacks elicit significant fear responses in European badgers and raccoons (Suraci et al. 2016). Poachers use dogs to hunt wildlife at Bwindi, and village dogs are also present. I thus expected wildlife at Bwindi to respond accordingly to dogs as predators. Research from other systems where dogs and human presence is prevalent shows that mammals are exposed to dog and human vocalizations (Parsons et al. 2016). Thus, there is sufficient reason to expect Bwindi mammals to be exposed to dog and ecotourist vocalizations since both dogs and ecotourists are present and have been recorded on camera traps in Bwindi (Mugerwa et al. 2013).

I also used vocalizations of an apex predator in African tropical rainforest ecosystems, the leopard, as a possible secondary positive control (Jenny & Zuberbuhler 2005; Schel & Zuberbuhler 2009; Kingdon et al. 2013). As an apex predator in tropical rainforest systems, leopards pose the greatest mortality threat to mammals in this system, killing everything from mice to elephants (Hart et al. 1996; Jenny & Zuberbuhler 2005; Hayward et al. 2006; Hayward & Kerley 2008; Kingdon et al. 2013; Thuppil & Coss 2013; du Preez et al. 2017; Mugerwa et al. 2017). Leopards vocalize for various reasons: marking territory, during courtship, advertising reproductive availability and during aggressive encounters or when with cubs (Bailey 2005; Kingdon et al. 2013). The leopard has been locally extinct in Bwindi for over 40 years, but playbacks of extirpated apex predators have been reported to elicit aversive fear responses in experiments on other mammals (Hettena et al. 2014). Playbacks of locally extinct bears induced a fear response in European badgers (Clinchy et al. 2016) and leopard playbacks elicited anti-predator behaviour in Guereza colobus monkeys (*Colobus guereza*) (Schel & Zuberbuhler 2009). For the case of mammals at Bwindi, I did not have expectations on how animals would

respond to leopard vocalizations because the recognition of leopards has been reported to be lost in some systems (Yorzinski et al. 2007) and retained in others (Schel & Zuberbuhler 2009). Nonetheless, why wildlife at Bwindi has retained the recognition of leopards is not the question I am addressing. But because animals can retain recognition of leopards decades after their extirpation, it provides me with means to test if wildlife perceive ecotourists as predators, by using leopard vocalizations as a secondary positive control. Therefore, I could be confident that my playbacks directly tested the impacts of ecotourism on Bwindi mammals.

2.4 Field procedures and playbacks used

I conducted the manipulation at 27 experimental sites ('sites') along game trails used by animals, within the designated ecotourism zones of the national park (Seiler & Robbins, 2016, Appendix A). I overlaid my experiment onto existing camera trap grids operated by the Tropical Ecology Assessment and Monitoring Network (TEAM, www.teamnetwork. org) (Mugerwa et al. 2013). TEAM is a global network of field sites in the tropics collecting data on biodiversity (terrestrial vertebrates and plants) to provide an early warning system for biodiversity loss in tropical rainforests. I used an existing TEAM grid because it allowed me to place my experiment at sites where I have previously used camera traps that recorded the presence of wildlife, ecotourists, and dogs (Mugerwa et al. 2013). Camera traps were spaced at 1 km, which was to maximise the probability of recording an adequate sample of terrestrial mammals at Bwindi (TEAM Network 2009; Ahumada et al. 2011). A 1 km spacing between camera trap sites is a well-established protocol in camera studies of medium-to-large mammals in tropical rainforests, in that it decreases the probability of non-independence between observations (DeFries et al. 2010; Ahumada et al. 2013; Rovero & Ahumada 2017). Therefore, a 1 km spacing between sites ensured spatial independence in trials between sites, i.e., individuals in two trials of the same species recorded at two sites 1 km apart are assumed to be different individuals.

I used a custom-made automated camera and playback system (the ABR, Suraci et al. 2017, Appendix B). The ABR consists of a stand-alone passive infrared motion detector with a fully adjustable sensitivity control (Qunqi HC-SR501, Shenzhen Qunqi Ltd., China) connected to an external speaker unit by a 6 m 18 AWG (Carol Ultra Flex)

water resistant cable. I set the units to play the playbacks in a continuous sequential loop, in the order: insect, ecotourist, dog, and leopard to the playback selected at the previous site. Each site received all four playback treatments playing in 6-hour blocks but in a different order. That is to say; if the first site received the treatments in the order of insect, ecotourist, dog, and leopard, the second site received the treatments in the order of ecotourist, dog, leopard, and insect. The units remained silent unless the motion sensor triggered the speaker; thereby permitting the broadcast of whatever sound was currently running following a 10 s delay for 10 s, allowing the behaviour of the animal to be recorded before and after playback. A motion-triggered camera trap that also recorded sound (Moultrie M-990i, Moultrie Products, LLC, USA), secured to a tree at the height of 20-25 cm from the ground at the opposite side of the trail, recorded the fear behavioural responses of the animals to the playbacks in 30 s long videos. I set the cameras with a 5 s interval between videos.

The ABRs operated for nine days: three days of pre-baiting (before the playbacks were set to be triggered) and six treatment days per site. Speaker positions were changed every three days to avoid habituation of animals to the direction of the sound source. I replaced speaker and camera batteries and memory cards every three days. Ideally, I could have sampled all the 27 sites simultaneously, but logistical constraints (e.g., workforce) precluded this. Therefore, I grouped the sites into a set of arrays (i.e., a collection of sites) consisting of three to six sites, grouped based on their ease of access from an available common camping site. I then sampled the arrays sequentially not simultaneously, meaning that the first array was sampled and remained in the forest for nine days. Immediately after that, the camera traps and ABRs were picked up, the batteries and memory cards replaced, and the replenished camera traps and ABRs immediately moved to the next array of sites for another nine days. Appendix C illustrates a general step-by-step workflow of the study activities.

I used Audacity 2.0.3 (http://audacity.sourceforge.net), an open source audio editor and recorder to compose separate playlists of sounds testing the impacts of ecotourism. Playlists included sounds of insects, people speaking English (to represent ecotourists), dog, and leopard, each with a minimum of eight exemplars (8 insects, 9

ecotourists, 11 dogs and 8 leopards). Exemplars included representative sounds made by the species: people speaking English in conversation or reading passages from a book (ecotourist); coughs, chuffs, growls, snarls, spits, hisses, and grunts (leopard); and barks, growls, and howls (dog). Sound files were acquired from online audio and video databases. Playbacks were broadcast at a volume of 80 dB at 1 m, using mp3 players (RCA TH1814WM, VOXX Accessories Corp, Orlando, FL) housed by and plugged into a weatherproof speaker (EcoExtreme, Grace Digital Inc., USA; 19.0 x 11.4 x 6.4 cm, 0.4 kg).

Because tropical rainforest wildlife naturally occur in extremely low densities, I baited each site. This had the benefit of attracting animals to the camera's view in addition to ensuring that they stayed in view long enough (before and during playback) to ensure that I recorded their responses, thereby maximizing data collection. Sites were baited every three days with dried Nile perch (*Lates niloticus*), dried silver cyprinid (*Rastrineobola argentea*) and peanut seeds. I placed the peanuts and the fish on the ground and a bait dispenser with fish stock and a scent lure of dried Nile perch attached to a pole above the ground. The variety in bait type aimed to target species of diverse dietary preferences including carnivores, omnivores and herbivores/granivores. I tested the effectiveness of the bait as a good attractant for Bwindi wildlife during a two-week pilot experiment (Suraci et al. 2017). The bait dispenser consisted of fish stock inside a plastic bottle with a single hole in its base, to allow fish stock to trickle on the ground. I attached the bait dispenser to a pole at the height of 80 cm from the ground (out of reach by the animals). The scent lure consisted of dried Nile perch placed inside perforated cans attached to a pole at the height of 10 cm from the ground, such that the animals can reach, lick and gnaw, but cannot consume the lure. I placed the bait immediately adjacent to a trail 2 m from the ABR units. I erected a "fence" of wooden sticks perpendicular to the trail on the side of the bait to corral any animal feeding on the bait into the view of the camera (Appendix D).

2.5 **Categorization of videos**

I recorded a total of 2,145 videos: 1,101 were of identifiable wildlife based on a field guide of African mammals (Kingdon 1997), whereas the others were of vegetation moving, or of birds or unidentifiable small mammals. Of these 1,101 videos, over 60 % (672) were recorded during the first three days of pre-baiting at each site, before the playbacks were set to be triggered. As detailed in my paper describing the ABR (Suraci et al. 2017), even when the playback is set to be triggered it does not always do so, setting a delay before the playback triggers has distinct advantages, as explained in the next sentence, but runs the risk that the animal will have left the field of view before the playback triggers. Successfully recording the animal's behaviour both before and after the playback is heard provides a powerful repeated-measures means of gauging its change in behaviour in response to the playback, within the timeframe of a given video (Suraci et al. 2017). Of the 429 videos recorded during the period when the playback was set to be triggered it did so in 245 videos, in 40 of which the animal was already out of view before the playback began, and in another 12 it did not come into view until after the playback had sounded. There were consequently 193 videos in which the animal's behaviour was successfully recorded both before and after the playback began.

Following a well-established protocol in camera trap studies (Azlan & Sharma 2006; Tobler et al. 2008; O'Brien 2011), I categorized video recorded responses as independent 'first' exposures when all of the following conditions were met: trials were recorded at different sites, different species were exposed, or animals heard different playback treatments. Animals at the same site of the same species were considered independent if separated by an interval of > 60 min. Where two or more videos of the same species at the same site were recorded < 60 min after that species was last exposed to the same playback treatment, I categorized the second and all subsequent videos together as a 'repeat' exposure bout. A 'repeat' exposure bout might entail the same animal hearing the same playback treatment in one video following its 'first' exposure, or up to 36 videos (median = 4). Applying this protocol to the 193 videos in which the animal's behaviour was recorded both before and after the playback began, I categorized

54 as independent 'first' exposures and the remainder as components of 22 'repeat' exposure bouts (Table 1).

Table 1. Species at Bwindi whose before vs. after responses to the playback treatments were recorded, ordered by descending body mass (in kg), based on Kingdon et al. (2013); the treatments each was exposed to (I = insect, E = ecotourist, D = dog, L = leopard); and the number of 'first' exposures, 'repeat' exposure bouts and total videos of each species recorded.

Species Common name *Latin name*	Mass (kg)	Treatments	Videos		
			First	Repeat bouts	Total
Elephant *Loxodonta africana*	5250.0	I, E, D	4	2	6
Bushpig *Potamochoerus larvatus*	70.6	I	1		1
Yellow-backed duiker *Cephalophus silvicultor*	69.3	I, E, D, L	22	8	89
Chimpanzee *Pan troglodytes*	38.1	E	1		1
Black-fronted duiker *Cephalophus nigrifrons*	13.9	I, D, L	4		4
African golden cat *Caracal aurata*	9.3	L	1		1
Side-striped jackal *Canis adustus*	8.5	E, L	4	3	26
Honey badger *Mellivora capensis*	7.7	I	1	1	2
L'Hoest's monkey *Allochrocebus lhoesti*	4.8	I	1		1
Marsh mongoose *Atilax paludinosus*	3.4	I, E, D, L	4	3	29

Two-spotted palm civet *Nandinia binotata*	2.0	E, D	2	1	6
Large-spotted genet *Genetta maculata*	1.8	E, L	3	2	14
Emin's giant pouched rat *Cricetomys emini*	0.9	I, E	3		3
Carruther's mountain squirrel *Funisciurus carruthersi*	0.2	E, D, L	3	2	10

2.6 **Behavioural measures**

In determining how to quantify the behavioural responses to the playbacks I faced a challenge directly akin to that described in the Indian fable of the blind men and the elephant, insofar as an elephant's trunk or a duiker's posterior might be all that was perceivable or the animal repeatedly moved in and out of the camera's field of view. Regardless of the species, how much of the animal was in view, or whether every behaviour was readily classifiable (e.g. the swinging of an elephant's trunk was not), in the 193 videos in which the animal's behaviour was recorded both before and after the playback began, I could with certainty always quantify: 1) when the animal was first in view; 2) when it was last in view; and 3) when the playback began. Using these three values, I quantified the animals' behaviour by calculating the difference between the proportion of time the animal was present after playback minus the proportion of video recorded after playback, thus providing an index of the animal's behavioural response. If the animal's behaviour was unaffected by the playback, and it was in view throughout the 30 s of the video, the proportion of time it was present after the playback began, would be equal to the proportion of the video recorded, after the playback began. If the animal responded aversively by leaving upon hearing the playback, the proportion of time it was present after the playback would be less than the proportion of the video recorded after the playback. An example showing how the index is calculated is given in appendix E.

The value of the index may vary from - 1.0 to + 1.0; zero denoting no effect, a negative indicating an aversive effect, and a positive an attractant effect. To verify that values generated using this index reflected readily recognizable responses, and provide an accurate gauge of what the animals' response, I scored 'first' exposure videos of yellow-backed duikers. I focused on duikers because these were the most numerous data (Table 1), and the responses of duikers were readily recognizable because given their body size, the entire animal (not just a portion of it) was almost always within the camera's view. I subsequently compared the value of the index between videos in which the duiker either remained standing after hearing the playback, or walked or ran away (figure 1). The value of the index reflected the differences between these readily recognizable responses. When there was no response to the playback and the duiker remained standing, the median value of the index was effectively zero (0.02), denoting no effect. When the animal showed a moderately aversive reaction by walking away, the median value of the index was -0.17, which was distinct from the index values associated with standing (figure 1; Mann-Whitney $U_{2,10} = 0.0$, $p = 0.030$). When the animal showed a strongly aversive reaction by running away, the median value of the index was -0.38, completely distinct from the values associated with remaining standing (figure 1; Mann-Whitney $U_{10,12} = 4.0$, $p < 0.001$). The value of the index thus clearly differed in accord with clearly different responses, but at the same time provided a single integrative measure enabling a quantitative comparison between these distinct behaviours.
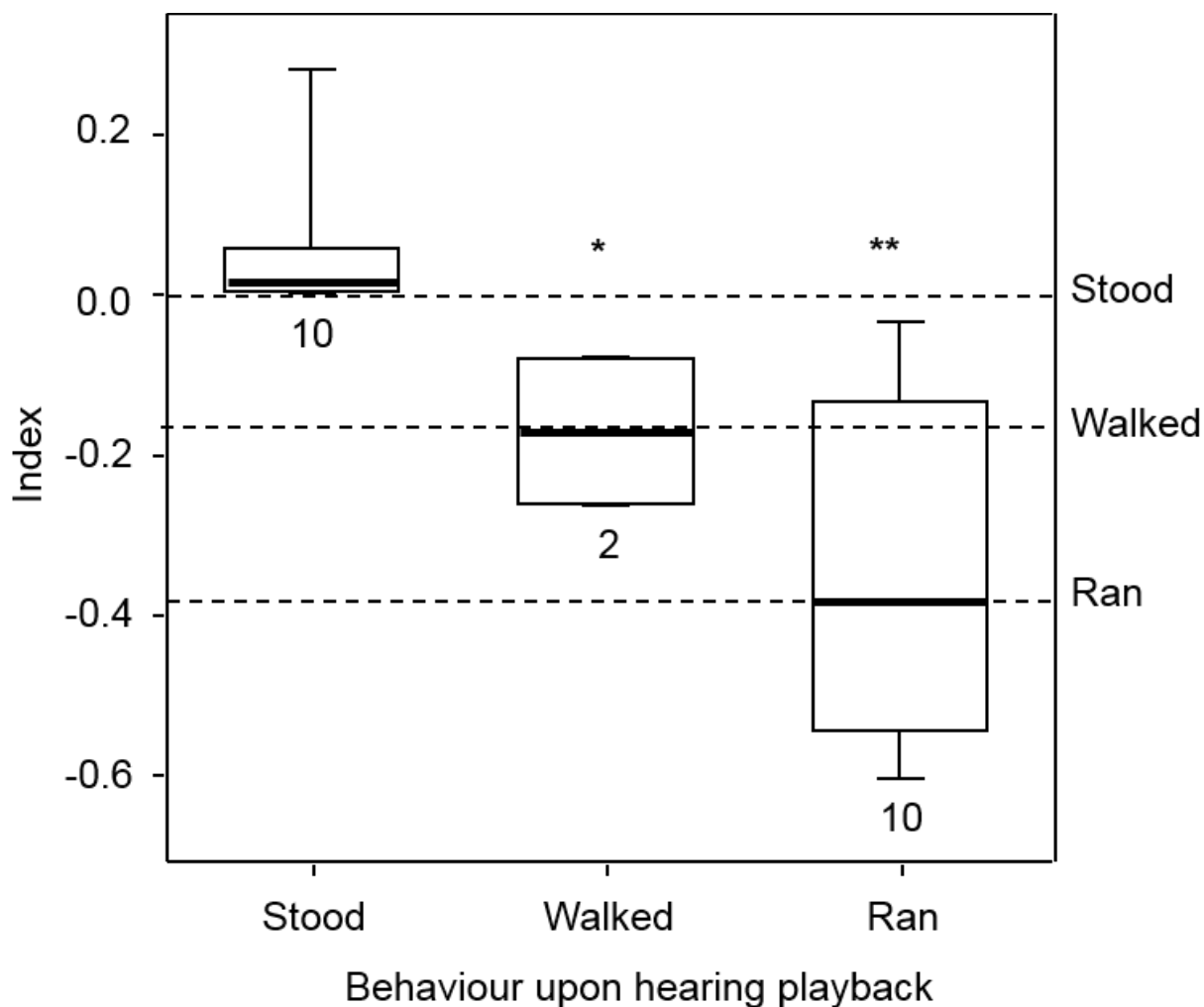
Figure 1. Values of the index quantifying the fear behavioural response of yellow-backed duikers to the playback treatments, calculated as the difference between the proportion of time the animal was present after the playback minus the proportion of the video recorded after the playback. Data are only for 'first' exposure videos of yellow-backed duikers in which the animal either remained standing after hearing the playback (stood) or walked or ran away. Box plots illustrate the median (bold horizontal line), upper and lower quartiles (box), and 5th and 95th percentiles (whiskers). Numbers below each box indicate sample size. The asterisks indicate a significant difference in index values in comparison to standing. Dotted lines indicate median index values (left axis of figure) corresponding to each of the behaviours (right axis of figure).

My straightforward index provided an additional advantage in permitting me to readily quantify habituation to the playback treatments, by calculating the average index value among the videos in each 'repeat' exposure bout. Here, I define habituation as the waning of wildlife's aversive response following repeated exposure to playback treatments, as measured by the change in the index from negative to zero values. If the animal habituated to the playback over the course of a 'repeat' exposure bout, the average value of the index among the videos in that bout may be expected to approach zero, as the animal became less likely in successive videos to leave after hearing the playback. The number of successive videos in a 'repeat' exposure bout is not a sufficient indicator of habituation, because if the animal reacted as aversively to the playback in each subsequent video as it did upon its 'first' exposure it cannot be said to have habituated, regardless of how many times it returned, i.e. how many successive videos there were.

2.7   Statistical analyses

To corroborate that the index enabled the comparison of responses between diverse species with different natural histories and cognitive ability, and verify that the pattern of responses to the playback treatments in yellow-backed duikers, for which there was the most data (Table 1), was representative of species at Bwindi in general, I conducted a two-way ANOVA of the rank-transformed index values of all 'first' exposure videos, assessing the effect of species identity (yellow-backed duikers vs. all other species combined) and playback treatment. The factor species identity was comprised of two groups; group 1 being all trials of the yellow-backed duiker only (n = 22), and group 2 being all trials of all the other 13 non yellow-backed duiker species pooled together (n = 32). Therefore, the two-way ANOVA did not use species identity with 14 species identities, but two identities (yellow-backed duiker vs. everything else that is not a yellow-backed duiker).

The pattern of responses to the playback treatments shown by yellow-backed duikers was the same as in all other species (figure 2), as verified by there being no significant interaction between species identity and the pattern of responses to the playback treatments ($F_{3,46} = 0.40$, $p = 0.752$). To ascertain that the non-significant interaction term between species identity and the pattern of responses to playbacks is not

an artifact of low power, I conducted a power analysis to estimate the number of first exposure trials that would be needed to detect a significant interaction effect with 80% power at 5% level of significance. The analysis revealed that a total sample size of 179 first exposure trials would be needed to have 80% power to detect a significant interaction effect. The estimated total sample size from the power analysis is three-fold my current sample size (n = 54), indicating that effect due to the interaction is indeed low.

The value of the index in yellow-backed duiker videos was consistently less negative regardless of playback treatment, resulting in there being a significant main effect of species identity ($F_{1,46}$ = 4.15, p = 0.047). In my paper describing the ABR, we reported that animals that ate the bait stayed in view longer, and larger animals took longer to leave the camera's field of view (Suraci et al. 2017). The less negative value of the index in yellow-backed duikers, indicating that they were slower to leave the camera's field of view upon hearing the playback, is thus consistent with their typically eating the bait and being the third largest species filmed (Table 1).

After ascertaining that all species as a community responded comparably to treatments, I then used the index to test if playback treatment affected the responses of wildlife. I tested the effect of ecotourists and known local predator playback treatments on the fear behavioural responses of mammals at Bwindi using Kruskal-Wallis' H-test, followed by Dunn's post-hoc tests (Zar 2010) which compares the significance of each treatment relative to the control (insect). I used non-parametric tests because the index values were not normally distributed (Shapiro-Wilk, W = 0.85, p < 0.001), and because non-parametric tests are more robust and conservative (Zar 2010). I tested the effect of playback treatment on the value of the index in each of the 54 'first' exposure videos, and then evaluated if treatment affected habituation to the playbacks, by testing the effects of the different playbacks on the average value of the index in each of the 22 repeat exposure bouts (Table 1). For both analyses, the independent variable was playback treatment and the dependent variable was the index.
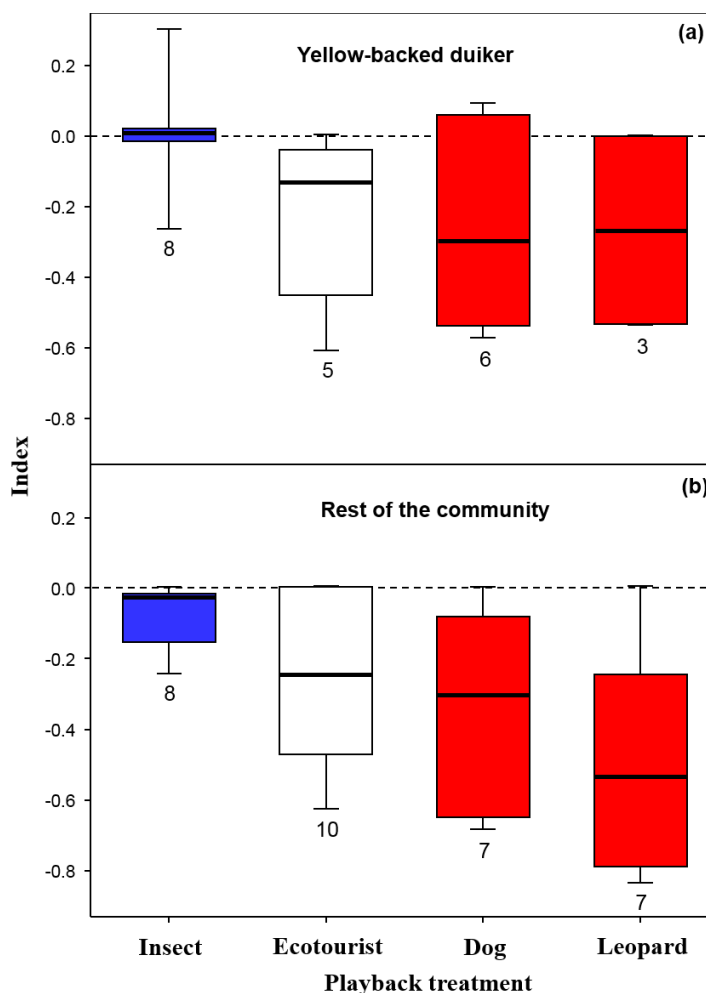
Figure 2. Responses of yellow-backed duikers (a) and rest of the community (all other species combined) (b), upon their 'first' exposure to each of the playback treatments; as quantified by the index calculated as the difference between the observed proportion of time the animal was present after the playback minus that expected if there was no effect. Note that the y-axis scale is the same in both panels. Blue signifies the non-predator control treatment (insect), white denotes ecotourists, red denotes the predator positive controls; extant introduced predator (dog) and the native extirpated apex predator (leopard). Box plots illustrate the median (bold horizontal line), upper and lower quartiles (box), and 5th and 95th percentiles (whiskers). Numbers below each box indicate sample size.

Chapter 3

3　Results

I successfully recorded before vs. after responses to the playback treatments in 14 of the 25-mammal species recorded present on camera traps at Bwindi (Treves et al. 2010; Mugerwa et al. 2013, Appendix F). Species size ranged from elephants to squirrels (Table 1). The median value of the index when animals heard insect playbacks was effectively zero (-0.02, 'first' exposures; 0.00, 'repeat' exposure bouts), verifying that insects were a non-threatening control with no effect on behaviour, and corroborating my use of Dunn's post-hoc tests comparing treatments vs. insects as a control (Zar 2010).

Playback treatment significantly affected the responses of individuals upon their 'first' exposure (figure 3a; K-W $H_{3,54}$ = 12.08, p = 0.007). Wildlife at Bwindi did not demonstrate a significant response to hearing ecotourist playbacks upon their 'first' exposure (figure 3a; Q_4 = 2.06, p = 0.122), and responded by only walking away slowly after hearing ecotourist vocalizations (median fear behavioural index = -0.18). As expected, wildlife at Bwindi demonstrated a significant aversive reaction upon their 'first' exposure to hearing their extant introduced large carnivore predator, the dog (figure 3a; Q_4 = 2.56, p = 0.034), to which they quickly walked away (median fear behavioural index = -0.30). Wildlife at Bwindi responded most strongly to hearing their native large carnivore apex predator, the leopard, upon their 'first' exposure, demonstrating a highly significant aversive reaction (figure 3a; Q_4 = 3.15, p = 0.005), to which they ran away from the playback (median fear behavioural index = -0.52).

Playback treatment also significantly affected habituation to the playbacks, judged by the average responses in 'repeat' exposure bouts (figure 3b; K-W $H_{3,22}$ = 9.45, p = 0.024). The aversive response of Bwindi wildlife to ecotourist playbacks faded quickly following repeated exposures to ecotourist vocalizations, responding non-significantly to 'repeat' exposure bouts of ecotourist playbacks (figure 3b; Q_4 = 1.43, p = 0.466), with a median fear behavioural response being effectively zero (< - 0.00), indicating habituation. Bwindi wildlife did not wholly habituate to hearing dog playbacks, as they also demonstrated a significant aversive reaction to hearing dogs in 'repeat' exposure bouts

(figure 3b; $Q_4 = 2.71$, $p = 0.020$; median fear behavioural index value = -0.19); and they showed a strong trend towards not wholly habituating to hearing leopard playbacks in 'repeat' exposure bouts (figure 3b; $Q_4 = 2.20$, $p = 0.086$), with a median fear behavioural index value of -0.13.
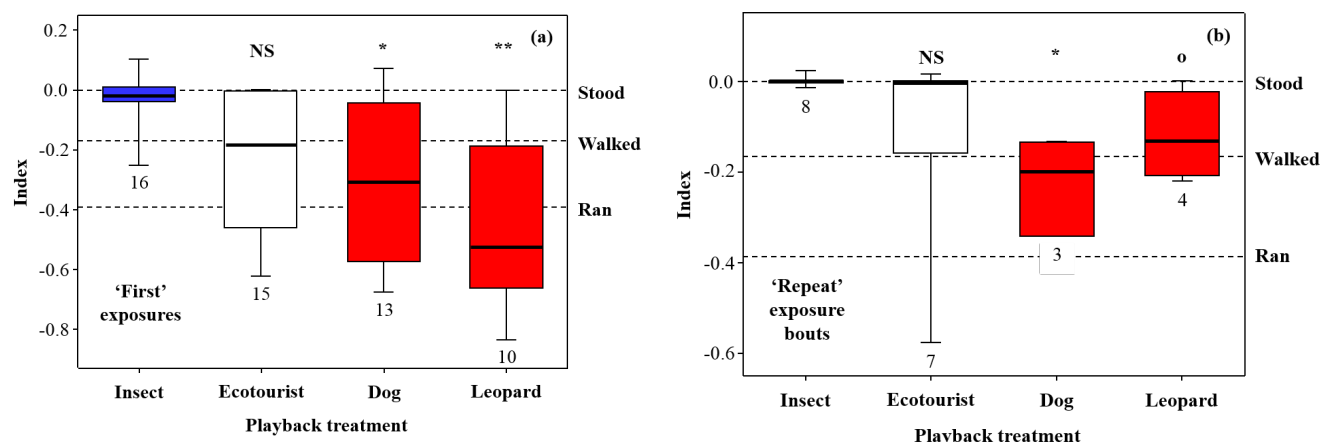
Figure 3. Responses of all species to each of the playback treatments upon their 'first' exposure (a), and as determined from the average response in each 'repeat' exposure bout (b) as quantified by the index calculated as the difference between the observed proportion of time the animal was present after the playback minus that expected if there was no effect. Note that the y-axis scale is less in panel (b). Blue denotes the non-predator control treatment (insect), white denotes an extant potential predator (ecotourist), red denotes the predator positive controls; extant introduced predator (dog) and the native extirpated apex predator (leopard). Box plots illustrate the median (bold horizontal line), upper and lower quartiles (box), and 5th and 95th percentiles (whiskers). Numbers below each box indicate sample size. Symbols signify significance of Dunn's post-hoc tests comparing treatment vs. the control (insect): **$p < 0.01$, *$p < 0.05$, °$p < 0.10$, NS (non-significant). Dotted lines indicate median index values (left axis of figure) corresponding to each of the behaviours (right axis of figure), in reference to the yellow-backed duiker median index values for each of the corresponding readily classifiable behaviours.

Chapter 4

4   Discussion

My results suggest that wildlife at Bwindi do not perceive ecotourists as predators, and there may be limited effects of ecotourism on wildlife at Bwindi, which responded to playbacks representing ecotourists as they did to insect sounds (non-threatening control). My results additionally indicate that wildlife at Bwindi recognize dogs and leopards as predators. Upon first exposure to ecotourist vocalizations, wildlife did not respond significantly different from negative control vocalizations, with animals merely walking away from the site following human voice playbacks (figure 3a). In contrast, wildlife responded significantly to vocalizations of their local predators upon first exposure, by walking away quickly or running away from the site after hearing dog and leopard vocalizations respectively (figure 3a). Wildlife seemed to habituate to ecotourist vocalizations following repeated exposures, but fearful responses of wildlife to both dog and leopard vocalizations continued even after repeated exposures, completely not habituating to dogs, and a strong trend towards not habituating to leopards (figure 3b). This is the first experimental study to test wildlife response to ecotourism in a protected area. By demonstrating that wildlife at Bwindi can accurately discern the level of threat posed by ecotourists from that of local predators and a non- predator, I provide evidence that ecotourism may not have negative impacts on wildlife in protected areas.

4.1   Response of Bwindi wildlife to ecotourists

My findings contrast those from other studies which have reported strong anti-predator behavioural responses of wildlife to ecotourists (Duschene et al. 2000; Stankowich & Blumstein 2005; Stankowich 2008; Ciuti et al. 2012a; Trimmer et al. 2017). The difference in results may be that previous studies have been conducted in areas where humans are sources of mortality such that human presence in general, including the benign presence of ecotourists is perceived as threatening by wildlife. It is worth mentioning that although poaching occurs at Bwindi, wildlife is poached with wire snares and dogs, perhaps, providing insufficient exposure to human voices to allow animals associate humans with mortality risk, as it is the case in protected areas where humans

hunt or persecute wildlife. Using human cues, experiments have indeed shown that wildlife in areas where humans are sources of mortality often exhibit fearful responses to humans (Bates et al. 2007; Yorzinski & Ziegler 2007; Stankowich 2008; Ciuti et al. 2012b; McComb et al. 2014; Clinchy et al. 2016; Smith et al. 2017).

In my study, vocalizations of people speaking English do not represent humans who pose any lethal threat to wildlife at Bwindi. I make a notable comparison with Clinchy et al. (2016) who used the same human playbacks as I used at Bwindi but reported a significant fearful response of European badgers in Britain to human vocalization playback treatments. This is because English speakers in Britain pose the greatest mortality risk to badgers by hunting and killing them for their alleged vermin behaviour (Tuyttens et al. 2000; Carter et al. 2007; Cassidy 2012; Cross et al. 2013). That Bwindi wildlife did not respond aversively to vocalizations of people speaking English, may indicate that wildlife at Bwindi perceive ecotourists as non-threatening. Ecotourists at Bwindi are indeed safe to wildlife insofar as the park agency guidelines on ecotourist behaviour prohibit ecotourists from reacting aggressively to wildlife, even when charged at or attacked by wild animals.

Investigating the specific mechanisms by which Bwindi wildlife recognize ecotourists was not the question my study was addressing. Nonetheless, I suggest that the presence of ecotourists at Bwindi has provided opportunities to wildlife to learn over time, through repeated exposures to English speakers, that this group of humans is safe (Blumstein 2002; Stankowich & Blumstein 2005). Animals may learn through experience over their lifetime to identify non-threatening environmental stimuli. For example, the badgers in the UK or the elephants in Amboseli National Park in Kenya, may have learned by witnessing human attacks on conspecifics and heterospecifics (observational learning) or surviving a human attack (inherited memory), that English (for badgers) or the Maasai (for elephants) speakers are sources of mortality.

Although shown here to have limited impacts on wildlife, given that wildlife in this study did not perceive ecotourists as predators, ecotourism may have indirect impacts on wildlife populations. For instance, habituation of wildlife to ecotourist presence may

increase wildlife vulnerability to predation by non-human predators, and where hunting is prevalent, to increased hunting, when wildlife become increasingly "bold" or lose anti-predator behaviour against humans in general, including threatening humans such as hunters (Geffroy et al. 2015). Habituation of wildlife to ecotourists may also bring wildlife in proximity with non-ecotourist communities (Whittaker & Knight 1998; Knight 2009; Seiler & Robbins 2016), causing conflict with human settlements, if wildlife pose harm to humans, agricultural fields or domestic animals (Packer et al. 2005; Maclennan et al. 2009; Dickman 2010; Liberg et al. 2012). Further, the presence of ecotourists in protected areas unintentionally excludes predators, because predators are often wary of humans and spatially avoid them (Berger 2007b). The presence of ecotourists may thus provide wildlife with safety from non-human predators, relaxing predation risk and eliciting reduced anti-predator behaviour in wildlife. For example, human presence around vervet monkeys (*Chlorocebus pygerythrus*) in Amboseli National Park in Kenya, deterred leopards from hunting the monkeys, thereby reducing vervet monkey predation by leopards (Isbell & Young 1993). However, in the absence of ecotourists, wildlife is re-exposed to the usual predators, which results in increased predation rates (Isbell & Young 1993). This is particularly true for protected areas where the intensity of ecotourism usually varies spatially or temporally, such that predator presence also varies accordingly. Wildlife may not encounter usual predators during the peak season when ecotourists are more abundant, but face a heightened predation risk during the low season when ecotourist presence is minimal. In protected areas with high ecotourist presence (e.g., the most popular National Parks in the United States, which receive more than 3 million ecotourists per year (National Park Service, 2016)), the cumulative effects of ecotourist presence could result in long-term changes in wildlife behaviour (e.g., altered habitat use; Sarmento & Berger, 2017). However, under regulated levels of ecotourist activity (including at Bwindi, where limits are placed on the number of ecotourists year round (Ahebwa et al., 2012)), I expect that any effects of ecotourism on wildlife will be minimal and maintained well within sustainable limits.

Previous correlative studies have reported that although the presence of ecotourists elicits negative responses from wildlife upon initial encounters (Bateman & Fleming 2017), these negative effects often wane over time and after repeated exposures

to ecotourists, indicating that wildlife habituate to ecotourists (Knight 2009; Geffroy et al. 2015). My results indeed support this conclusion, as wildlife at Bwindi quickly habituated to ecotourist vocalizations after repeated exposures (figure 3b), with wildlife median behavioural index increasing from a median of -0.18 (animals walking away slowly after hearing ecotourist vocalizations for first time) to zero (animals remaining standing at sites after repeated exposures to ecotourist vocalizations). Combining Bwindi wildlife's responses to first and repeated exposures to ecotourists and local predators, my findings further speak to the ability of wildlife to accurately discern threatening from non-threatening cues (Blumstein 2002; Hettena et al. 2014), where wildlife in this study habituated to the non-threatening ecotourists but demonstrated persistent aversive response to cues of actual predators (dogs and leopards), as wildlife that fails to respond to cues of its predator is at an elevated risk of death.

4.2 Dogs as sources of fear in wildlife at Bwindi

Whilst demonstrating that ecotourism may not have negative impacts on wildlife, I show that dogs may pose a significant predatory threat to wildlife at Bwindi as has been reported elsewhere (Vanak & Gompper 2009; Silva-Rodriguez & Sieving 2012; Hughes & Macdonald 2013). Dogs have been reported to cause reductions in wildlife abundances as they are responsible for over 50% of the wildlife predation incidences in protected areas worldwide (Hughes & Macdonald 2013). The fearful behaviour in response dog vocalizations is particularly interesting, as dogs are introduced large carnivore predators at Bwindi, and they are present inside the park illegally as either poaching or village dogs (McNeilage et al. 2006; Millan et al. 2013; Mugerwa et al. 2013; Proboste et al. 2015). The impacts of dogs on wildlife are likely to be aggravated if dogs are used for poaching as is the case at Bwindi (Grignolio et al. 2011; Lindsey et al. 2013). Accordingly, the presence of dogs and the risk of mortality they represent elicits fear behavioural responses in wildlife (Randler 2006; Clinchy et al. 2016; Parsons et al. 2016; Suraci et al. 2016; this study), which may potentially affect species interactions and species abundances in a community. Suraci et al. (2016) demonstrated that in response to hearing dog vocalizations, raccoons reduced foraging, which in turn increased the abundance of the raccoon's prey (red rock crab, *Cancer productus*), which also in turn reduced

abundances of the red rock crab competitor (staghorn sculpin, *Leptocottus armatus*) and red rock crab prey (periwinkle snail, *Littorina scutulata*).

Dogs vocalize regularly, and wildlife may be expected to be frequently exposed to and learn dog vocalizations (Blumstein 2002). Auditory predator recognition is dependent upon experience for proper performance (Blumstein 2002; Schel & Zuberbuhler 2009). The ability of wildlife at Bwindi to recognize dogs as predators based on vocalizations may be a learned experience through direct ecological interactions with dogs within the lifetime, especially for long-lived species such as elephants (Blumstein 2002; Hettena et al. 2014). Research on ungulates has shown that wildlife can learn to recognize predator cues in as short as one generation of the predator's presence (Berger et al. 2001; Berger 2007a). However, for short-lived species such as small herbivores and carnivores, the ability to recognize dogs as predators may have been acquired through both ecological and evolutionary processes. This is because dogs have been present in Bwindi for decades to allow a direct interaction between dogs and wildlife, and over evolutionary time to allow antipredator behaviour to be 'hard-wired' (Blumstein 2002, 2006; Hettena et al. 2014). While my results do not allow me to directly test the exact predator recognition mechanism of dogs by wildlife at Bwindi, I suggest that Bwindi wildlife's ability to recognize cues of dogs may depend, at least in part, on experience with dogs as predators regardless whether as poaching or village dogs (Berger et al. 2001; Blumstein 2002; Berger 2007a).

4.3 Fear behavioural response of Bwindi wildlife to leopards

Using leopard vocalizations as a potential secondary positive control treatment in my experiment to test the fear of ecotourists by wildlife proved successful, as wildlife at Bwindi responded fearfully to their native apex large predator, with no evidence of habituating to leopard vocalizations (figure 3a and b). Although out of scope for my study, this result raises an interesting question regarding the retained recognition of leopards by Bwindi mammals even though the large carnivore has been locally absent in the park for over 45 years (Butynski 1984; Kingdon et al. 2013). Prey populations may cease responding to predator cues over as few as several generations, but may also persist

for thousands of years following isolation from predators (Blumstein 2002; Blumstein & Daniel 2005). Some species of ungulates; bison (*Bison bison*), caribou (*Rangifer tarandus*), elk and moose (*Alces alces*) were experimentally shown to have lost recognition of wolves and grizzly bears after as short as 50 years of separation (Berger 1999; Berger et al. 2001; Berger 2007a). The retained recognition of leopards may highlight the important role leopards played as the only apex predators in this system before leopards were extirpated by humans. Retaining fear of leopards suggests that it provides a fitness benefit to wildlife at Bwindi, perhaps because leopard predation is an important force of selection and a source of high lethality in African tropical forest ecosystems (Kingdon et al. 2013), such that leopard recognition and associated antipredator behaviour is "hard-wired" to persist over an evolutionary time scale (Blumstein 2002).

Vocalizations of leopards elicited significant antipredator behaviour in Guereza colobus monkeys, even though this population had been isolated from leopards for over 40 years, a period longer than the individual's lifespan (Schel & Zuberbuhler 2009), indicating that perhaps, African forest mammals can retain recognition for leopards even without prior experience. Further, species which occur at Bwindi constitute a major component of the leopard's diet in African forests where leopards are still present (Hart et al. 1996; Jenny & Zuberbuhler 2005; Hayward et al. 2006; Hayward & Kerley 2008; du Preez et al. 2017; Mugerwa et al. 2017), hence I expect that leopards hunted mammals at Bwindi before their extirpation and the fearful response of Bwindi wildlife to leopard auditory cues is an innate and a hard-wired response. Bwindi mammals possibly co-existed in a multi-predator system consisting of leopards, dogs, and humans. Although leopards are now extirpated, poaching and village dogs are still present, and their presence may be sufficient to maintain appropriate antipredator behaviour in Bwindi mammals as predicted by the multi-predator hypothesis (Blumstein 2006). The multi-predator hypothesis suggests that appropriate anti-predator behavior may persist in prey populations following the removal of some but not all predators, so long as prey has other existing predators from which it must defend itself (Blumstein 2006).

Understanding the retention or loss of anti-predator behaviour in wildlife has important implications for large carnivore (apex predator) reintroduction programs and wildlife management (Berger et al. 2001; Blumstein 2002; Berger 2007a). The fearful behavioural response of wildlife at Bwindi to leopard playbacks may suggest a missing ecosystem function large carnivore apex predators provide, which may be conceivably filled by the reintroduction of leopards. Indeed, the fact that Bwindi wildlife still recognize leopard cues provides some optimism that wildlife at Bwindi would not suffer a similar fate as the moose in Sweden and the United States. Recolonizing bears and wolves in Sweden and the United States disproportionately killed moose which had lost their recognition of, and the danger bears and wolves posed (Berger et al. 2001). However, like elsewhere, the reintroduction of a large carnivore apex predator at Bwindi is a contentious subject considering the high predatory threat leopards may pose to species of high conservation and economic value, such as the mountain gorillas, not to mention the high potential of human-leopard conflict (Mech 1995; Ripple & Beschta 2004; Manning et al. 2009; Svenning et al. 2016). I wish to highlight that it is not my intention to advocate for leopard reintroduction at Bwindi insofar as this is a broader discussion for relevant stakeholders at Bwindi to consider.

4.4 Challenges of studying human impacts on wildlife in African forest protected areas

Studying the impacts of human activity in protected areas brings a lot of challenges. For instance, in most protected areas, both legal and illegal human activity often co-occur, making it challenging for both researchers and wildlife managers to discern the impacts due to the various human activities. Hunting and poaching are often conducted with dogs (Grignolio et al. 2011; Lindsey et al. 2013), and wildlife may respond similarly to both hunting and poaching dogs. African protected areas present a particular challenge in that on top of hunting and poaching with dogs, village dogs are ubiquitous and arguably pose the same predatory threat as hunting/poaching dogs (Boyko et al. 2009; Grignolio et al. 2011; Lindsey et al. 2013). In such protected areas, teasing apart the effects of hunting vs. poaching vs. village dogs may be challenging because researchers are more likely to test wildlife behavioural response to dogs in general, not responses to hunting vs. poaching

vs. village dogs. Although there is an increased interest among researchers to test the cognitive ability of wildlife to discern among human activity auditory and visual cues that pose different levels of threat (Bates et al. 2007; McComb et al. 2014; this study), there remains a challenge for wildlife managers to discern the human impacts that greatly overlap in characteristics.

Studying the impacts of ecotourism (and human activity in general) on tropical rainforest wildlife is challenging considering that these animals are naturally cryptic and often occur in low densities (Linkie et al. 2008), not to mention the dense vegetation of tropical rainforests that makes it notoriously hard to observe animals readily. Indeed, evidence of their presence often relies on paw or footprints, scratches on tree trunks and a plethora of noises. This challenge is evident insofar as most studies to date have inferred the effects of ecotourism on wildlife from the spatial or temporal relationships between wildlife and ecotourists (Klein et al. 1995; Duchesne et al. 2000; Mullner et al. 2004). Yet any such association may not be due to avoidance or fearfulness in wildlife of ecotourists, but a response to prey or non-human predator, with the wildlife's behaviour actually being determined by its response to its prey or predator (Duschene et al. 2000; Harmsen et al. 2009; Harmsen et al. 2011; Mugerwa et al. 2017).

Audio playback experiments provide a powerful and reliable means of simulating a naturally rare event in free-ranging animals and are a promising method of studying predator-prey interactions and testing anti-predator responses (Hettena et al. 2014; Suraci et al. 2017). More recently (and also in this study), audio playback experiments have been integrated with camera traps, providing a completely non-invasive robust means for testing how free-ranging wildlife respond to sounds of humans as predators. Nevertheless, the meager detections/trials of especially rare species often limit comprehensive statistical analysis of behavioural responses of individual species to treatments as I have highlighted in chapter 2 (also see table 1). To increase the number of trials available for analysis for this particular study, perhaps I did not need to do the pre-baiting (baiting the sites but with no playbacks set to be triggered for the first three days), but rather broadcast playbacks throughout the whole nine-day experiment period. Sixty percent of all trials were recorded during the pre-baiting period of the experiment, but

these could not be used to test the responses of wildlife to ecotourists because the playback treatments were not set to be triggered. The number of trials recorded for species may also be increased by trapping animals and having tracking devices attached (e.g., Smith et al. 2017). Tracking the animals will then allow targeted placement of playback experiments, in areas of the park where the animals are present then. However, such studies will require considerable time, budget and effort.

Using bait or attractants or lures is common in experimental studies, and indeed a proven remedy to increase detections/trials of free-ranging animals in camera trap based studies investigating animal behaviour (du Preez et al. 2014; Burton et al. 2015; Suraci et al. 2017). However, different species may respond differently to attractants, with some showing interest in bait and others not (Suraci et al. 2017). Therefore, choosing the right bait that is attractive to a suite of species may be challenging. Further choosing the most appropriate baiting strategy is challenging, especially when working in rural, remote sites, where automated baiting devices are unavailable. For example, in this study, it is plausible that the dramatic drop in recorded trials between pre-baiting and treatment days was because my baiting strategy for this particular study was ineffective. I applied visual and olfactory bait at experimental sites on visit days: 1, 4 and 6, meaning that animals were attracted to the sites by odour and they consumed all the bait on day 1. But, on visiting the sites on days 2 and 3, the animals only got the odour but no bait to consume. It is therefore likely that animals learned that the odour did not come with a reward, and they did not return to the sites beyond day 3 of the experiment. An automated baiting devise to allow continuous replenishing of the visual bait, may have, perhaps ensured that animals received both the odour and reward on all the days they visited the sites.

4.5 Future research directions

My research has shown that wildlife may accurately perceive cues of benign human types (e.g., ecotourists) as non-threatening. Experiments that simultaneously test behavioural responses of a wildlife community to cues of local language speakers and ecotourists are needed to elucidate further wildlife's cognitive ability to discern the level of threat posed by different human types. For instance, in protected areas like Bwindi, it is the local people speaking native languages, and not ecotourists, who poach wildlife. It would be

interesting to compare the behavioural responses of wildlife to local people and ecotourists.

Further, elsewhere, it has been reported that the level of threat humans pose to wildlife differs between species and even with traits such as body size and trophic category (Macdonald et al. 2011; Darimont et al. 2015; Ripple et al. 2016). Large-bodied mammals, for instance, are hunted at higher rates than small-bodied mammals (Macdonald et al. 2011; Ripple et al. 2016). Similarly, large carnivore predators are hunted at higher rates than herbivores (Darimont et al. 2015). Experiments have neither compared the behavioural responses of carnivores vs. herbivores nor large vs. small-bodied mammals to cues of ecotourist (or humans in general) presence. An important note to make is that my study tested the impacts of ecotourism on a Bwindi wildlife community as a whole and not individual specific species. That said, my findings are pertinent to the management of Bwindi wildlife community, and opens opportunities to test the impacts of ecotourism on specific species, especially high conservation value species such as mountain gorillas.

4.6 Study overview

The objective of my thesis was to expand the field of predator-prey interactions while considering the fear ecotourists may induce in wildlife, which I assessed by examining the extent to which wildlife perceive ecotourists as predators. In chapter 1 of this thesis, I give a general background on fear in prey as induced by the presence of predators, with fear effects ranging from wildlife demography to changes in wildlife abundance at the community level. I reviewed how the presence of ecotourists may be a source of fear in wildlife, because humans in general, are major causes of mortality to wildlife. In chapter 2, I used an automated acoustic playback experiment to test if wildlife at a premier African protected area perceive ecotourists as predators. I achieved this by testing if wildlife respond fearfully to vocalizations that simulate the presence of ecotourists in contrast to local predators (dog and leopard, positive control) and a non-predator (insects, negative control). Through this manipulation, I combined knowledge of predator-prey interactions to investigate how ecotourism may impact wildlife in a protected area. In chapter 3, I present my findings, where I compared the fear behavioural response of

wildlife to ecotourists and local predators. In chapter 4, I discuss the general biological and management implications of my research and discuss my findings in light of the rapidly expanding ecotourism in protected areas (Balmford et al. 2015; Geffroy et al. 2015). In the same chapter, I give a study overview, summary and concluding remarks of this research.

4.7 Summary

This study demonstrates that ecotourists are not perceived as predators by wildlife at Bwindi, and thus, ecotourism may not negatively impact wildlife in this protected area. While testing for impacts of ecotourism on wildlife, by comparing wildlife response to ecotourist vs. local predators, I have been able to show that the presence of dogs inside the national park poses a major predatory threat to wildlife at Bwindi. The presence of dogs and the associated fear of predation they induce in wildlife may have long-term negative impacts on wildlife populations and ecosystem functioning as has been demonstrated elsewhere. Lastly, my experiment further showed that wildlife at Bwindi still recognize its long-extirpated apex predator, the leopard. Overall, the impacts of ecotourism on wildlife may be minimal, but the presence of dogs and the human extirpation of apex predators may have negative impacts on the wildlife community. Therefore, it is the presence of dogs and the fear it induces, and the extirpation of the only large apex predator, that are likely to have negative impacts on wildlife at Bwindi and not the presence of ecotourists as I hypothesized.

4.8 Conclusion

The global protected area network is expanding, currently covering 13% of the world's surface (Naughton-Treves et al. 2005; Watson et al. 2014). This unprecedented expansion has not gone unchallenged, with local communities often resisting protected areas, on the grounds of lost access to wildlife resources, and asking tough questions regarding the need for protected areas (Hamilton et al. 2000). Central to eliciting local and national support for protected areas, and justifying their need, protected area agencies use ecotourism as a strategy to attach economic value on protected areas (Balmford et al. 2009; Balmford et al. 2015). On the other hand, ecotourism has received resistance from

researchers, citing potential negative impacts of ecotourism on wildlife (Bateman & Fleming 2017), and even maybe a more serious problem if wildlife perceive as predators.

My study, the first experiment to test the responses of wildlife to ecotourists in a protected area, has shown that the impacts of ecotourism on wildlife are likely to be limited because wildlife in this study did not perceive ecotourists as predators. Although I acknowledge that my analysis treated all wildlife uniformly, despite the potential differences in natural history and cognitive ability, I highlight that my results apply to a wildlife community as a whole, not to particular species. Protected areas manage wildlife in aggregate as a community and occasionally specific species of concern. My research has tested how a wildlife community responds to ecotourism. The obvious next step would be to test the response of particular species of conservation concern such as mountain gorillas to ecotourism.

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Appendices

Appendix A: Map showing the location of Bwindi Impenetrable National Park (inset), ecotourism zones and experimental sites
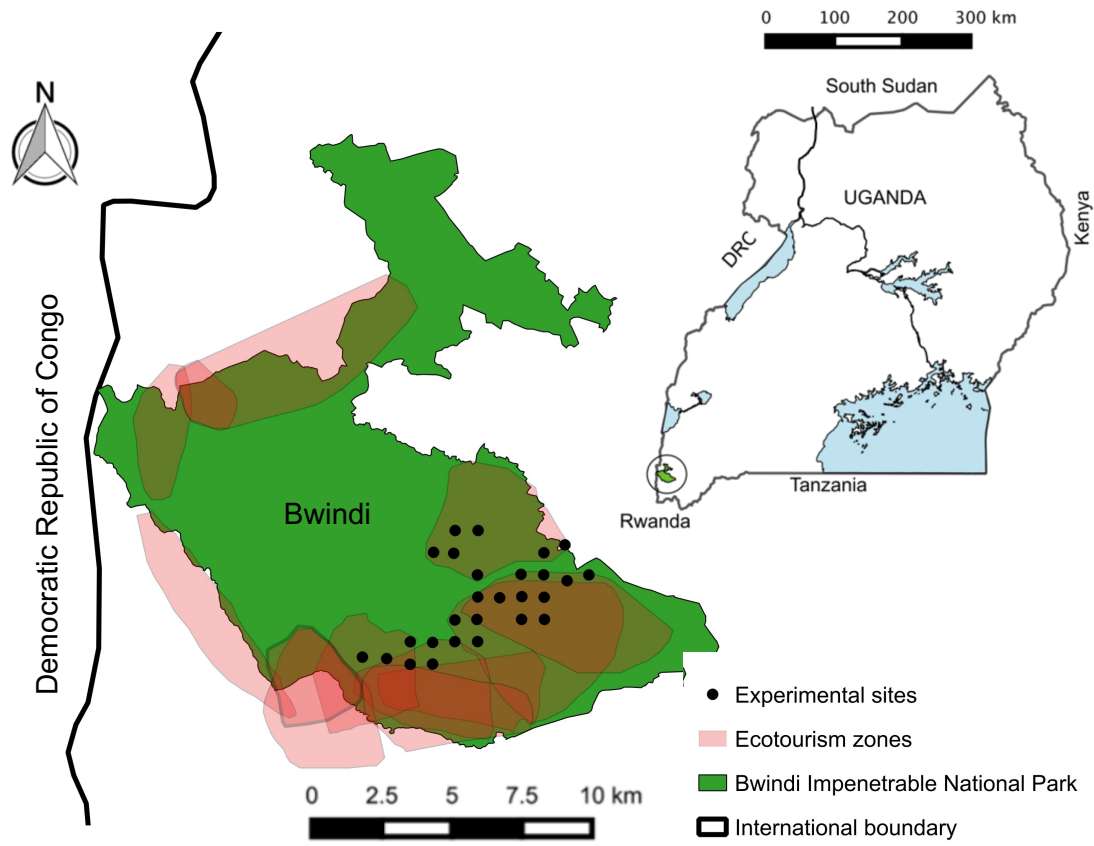
Appendix B: Picture of ABR (adapted from Suraci et al. 2017)
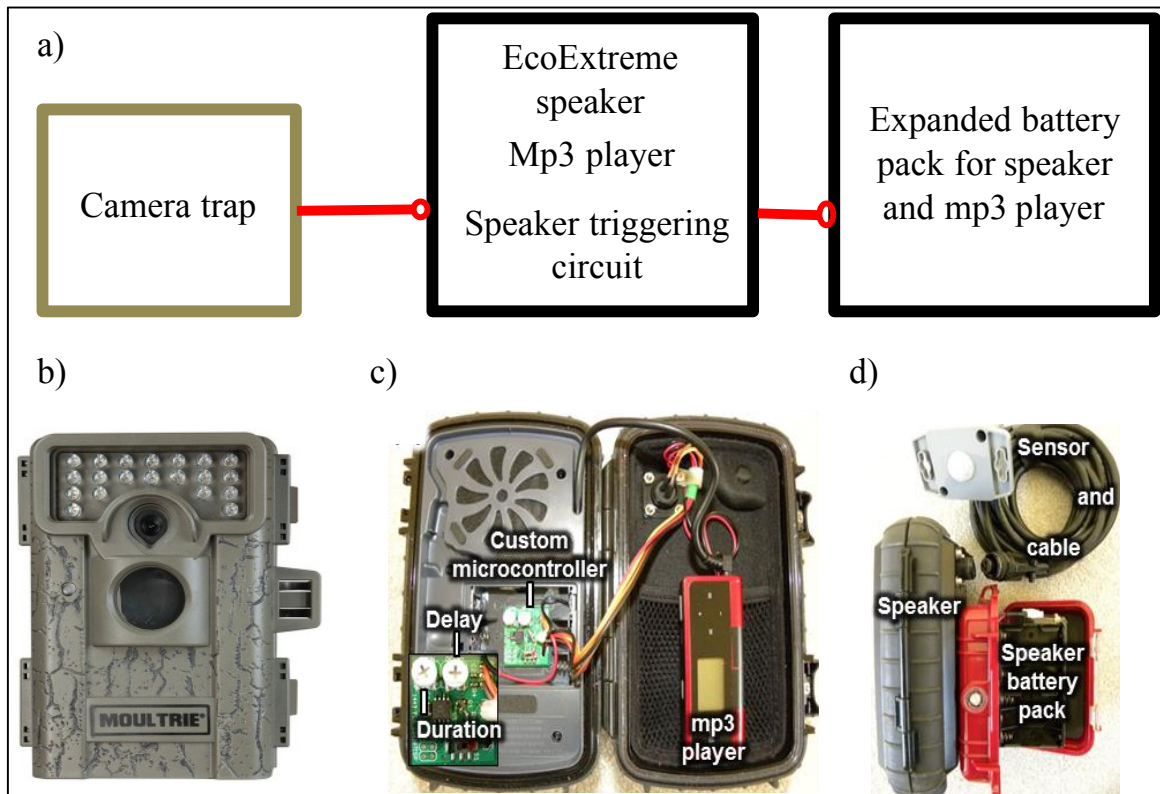
Appendix C: General workflow of the study activities. For details on baiting, camera set-up, playbacks and ABR, see section 2.3 (field procedures and playbacks used) under methods.

```
┌──────────────────────────────────┐
│ Grouping experimental sites into  │
│ arrays and preparing playback     │
│ playlists                         │
└──────────────────────────────────┘
                │
                ▼
┌──────────────────────────────────┐
│ Preparing array deployment plan   │
└──────────────────────────────────┘
                │
                ▼
┌──────────────────────────────────┐
│ Deploying ABRs in arrays          │
└──────────────────────────────────┘
                │
                ▼
```

First site visit
• Bait applied
• "Fence" built
• Camera set-up

◇ Pre-baiting Playbacks OFF ◇

START

3 days

Second site visit
• Bait applied
• Camera batteries replaced
• Camera card replaced
• ABR set-up

◇ Treatment Playbacks ON ◇

3 days

Third site visit
• Bait applied
• ABR positions changed
• Batteries replaced
• Memory cards replaced

◇ Treatment Playbacks ON ◇

3 days

Fourth site visit
• Fence put down
• Camera and ABR picked

END

Appendix D: ABR field set-up at Bwindi Impenetrable National Park

Appendix E: An example on how to calculate the index of animal's behavioural response to playback treatments from three data points scored from the video: when the animal is first seen, when the playback began and when the animal was last seen in video. For details on the index see section 2.5 (behavioural measures).

Animal first seen at frame 50   Playback begun at frame 140   Animal last seen at frame 160
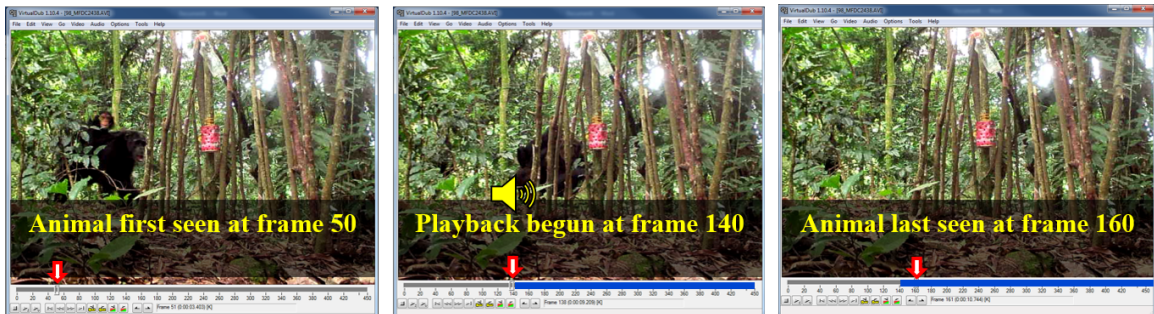
Proportion of time animal in view after playback began $= \dfrac{\text{Frame animal last seen} - \text{Frame playback begun}}{\text{Frame animal last seen} - \text{Frame animal first seen}}$

Proportion of video recorded after playback began $= \dfrac{\text{Total video length} - \text{Frame playback begun}}{\text{Total video length}}$

Proportion of time animal in view after playback began $= \dfrac{160 - 140}{160 - 50} = \dfrac{20}{110} = 0.18$

Proportion of video recorded after playback began $= \dfrac{450 - 140}{450} = \dfrac{310}{450} = 0.69$

Index of animal's behavioural response $= \quad 0.18 - 0.69 \quad = -0.51$

Appendix F: Table showing recorded species at Bwindi based on previous camera trap surveys of Treves et al. 2010 and Mugerwa et al. 2013. 1 and 0 indicate the presence or absence of the species in the respective studies. Both studies combined have recorded 25 medium-to-large mammal species at Bwindi.

Common name	Species	Treves et al. 2010	Mugerwa et al. 2013	Both studies
Black-fronted duiker	*Cephalophus nigrifrons*	1	1	1
Yellow-backed duiker	*Cephalophus silvicultor*	1	1	1
Lhoesti monkey	*Allochrocebus lhoesti*	1	1	1
African golden cat	*Caracal aurata*	1	1	1
Chimpanzee	*Pan troglodytes*	1	1	1
Olive baboon	*Papio anubis*	1	1	1
Emin's giant pouched rat	*Cricetomys carruthersi*	0	1	1
Servaline genet	*Genetta servalina*	0	1	1
Carruther's mountain squirrel	*Funisciurus carruthersi*	0	1	1
African brush-tailed porcupine	*Atherurus africanus*	0	1	1
Common bushpig	*Potamochoerus larvatus*	1	1	1
Greater Cane Rat	*Thryonomys swinderianus*	0	1	1
Mountain gorilla	*Gorilla beringei*	1	1	1

Side stiped jackal	*Canis adustus*	1	1	1
Marsh mongoose	*Atilax paludinosus*	1	1	1
African civet	*Civettictis civetta*	1	1	1
Sitatunga	*Tragelaphus spekii*	0	1	1
Honey badger	*Mellivora capensis*	0	1	1
Demidoff's dwarf galago	*Galago demidoff*	0	1	1
Two-spotted palm civet	*Nandinia binotata*	0	1	1
African elephant	*Loxodonta africana*	1	0	1
African wildcat	*Felis silvestris*	1	0	1
African white-bellied pangolin	*Phataginus tricuspis*	1	0	1
Weyn's duiker	*Cephalophus weynsi*	1	0	1
Red-flanked duiker	*Cephalophus rufilatus*	1	0	1
Total number of species reported present		16	20	25

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Education
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Teaching Assistant
Plant Reproductive Biology, and Tree Improvement, Makerere University   2009

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Publications

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Conferences and Presentations

(September 2017) Invited speaker: The future is not that golden: conflict with humans, poaching, and conservation of African golden cats. First International Small wild cat Conservation Summit, Kent, England.

(June 2017) Anthropogenic effects on the ecology of fear in African forest mammals. 54th Annual conference of the Animal Behaviour Society, Toronto, Canada.

(January 2016) Experimentally testing wildlife's fear of humans to quantify the impacts of illegal hunting on tropical biodiversity. Predator-Prey Interactions Meeting, Gordon Research Conferences, California, USA.

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(June 2011) A camera trap assessment of terrestrial vertebrates in Bwindi Impenetrable National Park, Uganda. SCB+ATBC meeting, Arusha, Tanzania.

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