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A new Automated Behavioural Response system to integrate playback experiments into camera trap studies

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Summary

1. How animals respond to anthropogenic disturbances is a core component of conservation biology and how they respond to predators and competitors is equally of central importance to wildlife ecology. Camera traps have rapidly become a critical tool in wildlife research by providing a fully automated means of observing animals without needing an observer present, permitting data to be collected on rare or elusive species and infrequent events. Snapshots from camera traps revealing a species' presence have been the principal data used to date to gauge behaviour; but, lacking experimental controls, such data permit only correlational analyses potentially open to confounding effects. Playback experiments provide a powerful means to *directly* test the behavioural responses of animals, enabling strong inferences and rigorous conclusions not subject to the potential confounds affecting the interpretation of snapshot data; the principal factor to date limiting the use of playback experiments being the need to have an observer present.

2. We developed an Automated Behavioural Response system (ABR) comprising a custom-built motion-sensitive speaker system that can be paired with any commercially available camera trap, providing the means to conduct playback experiments directly testing the behavioural responses of any species that can be 'caught' on a camera trap.

3. We describe field tests in Uganda, Canada and the USA, experimentally testing the effects of anthropogenic disturbances and interactions among large carnivores, in species as diverse as elephants, black bears, chimpanzees and cougars; experiments that would be completely infeasible without the ABR. We evaluate factors affecting the rate of successful data collection in the experiments in Uganda and Canada, and detail how we maximized the system's performance in the USA experiment.

4. By integrating the power playback experiments provide to directly and rigorously test behavioural responses with the capacity camera trapping affords to study virtually any animal anywhere, the ABR can both greatly expand the range of research questions addressed by conservation biologists and wildlife ecologists and qualitatively improve the rigour of the resulting conclusions. We discuss various ways to optimize the ABR's performance in any circumstance, and the many novel research opportunities made available by this new methodology.

Key-words: acoustic cues, animal behaviour, automated playback system, behavioural response, conservation biology, motion sensor, observer effects, remote monitoring, video data, wildlife ecology

Introduction

How animals respond to humans, their commensals (e.g. dogs), and anthropogenic disturbances, are central questions in conservation biology (Frid & Dill 2002; Caro 2007; Francis & Barber 2013; Oriol-Cotterill *et al.* 2015; Smith, Wang & Wilmers 2015); and quantifying how animals respond to predators and competitors is similarly central to behavioural, population and community ecology (Lima & Dill 1990; Schmitz 2010; Zanette *et al.* 2011; Suraci *et al.* 2016). Camera traps have rapidly become a critical tool in both conservation biology and wildlife ecology in large part because they provide a fully automated means of observing wildlife that avoids the potentially confounding effects and logistical challenges of needing to have an observer present, and can thus capture information on rare or elusive species and infrequent events

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(Rowcliffe *et al*. 2011, 2012, 2014; Hamel *et al*. 2013; Burton *et al*. 2015; Heinicke *et al*. 2015; Weinstein 2015). Snapshots from camera traps have been used to interpret how animals may be responding to, e.g., humans, predators or competitors, by avoiding them in space or time, for instance through the use of occupancy models to test hypotheses regarding species co-occurrence (O'Connell & Bailey 2011), or the comparison of activity patterns to test for temporal avoidance (e.g., Brook, Johnson & Ritchie 2012). The correlational nature of many camera trap studies, however, may leave them open to several well-described sources of bias that could complicate the interpretation of results (Rowcliffe *et al*. 2012, 2014; Hamel *et al*. 2013; Burton *et al*. 2015), particularly when testing hypotheses regarding wildlife behavioural responses. Moreover, while snapshots and the well-developed methods for handling these data (O'Connell & Bailey 2011; Rowcliffe *et al*. 2014; Burton *et al*. 2015) have provided valuable insights into species interactions, still images provide only relatively coarse-scale information on behavioural responses. Most modern camera traps are capable of recording both audio and video, though only a very small subset of camera trap studies have yet made use of this capability to directly record the behavioural responses of animals in real-time (Rowcliffe *et al*. 2012; Weinstein 2015).

Playback experiments provide a powerful, comparatively easily implemented and readily interpretable means of directly testing the behavioural responses of animals (Durant 2000a; Clinchy *et al*. 2011; Zanette *et al*. 2011; Suraci *et al*. 2016), and have accordingly been employed in hundreds of wildlife studies to quantify how animals respond to the sounds of humans (e.g., elephants, McComb *et al*. 2014), dogs (e.g., raccoons, Suraci *et al*. 2016), anthropogenic noise (Francis & Barber 2013), predators (180 experiments on everything from toads to elephants, reviewed in Hettena, Munoz & Blumstein 2014), competitors (e.g., black bears and cougars, Suraci *et al*. 2016; hyenas and African wild dogs, Webster, McNutt & McComb 2012), potential mates (e.g., lions, McComb *et al*. 1993) and numerous other stimuli (King 2015). To date, the principal logistical constraint on conducting such experiments has been the need to have an observer present to locate subjects and operate the equipment, with the result that most playback experiments have been restricted to quantifying the responses of relatively common, diurnally active animals, that are not hyper-sensitive to the presence of humans. This constraint has largely precluded the use of playback experiments in conservation biology (Pimm *et al*. 2015; Thuppil & Coss 2015), as well as studies of more elusive wildlife like large carnivores living in remote or heavily forested habitats.

Here, we describe an Automated Behavioural Response system (ABR) combining all the advantages camera trapping derives from not needing to have an observer present, with the power playback experiments provide to directly and rigorously test research hypotheses regarding behavioural responses. The ABR is designed to be easily integrated into any camera trap study, providing the means to directly experimentally test the behavioural responses of any species that can be 'caught' on a camera trap. The ABR permits the *direct* testing of behavioural responses by presenting a cue (sound) from the stimulus of interest (e.g. human, predator or competitor) when the animal is present, and video recording its reaction; its reaction being the dependent variable of interest. Because the ABR permits different cues to be presented (control vs. treatment) it further provides the means to *experimentally* test behavioural responses, enabling strong inferences and robust conclusions (Zanette *et al*. 2011; Suraci *et al*. 2016). Utilizing the ABR, the contrasting response to the treatments is what is of interest, not how or why the animal came to be in front of the camera. The animal's presence and timing the cue to be present when the animal is, are simply limiting factors determining the rate of successful data collection. We discuss means of increasing the rate at which animals are present, such as setting the ABR where animals are 'corralled' into view, and means of increasing the rate at which the cue is successfully timed to coincide with the animal's presence, such as using attractants to help keep the animal in view.

The direct testing of behavioural responses the ABR enables is fundamentally different from the indirect assessment of behaviour derived from snapshots revealing a species' presence, which has been the principal means used to date to gauge responses using camera trap data (Bridges & Noss 2011; Burton *et al*. 2015). Utilizing the ABR, the animal's presence is simply, and obviously, a necessary precursor to measuring its reaction to the cue presented. This is in contrast with snapshot studies, where the animal's presence is itself the dependent variable. While factors that limit species' presence represent potential confounds that may complicate the interpretation of snapshot data (Rowcliffe *et al*. 2011, 2012, 2014; Hamel *et al*. 2013; Burton *et al*. 2015), these simply represent potential impediments to overcome in maximizing the performance of the ABR. Additionally, whereas factors such as camera placement or the use of attractants may represent sources of bias in standard correlational camera trapping studies because they may affect the probability of detecting an animal's presence (Hamel *et al*. 2013; Burton *et al*. 2015), provided these factors increase the animal's presence in front of the camera, they can, in contrast, actually represent opportunities to increase the rate of data collection in the context of the controlled experimental tests of behavioural responses possible with the ABR (but see Supplementary Discussion regarding potential disadvantages of using attractants).

We provide a technical description of two versions of the ABR, and detail our successful use of the ABR in three experiments it would have otherwise been infeasible to conduct: assessing the extent and intensity of illegal hunting (Ahumada *et al*. 2011; Harrison *et al*. 2015) in tropical montane forest in Uganda (B. Mugerwa *et al*. unpubl. data); testing behavioural interactions among large carnivores only very rarely directly recorded (Allen *et al*. 2015), in remote temperate rain forest in Canada (J. Suraci *et al*., unpubl. data); and quantifying cougar responses to anthropogenic disturbances it has previously been impossible to experimentally test (Wilmers *et al*. 2013; Smith, Wang & Wilmers 2015), in coastal montane habitats in the USA (J. Smith *et al*. unpubl. data). Utilizing the ABR, we successfully tested the responses of animals from the size of elephants (5250 kg) to black bears (89·5 kg) to squirrels (0·2 kg).

We evaluate the factors influencing how effective the two variants of the ABR were at quantifying the responses of animals to playbacks in the experiments conducted in Uganda and Canada, and detail how we maximized the ABR's performance in the USA experiment. We discuss the variety of means available to optimize the ABR's performance in any circumstance, and the many opportunities the ABR provides to rigorously experimentally test questions of central importance in both conservation biology and wildlife ecology which were previously infeasible to answer (Zanette *et al*. 2011; Pimm *et al*. 2015; Suraci *et al*. 2016).

Technical description

The ABR is comprised of a custom-made, motion-sensitive speaker unit, designed to be used with any commercially available, audio- and video-enabled camera trap (Fig. 1a,b). The unit consists of an off-the-shelf shockproof and waterproof speaker (EcoExtreme, Grace Digital Inc., San Diego, CA, USA; 19·0 × 11·4 × 6·4 cm, 0·4 kg) modified to incorporate a custom microcontroller (Fig. 1c; see Supporting Information for circuit diagram and description) and input port for an external motion sensor (Fig. 1d,e). The microcontroller detects an incoming digital trigger from the attached sensor (Fig. 1a; see below) and activates the speaker by permitting current to pass from a custom battery pack (Fig. 1d) to the speaker's battery terminals. Potentiometers on the microcontroller (Fig. 1c) allow the user to adjust two playback parameters: (1) the delay between triggering of the motion sensor and the start of the playback; and (2) the duration of the playback. The range of values can be pre-programmed by the user (using program "motion.c", included in Supporting Information). The inclusion of the delay permits the recording of behaviour prior to the playback broadcasting, providing a powerful means to gauge any change in behaviour in response to the playback in the timeframe of a given video (see Video S1).

The ABR is designed for use with any AAA battery-powered audio (e.g. mp3) player (Fig. 1c). A custom battery pack in a weatherproof case (Fig. 1d; Pelican 1010 Micro Case, Pelican Products Inc., Torrence, CA, USA; 14·0 × 10·0 × 6·0 cm, 0·2 kg) takes 12 AA batteries, providing extended battery life to the speaker and audio player. When first powered on, most digital audio players require several seconds before playing a sound file. For this reason, the ABR is designed such that the audio player is continuously active (i.e., not connected to the motion sensor), but the system remains

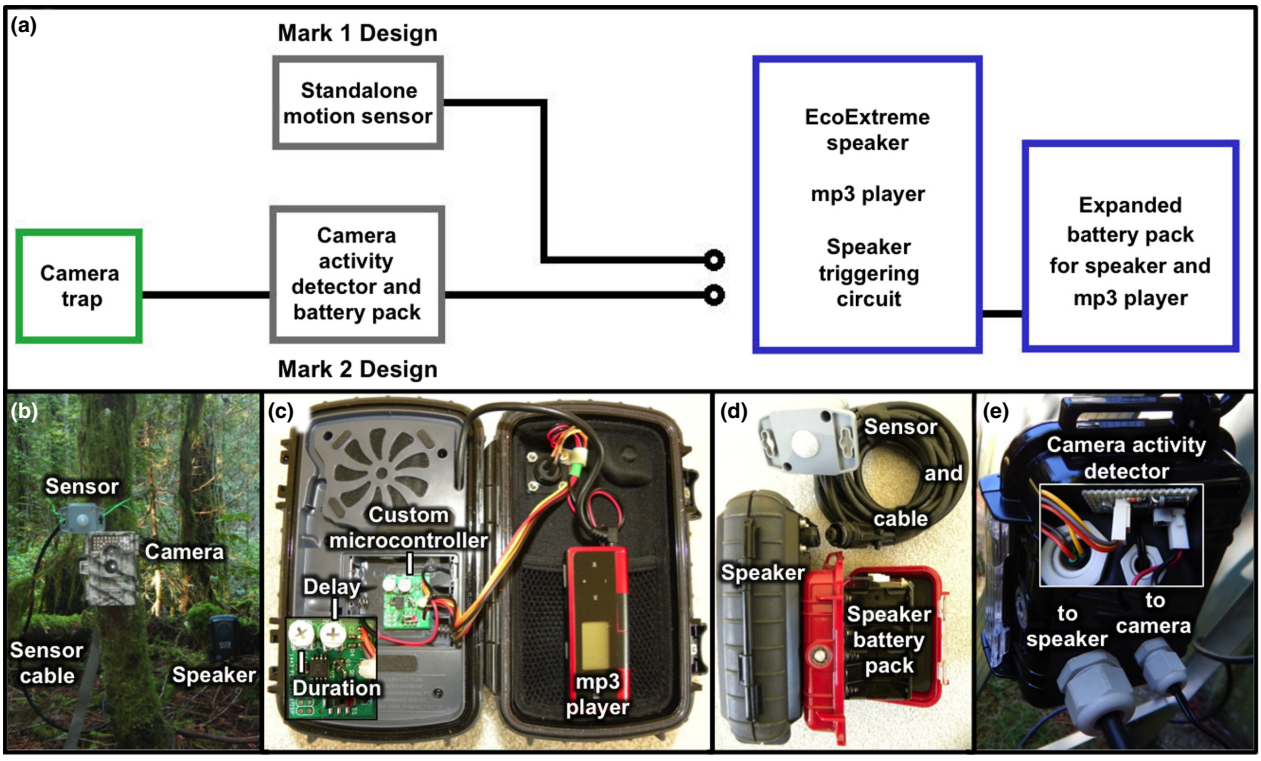

Fig. 1. Design of the Automated Behavioural Response system (ABR). (a) Diagram detailing the major components of the Mark 1 and Mark 2 designs. (b) Mark 1 design deployed in the field, illustrating the positioning of the speaker's standalone motion sensor ('Sensor') adjacent to the commercially purchased camera trap ('Camera'), and the 6 m cable ('Sensor cable') leading from the sensor to the custom speaker unit ('Speaker'). (c) Internal features of the speaker unit, revealing the 'Custom microcontroller' and commercially purchased 'mp3 player', the inset detailing the potentiometers on the microcontroller that permit the user to adjust the 'Delay' before the playback is broadcast and its 'Duration'. (d) Photo displaying, the standalone motion sensor ('Sensor') and attached 6 m 'cable' used in the Mark 1 design, and the external features of the speaker unit showing the (open) expanded battery pack ('Speaker battery pack') attached to the back of the 'Speaker'. (e) Photo showing the 'Camera activity detector' used in the Mark 2 design indicating the two external cables ('to speaker' and 'to camera') connecting the unit to the speaker and camera, respectively, the inset showing the circuitry inside the unit that detects when the camera is triggered and turns the speaker on.

silent unless the speaker is triggered by the motion sensor; thereby permitting a playback to be broadcast immediately upon the speaker being triggered. In the field tests described below, we used inexpensive mp3 players (Fig. 1c; RCA TH1814WM, VOXX Accessories Corp., Carmel, IN, USA), which ran continuously for up to 7 days. Speaker battery life will depend on how frequently the system is triggered but was much longer than 7 days in our field tests.

We designed the ABR to be activated by either (Fig. 1a) a standalone motion sensor (Mark 1) or the triggering of the camera trap (Mark 2). In the Mark 1 design, the speaker is connected by a 6 m cable to a passive infrared motion detector module with a fully adjustable sensitivity control (Qunqi HC-SR501; Shenzhen Qunqi Ltd., Shenzhen, China), housed in a weather-proof casing (Fig. 1b,d). Using the Mark 1's standalone motion sensor, an animal may trigger the camera trap but not the speaker (see Video S7), which has advantages in certain applications (see Discussion). In the Mark 2 design (Fig. 1a), the speaker is connected to the camera trap's DC power port and triggered by the camera itself, ensuring a playback is broadcast every time the camera is triggered and a video is recorded. A custom-built 'camera activity detector' (Fig. 1a,e) is positioned between the camera and speaker, consisting of a weather-proof case (Pelican 1010 Micro Case) housing a battery pack to power the camera and a custom current detector circuit (see Supporting Information for circuit diagram and description), which sends a digital trigger to the speaker whenever the camera draws power from the battery pack to record a video.

Materials and methods

FIELD TEST LOCATIONS

We tested the ABR at three dramatically different field locations: Bwindi Impenetrable National Park in Uganda ('Bwindi'); Clayoquot Sound Biosphere Reserve, B.C., Canada ('Clayoquot'); and the Santa Cruz Mountains, California, USA ('Santa Cruz'). Field tests in Bwindi used only Mark 1 ABRs, and were conducted from 17 February to 3 April 2015 as part of a study testing the behavioural responses of animals to sounds associated with illegal hunting, i.e., humans and hunting dogs (B. Mugerwa *et al.* unpubl. data; Video S1). In Clayoquot, both Mark 1 and Mark 2 designs were tested. Clayoquot trials were conducted between 8 April and 27 August 2015 as part of a study testing the responses of other carnivores to cougars (J. Suraci *et al.* unpubl. data; Video S2). Santa Cruz field tests were conducted from 3 December 2015 to 19 March 2016 as part of a study on the behavioural responses of cougars to anthropogenic disturbances (J. Smith *et al.* unpubl. data; Wilmers *et al.* 2013; Smith, Wang & Wilmers 2015; Video S3), and used only Mark 2 ABRs. For full site descriptions and field methods, see Supplementary Methods and Table S1.

FIELD SET-UP

For all field tests, we used Moultrie M-990i camera traps (Moultrie Products, LLC, Alabaster, AL, USA) positioned at a height of 0·5–1 m (Fig. 1b) and programmed to record 30 s videos with a 5 s recovery time. In Mark 1 design trials, the standalone motion sensor was set to a consistent sensitivity level, and positioned immediately adjacent to the camera trap to maximize overlap with the camera's detection area (Fig. 1b). In all trials, the speaker was positioned 3 m from the camera trap (Fig. 1b) and broadcast 10 s playbacks at a volume of 80–90 dB at 1 m.

In Bwindi, ABRs were set 2 m from active game trails (to corral animals into view), baited with both food and a scent lure (see Supplementary Methods), and set to broadcast following a 10 s delay, permitting us to record both pre- and post-playback behaviour (Video S1). In Clayoquot, ABRs were set along shorelines at the level of the high tide line (0–3 m from the forest edge) to film intertidal foraging mammals. The large tidal fluctuations in Clayoquot meant that, at low tide it was often possible for animals to pass far from the ABR motion sensor at distances of up to 20 m, and that baiting was not possible, as the high tide would wash away any bait. Because no bait was used, ABRs in Clayoquot were set to broadcast after only a 1 s delay (Video S2). In Santa Cruz, we used the cougars' own deer kills as an attractant, deploying ABRs at sites where cougars cached a deer carcass the previous night (see Supplementary Methods). The camera trap connected to the ABR was positioned 3 m from the carcass, and a second camera trap not connected to the ABR was positioned 4 m from the carcass, opposite the camera trap with the ABR attached (Video S3). The ABRs here were set to broadcast following a 10 s delay. For additional details on field set-ups see the Supplementary Video Descriptions.

ABR SUCCESS METRICS

We considered any video of an animal to be a trial of the ABR's performance and calculated three success metrics: (1) *proportion triggered* - the proportion, out of all trials, in which the speaker triggered, broadcasting a playback; (2) *proportion observable* - the proportion, from among those trials in which the speaker triggered, in which the animal remained in view long enough for its response to the playback to be observed; and (3) *overall success rate* - the proportion, out of all trials, in which the speaker triggered *and* the animal remained in view long enough for its response to the playback to be observed. Note that in Mark 2 design trials, the *proportion triggered* necessarily equals 100% because the camera itself triggers the speaker and there thus cannot be a video without a playback, meaning the *proportion observable* and *overall success rate* are necessarily equivalent.

STATISTICAL ANALYSES – FACTORS AFFFECTING ABR SUCCESS

At both Bwindi and Clayoquot the ABRs were successful in quantifying the behavioural responses of a remarkably diverse array of species, which varied enormously in body size and occupied multiple ecological roles. For each species, we identified its average body mass and 'functional group', i.e. herbivore, carnivore or omnivore (See Supplementary Methods and Table S2). At Bwindi, one species of bird and multiple 'Unidentified small rodents' were recorded (Table S2), which we excluded from our analyses of the effects of species body mass, functional group, and pre-playback behaviour, on ABR performance (see Supplementary Methods).

We tested for differences in ABR success using the Mark 1 design between Bwindi and Clayoquot by performing chi-squared tests. To elucidate the causes of any such differences, we tested the effect of location (Bwindi vs. Clayoquot), species body mass, and their interaction, on each ABR success metric, using ANCOVAs (Table S3).

At Bwindi the ABRs were baited with food and a scent lure. To quantify whether animals were interested in these attractants a single

observer (BM) scored each animal's pre-playback behaviour as either 'foraging' (feeding, sniffing the bait) or not (vigilant, transiting). We calculated the proportion of trials in which each species was seen foraging and tested if this was associated with species body mass using a Spearman rank test. We then tested whether pre-playback 'foraging' predicted ABR success using binomial generalized linear mixed effects models (GLMM) that included pre-playback behaviour, species functional group and their interaction as fixed effects (Table S4).

Finally, we tested whether the Mark 2 design increased the *overall success rate* at Clayoquot in comparison to the Mark 1 design, using a chi-squared test. For full details on these statistical analyses, see Supplementary Methods.

Results

Using our new ABRs we successfully recorded hundreds of behavioural responses to playbacks at each of two remote, logistically challenging and dramatically different field sites (Bwindi, $n = 409$; Clayoquot, $n = 192$; Table S2), providing us with sample sizes that gave us plenty of statistical power to successfully test our research hypotheses regarding the behavioural responses of animals at Bwindi to sounds associated with illegal hunting (B. Mugerwa *et al.* unpubl. data) and interactions among carnivores at Clayoquot (J. Suraci *et al.* unpubl. data). The ABR provided a unique ability to experimentally test the behavioural responses of rare and cryptic species it would otherwise be virtually impossible to assess. We successfully recorded the behavioural responses of forest elephants (Video S5), chimpanzees (Video S6), African golden cats (Africa's least-known felid; Video S9), yellow-backed duikers (a forest antelope; Video S1), side-stripped jackals (Video S7), large-spotted genets (Video S8), and 11 other species in Bwindi; and black bears (Video S2), wolves (Video S10), raccoons (Video S11), mink (Video S12) and five other species in Clayoquot (Table S2).

'Corralling', and the use of attractants, both improved the probability of successfully recording a behavioural response to a playback. At Bwindi, ABRs were placed along game trails, effectively 'corralling' animals into range of the speaker motion sensor, and we also used edible bait and a scent lure as attractants to help keep animals in view long enough to ensure their responses were recorded (e.g. Video S1; see Supplementary Methods). We were unable to do either at Clayoquot and correspondingly every ABR success metric was significantly higher at Bwindi than Clayoquot (comparing trials at Bwindi vs. Mark 1 design trials at Clayoquot): *proportion triggered* (72% [Bwindi] vs. 58% [Clayoquot], $\chi^2_1 = 9{\cdot}49$, $P = 0{\cdot}002$); *proportion observable* (86% vs. 66%, $\chi^2_1 = 17{\cdot}56$, $P < 0{\cdot}001$); *overall success* rate (62% vs. 38%, $\chi^2_1 = 24{\cdot}26$, $P < 0{\cdot}001$; Table S2).

Passive motion sensors are more likely to detect larger species at a longer range, meaning corralling animals into range ought to help more in ensuring smaller species trigger the playback; thereby making the *proportion triggered* by smaller species more comparable to that of larger species. Where animals are induced to move directly in front of the ABR system, as at Bwindi, the *proportion triggered* ought to thus vary less with species body mass than where corralling is not used and animals can pass at much greater distances, as in Clayoquot. This is precisely the pattern we observed. Considering both sites together (all trials at Bwindi and Mark 1 design trials at Clayoquot) *proportion triggered* varied significantly less with species body mass at Bwindi than at Clayoquot (species body mass by location interaction, $F_{1,19} = 8{\cdot}19$, $P = 0{\cdot}010$; Table S3). Taking each site separately, *proportion triggered* did not vary significantly with species body mass at Bwindi ($F_{1,13} = 0{\cdot}35$, $P = 0{\cdot}564$), but did at Clayoquot ($F_{1,6} = 7{\cdot}74$, $P = 0{\cdot}032$) because at Clayoquot smaller species were less likely to trigger the playback (Tables S2 and S3).

Use of attractants can help ensure smaller species are kept in view long enough for their behavioural responses to the playback to be recorded, improving the *proportion observable*. At Bwindi there was no significant relationship between species body mass and *proportion observable* ($F_{1,12} = 1{\cdot}19$, $P = 0{\cdot}296$) but at Clayoquot there was ($F_{1,6} = 9{\cdot}84$, $P = 0{\cdot}020$; here considering Mark 1 design trials), because at Clayoquot the responses of smaller species were less likely to be recorded. As detailed below, this effect at Clayoquot results from larger species lumbering by at a slow enough pace that their responses are reliably recorded even in the absence of attractants (Video S2). At Bwindi, our use of attractants evidently successfully counteracted any resulting species body mass effect on *proportion observable*, because smaller species tended to be more interested in the attractants. All but one species (mountain gorillas) showed some interest, gauged by their 'foraging' prior to the playback (e.g. Video S1; see Supplementary Methods), and smaller species were apparently more interested, as there was a strong negative trend between species body mass and the proportion of trials in which animals were seen foraging prior to the playback (Spearman $r = -0{\cdot}51$, $P = 0{\cdot}052$).

Considering the Bwindi results irrespective of body mass, our use of attractants to help keep animals in view definitely increased the *proportion observable* as evidenced by this being significantly greater (Wald's $\chi^2_1 = 5{\cdot}26$, $P = 0{\cdot}022$) among animals interested in the attractants, i.e. those that 'foraged' prior to the playback (Video S1), compared to those that did not (Video S9). Our use of attractants was in fact so successful at helping keep animals in place it had the unexpected effect of slightly decreasing the *proportion triggered* among those seen foraging, because their slight movements while feeding were sometimes insufficient to trigger the speaker's motion sensor (as illustrated in Video S7; Table S4). This could easily be rectified by either: (1) increasing the fully adjustable sensitivity of the Mark 1 speaker motion sensor; or (2) using the Mark 2 design (see below). To interest as many different types of animals as feasible we used a combination of attractants (peanuts and dried fish; Supplementary Methods), and this was evidently successful, as there were no significant differences in ABR success metrics between herbivores, carnivores or omnivores (Functional group; Table S4).

Whereas, in the main, our use of attractants was very successful, there were exceptions, such as the African golden cat, which showed very little interest in the attractants (as illustrated in Video S9), the *proportion observable* and *overall*

success rate for this species consequently being disappointing low (Table S1). However, there is reason to expect the *overall success rate* for this species could be increased to well over 70%, by switching to use of the Mark 2 design and decreasing the delay setting to a minimum as done at Clayoquot. African golden cats were filmed for a median of 6 s (range = 1–16 s), and adopting these solutions at Clayoquot (see below) allowed us to achieve an *overall success rate* of 71% with animals (raccoons) filmed for a median of just 4·5 s (see Video S11).

Being unable to corral animals at Clayoquot, we developed the Mark 2 ABR design (Fig. 1), eliminating the speaker's standalone motion sensor and instead having the speaker's activation triggered by the camera's activation. The *proportion triggered* is thus eliminated as a variable because there is never a video recorded without the playback being triggered. Utilizing the Mark 2 design was successful in significantly increasing the *overall success rate* at Clayoquot from 38% to 75% ($\chi^2_1 = 41{\cdot}63$, $P < 0{\cdot}001$), resulting in a higher *overall success rate* than that achieved at Bwindi (62%, Table S2).

Being unable to use attractants at Clayoquot to help keep animals in view we decreased the delay before the playback sounded to just 1 s, rather than the 10 s delay used at Bwindi (Table S1). Large lumbering species like bears (see Video S2) took long enough to traverse the camera's field of view (median = 39 s, range = 3 to 71 s) that this reduction in the delay was largely unnecessary, and came at the cost of greatly reducing the ability to quantify pre- vs. post-playback changes in behaviour in a particular video (compare Videos S2 vs. S1). Smaller, faster-moving species, on the other hand, traversed the camera's field of view in much less than 10 s, raccoons being 'on camera' a median of 4·5 s (range = 1–20 s) and mink a median of just 1 s (range = 1–5 s), and minimizing the delay setting was thus indispensable to recording the responses of these species. This was remarkably successful, as the *proportion observable* was 71% for raccoons and 44% for mink (Table S2). Thus, even for a species (mink) on camera a median of just 1 s we succeeded in obtaining 27 interpretable trials over the course of the Clayoquot study (see Video S12).

By applying lessons learned from the Bwindi and Clayoquot field tests, we succeeded in achieving a 100% *overall success rate* in field trials on cougars in Santa Cruz. Firstly, we used the Mark 2 ABR design, thereby ensuring that the playback triggered in 100% of trials. Secondly, we were fortunate to be able to use a very strong attractant perfectly tailored to each individual because it was the cougar's own food cache, which kept the animal in view, allowing us to confidently use the ABR's delay setting to capture any *change* in the individual's behaviour between prior to and after the playback sounded (Video S3; see Supplementary Methods). Finally, we further improved the likelihood of recording the individual's response to the playback by adding a second camera (not attached to the ABR system) positioned to obtain a 360° view of the area around the cougar's food cache, which was indeed indispensable to observing the animal's response in some cases (Video S4; see Supplementary Methods and Supplementary Video Descriptions).

Discussion

Our results demonstrate that our new ABR provides the capacity to conduct a playback experiment anywhere a camera trap can be deployed, and that with simple adjustments in set-up, the design selected (Mark 1 vs. Mark 2), and settings used (e.g. 1 vs. 10 s delay; see Table S1), the behavioural response of virtually any species that can be 'caught' on a camera trap can be readily tested. We discovered many additional advantages during our field tests, the foremost being just how many successful trials we obtained (Table S2) using a modest number of ABRs ($n = 10$) deployed over relatively short periods (Bwindi 45 days, Clayoquot 141 days). The modest cost of each ABR (<$200) helped in making our multiple studies financially feasible. The portability of the ABRs, being no bigger and weighing no more than a standard camera trap, made deployment manageable where long hikes to sites were required, as at Bwindi and Santa Cruz. That no more skill is required than is necessary to turn on an mp3 player and speaker meant the ABRs could be deployed by field assistants with minimal training. The ABRs proved fully waterproof, and withstood attacks by bears (Video S2) and buffeting by elephants (Video S5), demonstrating the durability of the system in demanding field conditions. Finally, these attacks and buffetings reinforced the principal advantage the ABR provides in not needing to have an observer present, because we were able to test the behavioural responses of many potentially dangerous animals (bears, wolves, cougars and elephants) without any safety concerns.

Corralling, the use of attractants, and a second camera, can all provide effective means of increasing the successful use of the ABR, as illustrated at Bwindi and Santa Cruz, but equally importantly, our success at Clayoquot demonstrates that none of these is strictly necessary. The best means of maximizing the ABR's performance depends on the circumstances and species being studied, and the research question of interest. The Mark 2 design, for example, is not always the best choice because, with the Mark 2, everything that triggers the camera triggers the speaker, be it swaying vegetation or dappled sunlight, which could lead to the speaker broadcasting playbacks when no animal is present in front of the camera. The sensitivity of the Mark 1's standalone motion sensor is fully adjustable and can be lowered to reduce such unwanted triggering, potentially making the Mark 1 the better choice, e.g. at windy sites or where the species of interest is large and thus likely to be detected by the motion sensor even when its sensitivity is lowered. For additional suggestions on how to optimize ABR set-up for a particular field application, see the Supplementary Video Descriptions and Supplementary Discussion.

We successfully obtained ample data for us to statistically test our research hypotheses, and found significant results in all three of our experiments, enabling us to answer questions of broad importance in conservation biology (responses to anthropogenic disturbance; Caro 2007; Frid & Dill 2002; Francis & Barber 2013; Oriol-Cotterill *et al.* 2015) and wildlife ecology (interactions among large carnivores; Allen *et al.*

2015; Périquet, Fritz & Revilla 2015) it would otherwise have been infeasible to address without the use of our new ABR (Pimm *et al*. 2015). The majority of species at Bwindi responded aversively to cues from humans (e.g., Videos S5 and S6), indicative of the likely intensity of illegal hunting (McComb *et al*. 2014; Harrison *et al*. 2015), and cougars in Santa Cruz similarly responded aversively to anthropogenic disturbance (Wilmers *et al*. 2013; Smith, Wang & Wilmers 2015). The ability the ABR provides to conduct playback experiments without the need to have an observer present is the principal factor that made both these experiments feasible, because given their aversion to humans, the species in question would almost certainly avoid an observer, making it infeasible to directly test their aversion. Not needing to have an observer present is also what made the Clayoquot experiment feasible, not just because large carnivores are potentially dangerous, as noted above, but also because they occur at low densities and are thus infrequently present; with the result that the average interval between successful trials was 7 days (see Video S2).

Playback experiments can and have been used to test the behavioural responses of animals to an enormous range of sounds, including the vocalizations of other animals (Hettena, Munoz & Blumstein 2014; King 2015), and anthropogenic noises (Francis & Barber 2013); and camera traps provide the means to remotely observe virtually any animal in the wild (Hamel *et al*. 2013; Burton *et al*. 2015). By combining playbacks and camera trapping the ABR now provides the opportunity to experimentally test the behavioural response of virtually any animal to any sound; as our experiments in Uganda, Canada and the USA, testing the responses of elephants (Video S5), black bears (Video S2), chimpanzees (Video S6) and cougars (Video S3), help illustrate. It is precisely because it is the camera that is doing the 'trapping' that camera trapping has been so rapidly adopted in so many studies, since this can obviate the need to physically live-trap animals, which is often infeasible and undesirable, particularly in conservation applications, where the species of interest are typically rare, cryptic and endangered (Rowcliffe *et al*. 2011, 2012, 2014; Hamel *et al*. 2013; Burton *et al*. 2015; Heinicke *et al*. 2015; Weinstein 2015). In our USA experiment, the cougars we studied had been live-trapped to fit them with GPS collars and the collar could have conceivably been equipped with some device to remotely trigger a playback (e.g., Lendvai *et al*. 2015), but this was not possible in our experiments in Uganda and Canada, where live-trapping endangered forest elephants, for example, was neither feasible nor desirable. Live-trapping necessarily requires one or more observers to be present. The ABR is specifically designed for use in conjunction with camera trapping precisely because of the capacity camera trapping affords to study virtually any animal anywhere without the need to have an observer present.

Directly experimentally testing the reactions of animals to the stimulus of interest solves many of the problems identified with the current use of camera trapping in attempting to understand how animals respond to humans, predators or competitors (Bridges & Noss 2011; Rowcliffe *et al*. 2012, 2014; Burton *et al*. 2015). The ABR thus not only greatly expands the range of research questions that can be addressed by conservation biologists and wildlife ecologists, but also qualitatively improves the strength of the inferences supporting the resulting answers and the rigour of the resulting conclusions (Zanette *et al*. 2011; Suraci *et al*. 2016).

Author's contributions

J.P.S., M.C., L.Y.Z. and M.D. conceived of, designed, and developed the ABR system. J.P.S., M.C., B.M., D.W.M., J.A.S., C.C.W. and L.Y.Z. conceived of the field tests. J.P.S., B.M. and J.A.S. carried out the fieldwork, with help from M.C., L.Y.Z. and C.C.W. J.P.S. conducted the statistical analyses. J.P.S. and M.C. led the writing of the manuscript, with critical input from all authors.

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Data accessibility

All data required to replicate the analyses in this article are available in the supplementary information (Supplementary Table S2 and Data S1).

References

Ahumada, J.A., Silva, C.E.F., Gajapersad, K. *et al*. (2011) Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **366**, 2703–2711.

Allen, M.L., Elbroch, L.M., Wilmers, C.C. & Wittmer, H.U. (2015) The comparative effects of large carnivores on the acquisition of carrion by scavengers. *American Naturalist*, **185**, 822–833.

Bridges, A.S. & Noss, A.J. (2011) Behavior and activity patterns. *Camera Traps in Animal Ecology: Methods and Analyses* (eds A.F. O'Connell, J.D. Nichols & K.U. Karanth), pp. 57–70. Springer, Tokyo, Japan.

Brook, L.A., Johnson, C.N. & Ritchie, E.G. (2012) Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology*, **49**, 1278–1286.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E. & Boutin, S. (2015) Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, **52**, 675–685.

Caro, T. (2007) Behavior and conservation: a bridge too far? *Trends in Ecology & Evolution*, **22**, 394–400.

Clinchy, M., Schulkin, J., Zanette, L.Y., Sheriff, M.J., McGowan, P.O. & Boonstra, R. (2011) The neurological ecology of fear: insights neuroscientists and ecologists have to offer one another. *Frontiers in Behavioral Neuroscience*, **5**, 21.

Durant, S.M. (2000a) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.

Francis, C.D. & Barber, J.R. (2013) A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment*, **11**, 305–313.

Frid, A. & Dill, L.M. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 11.

Hamel, H., Killengreen, S.T., Henden, J.-A., Eide, N.E., Roed-Eriksen, L., Ims, R.A. & Yoccoz, N.G. (2013) Towards good practice guidance in using camera-traps in ecology: influence of sampling design on validity of ecological inferences. *Methods in Ecology and Evolution*, **4**, 105–113.

Harrison, M., Baker, J., Twinamatsiko, M. & Milner-Gulland, E.J. (2015) Profiling unauthorized natural resource users for better targeting of conservation interventions. *Conservation Biology*, **29**, 1636–1646.
Heinicke, S., Kalan, A.K., Wagner, O.J.J., Mundry, R., Lukashevich, H. & Kühl, H.S. (2015) Assessing the performance of a semi-automated acoustic monitoring system for primates. *Methods in Ecology and Evolution*, **6**, 753–763.
Hettena, A.M., Munoz, N. & Blumstein, D.T. (2014) Prey responses to predator's sounds: a review and empirical study. *Ethology*, **120**, 427–452.
King, S.L. (2015) You talkin' to me? Interactive playback is a powerful yet underused tool in animal communication research. *Biology Letters*, **11**, 20150403.
Lendvai, A.Z., Akçay, Ç., Weiss, T., Haussmann, M.F., Moore, I.T. & Bonier, F. (2015) Low cost audiovisual playback and recording triggered by radio frequency identification using Raspberry Pi. *PeerJ*, **3**, e877. doi:10.7717/peerj.877
Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
McComb, K., Pusey, A., Packer, C. & Grinnell, J. (1993) Female lions can identify potentially infanticidal males from their roars. *Proceedings of the Royal Society of London B: Biological Sciences*, **252**, 59–64.
McComb, K., Shannon, G., Sayialel, K.N. & Moss, C. (2014) Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. *Proceedings of the National Academy of Sciences*, **111**, 5433–5438.
O'Connell, A.F. & Bailey, L.L. (2011) Inference for occupancy and occupancy dynamics. *Camera Traps in Animal Ecology: Methods and Analyses* (eds A.F. O'Connell, J.D. Nichols & K.U. Karanth), pp. 57–70. Springer, Tokyo, Japan.
Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C. & Macdonald, D.W. (2015) Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, **124**, 1263–1273.
Périquet, S., Fritz, H. & Revilla, E. (2015) The Lion King and the Hyaena Queen: large carnivore interactions and coexistence. *Biological Reviews*, **90**, 1197–1214.
Pimm, S.L., Alibhai, S., Bergl, R., Dehgan, A., Giri, C., Jewell, Z., Joppa, L., Kays, R. & Loarie, S. (2015) Emerging technologies to conserve biodiversity. *Trends in Ecology and Evolution*, **30**, 685–696.
Rowcliffe, J.M., Carbone, C., Jansen, P.A., Kays, R. & Kranstauber, B. (2011) Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution*, **2**, 464–476.
Rowcliffe, J.M., Carbone, C., Kays, R., Kranstauber, B. & Jansen, P.A. (2012) Bias in estimating animal travel distance: the effect of sampling frequency. *Methods in Ecology and Evolution*, **3**, 653–662.
Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C. & Jansen, P.A. (2014) Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, **5**, 1170–1179.
Schmitz, O.J. (2010) *Resolving Ecosystem Complexity (MPB-47)*. Princeton University Press, Princeton, NJ, USA.
Smith, J.A., Wang, Y. & Wilmers, C.C. (2015) Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society of London B: Biological Sciences*, **282**, 20142711.
Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y. (2016) Fear of large carnivores causes a trophic cascade. *Nature Communications*, **7**, 10698.
Thuppil, V. & Coss, R.G. (2015) Playback of felid growls mitigates crop-raiding by elephants *Elephas maximus* in southern India. *Oryx*, **50**, 329–335.
Webster, H., McNutt, J.W. & McComb, K. (2012) African wild dogs as a fugitive species: playback experiments investigate how wild dogs respond to their major competitors. *Ethology*, **118**, 147–156.
Weinstein, B.G. (2015) MotionMeerkat: integrating motion video detection and ecological monitoring. *Methods in Ecology and Evolution*, **6**, 357–362.
Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V. & Williams, T. (2013) Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS ONE*, **8**, e60590.
Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M. (2011) Perceived predation risk reduces the number of offspring songbirds produce per year. *Science*, **334**, 1398–1401.

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Supporting Information

Details of electronic Supporting Information are provided below.

Circuit Diagram. Diagrams, written descriptions and component lists for the two custom-built circuits used in the ABR (the speaker microcontroller and the camera current detector).

Program "Motion". Custom program (written in C) for specifying the range of ABR speaker duration and delay values.

Table S1. Summary of the three experiments described in the main text, which provided the first field tests of the functionality and performance of the ABR.

Table S2. Species from which trials were obtained during field tests of the ABR in Bwindi and Clayoquot.

Table S3. Results from ANCOVAs testing the effects of location (Bwindi vs. Clayoquot) and species body mass on ABR success metrics, considering trials using the Mark 1 design.

Table S4. Results from Generalized Linear Mixed Effects Models testing the effects of pre-playback behaviour and functional group (herbivore, carnivore or omnivore) on ABR success metrics at Bwindi.

Supplementary Methods and Discussion: Includes additional details on study sites and experimental design for the three field tests and further details on the statistical analyses presented in the main text. Additional suggestions for optimizing ABR performance are also discussed.

Video Descriptions: Descriptions of Videos S1 to S12, illustrating aspects of the videos relevant to optimizing performance of the ABR in the field.

Data S1. Data used in analysing the effect of attractants on ABR performance (i.e., the analysis presented in Table S4).

Supplementary Videos. See Video Descriptions file for detailed descriptions.

Video S1. Yellow-backed duiker – Bwindi.

Video S2. Black bear – Clayoquot.

Video S3. Cougar – Control Playback – Santa Cruz.

Video S4. Cougar – Dog Playback – Santa Cruz.

Video S5. Elephant – Bwindi.

Video S6. Chimpanzee – Bwindi.

Video S7. Side-striped jackal – Bwindi.

Video S8. Large-spotted genet – Bwindi.

Video S9. African golden cat – Bwindi.

Video S10. Grey wolf – Clayoquot.

Video S11. Raccoon – Clayoquot.

Video S12. Mink – Clayoquot.