1 **Suitability of acoustics as non-lethal deterrents for macropodids: the**

2 **influence of origin, delivery, and anti-predator behaviour**

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12 Short-title: Acoustic deterrents for macropodids

13

1 Abstract

2 **Context.** Auditory devices used to deter wildlife are a potentially humane and effective

3 way of minimising deleterious interactions with humans and their livelihoods and have

4 been used successfully for many species around the world. Acoustic cues can be used to

5 manipulate anti-predator behaviour, encouraging animals to forage elsewhere. Employing

6 acoustics derived from natural sources to make use of innate behavioural responses has

7 been suggested to outperform novel or artificial sounds, however, anti-predator strategies

8 vary among sympatric species and will influence the utility of acoustic stimuli for deterring

9 wildlife.

10 **Aims.** We aimed to test the interaction between the source of origin (natural or novel) and

11 species traits (anti-predator strategy – grouping behaviour) on the efficacy of using acoustic

12 stimuli to elicit alarm responses for two species in the family Macropodidae commonly

13 associated with browsing on forest plantation seedlings; the red-necked pademelon

14 (*Thylogale thetis*) and the red-necked wallaby (*Macropus rufogriseus banksianus*).

15 **Methods.** We tested these factors in captivity using playback experiments of acoustic

16 stimuli and monitored the behavioural responses of subjects.

17 **Results.** Red-necked pademelons exhibited strong responses to bioacoustic and novel

18 stimuli but did not greatly differentiate amongst them. Short-term habituation to predator

19 calls was detected but responsiveness to novel sounds increased. Red-necked wallabies

20 most strongly responded to conspecific distress calls, showing no sign of short-term

21 habituation.

1   **Conclusions.** Results from this and other studies suggest that bioacoustic deterrents,

2   particularly those utilising natural conspecific sounds aimed at communicating danger,

3   have the potential to play an important role in non-lethal wildlife management, but that

4   responsiveness varies with the form of anti-predator strategies employed.

5   **Implications.** If alarm responses translate into subjects vacating targeted areas then there is

6   some potential to implement non-lethal acoustic deterrents for macropodids alongside other

7   management measures aimed at preventing impacts on primary production.

8   Problematically, our experiments showed that without accurate acoustic delivery,

9   particularly of sounds with infrasonic components, the development of effective

10   bioacoustic deterrents may remain stymied.

11   *Key words*: bioacoustics, alert behaviour, non-lethal management, *Macropus rufogriseus*

12   *banksianus*, *Thylogale thetis*, conspecific signalling, species traits

13

1   Introduction

2   As the global trend of human population increase intensifies the need to secure and

3   maximise resource production, conflict resolution between primary industries and

4   biodiversity conservation will become increasingly important. Wildlife often struggle to

5   maintain viable populations in modified and fragmented landscapes (Hobbs 2005) and can

6   unwittingly cause conflict when they seek additional resources from land allocated to

7   production. There is therefore great need to foster both environmental and production

8   sustainability, maximising the long term persistence of wildlife in a manner that conforms

9   to societal expectations of environmental and human well-being (Hassan *et al.* 2005;

10   Pereira *et al.* 2005) and the ethical treatment of animals (Bekoff 2010).

11   Traditional approaches to minimising wildlife interactions with agricultural and forestry

12   industries have focussed on the poisoning and shooting of both native and non-native

13   species (e.g. Choquenot and Warburton 2006). There is, however, increasing pressure to

14   develop non-lethal control methods that reduce economic loss to industries using

15   sustainable and humane strategies (Reiter *et al.* 1999; Eason *et al.* 2010). One such

16   technique is the use of deterrents, which act to discourage the target species from accessing

17   a specific area. Although research remains in its infancy (Eason *et al.* 2010) and has

18   generally proven ineffective (e.g. Bender 2003; VerCauteren *et al.* 2005; Brown *et al.*

19   2006; Ramp and Croft 2006; Edgar *et al.* 2007), a number of successful cases exist (Maes

20   *et al.* 2004; Baker *et al.* 2005; Graham *et al.* 2009; Gotz and Janik 2010). When targeted

21   towards biologically-relevant behavioural repertoires, the potential for developing effective

22   deterrents appears plausible. More often than not, the weak link in experimentation appears

1   to be the ability to deliver the stimulus in an appropriate manner. Applying cues singly and

2   in isolation from other cues may lead to an estrangement from the behavioural process

3   (Lima and Dill 1990).

4   Recent research has focused on exploiting an animal's sensory system to produce aversive

5   behaviour. Current deterrents include visual (Schafer and Penland 1985; Ramp and Croft

6   2006) and chemical deterrents (Atkinson and MacDonald 1994; Marks *et al.* 1995; Ramp *et*

7   *al.* 2005), with taste-aversion successfully used to reduce mammal browsing on forestry

8   plantations (Marks *et al.* 1995). Acoustic deterrents, in particular, tend to be non-intrusive

9   and have little or no adverse effects on animals. Novel sounds that may shock or startle

10   have been used to deter a variety of bird (Stickley *et al.* 1972), marine (Mueller-Dombois

11   and Ellenberg 1974; Knudsen *et al.* 1997; Kastelein *et al.* 2005) and mammal species

12   (Sprock *et al.* 1967; Macedonia and Yount 1991; Weary and Kramer 1995; Slobodchikoff

13   2002; Searcy and Caine 2003; Gilsdorf *et al.* 2004). In contrast, research using bioacoustics

14   as deterrents is limited (but see Biedenweg *et al.* 2011). Bioacoustic sounds may originate

15   from conspecifics as a warning to other individuals (or directed towards a perceived threat),

16   from heterospecifics with the same purpose, or may originate from predators (e.g. canid

17   howls). Given their biological and ethological origins, the use of bioacoustics as deterrents

18   would appear to be a fruitful area of research.

19   In Australia, species within the family Macropodidae (kangaroos, wallabies and rat-

20   kangaroos) are frequently targeted for control to prevent grazing and browsing damage to

21   agricultural crops and forestry plantations (Pietrzykowski *et al.* 2003). Many thousands of

22   animals are killed each year for this purpose, creating desire to find sustainable, humane

1   and cost-effective alternatives (Wiggins *et al.* 2010; Wiggins and Bowman 2011). Many

2   species in the family utilise vocalisations (Croft 1981; Coulson 1989) and have highly

3   developed anti-predator strategies (Blumstein *et al.* 2002). However, the specific form of

4   the anti-predator strategy employed may strongly influence the suitability of acoustic

5   deterrents for eliciting alarm responses. In particular, grouping behaviour, or lack thereof,

6   may determine the utility of different acoustic stimuli. Acoustic behaviour in the

7   Macropodidae requires further exploration and we address this knowledge gap by

8   examining the behavioural responses of two species of macropodids in captivity to seven

9   different bioacoustic and novel stimuli (two predator, three conspecific, one novel, and one

10 benign). We contrasted findings according to five different behavioural responses. We

11 hypothesised that vigilance responses would be strongest for bioacoustic stimuli,

12 particularly when originated from a conspecific. We highlight experimental difficulties in

13 the delivery of bioacoustic stimuli that require further investigation to enable bioacoustics

14 to potentially become a supplemental, non-lethal management tool.

15 **Methods**

16 *Study species and location*

17 We chose to study red-necked pademelons (*Thylogale thetis*) and red-necked wallabies

18 (*Macropus rufogriseus banksianus*) as they are close relatives of species that result in high-

19 profile conflict with plantation forests and agricultural practices in Tasmania (Wiggins *et*

20 *al.* 2010). Red-necked pademelons are sexually dimorphic, with males weighing an average

21 of 7 kg and females 4 kg (Strahan 2002). Pademelons are generally edge-specialists that

1   utilise open habitat adjoining dense forest for foraging at night, feeding on grasses and

2   herbs (Johnson 1980; Wahungu *et al.* 2001; Le Mar and McArthur 2005; While and

3   McArthur 2005). To reduce predation risk, red-necked pademelons forage in larger groups

4   and allocate more time to vigilance with increasing distance from cover (Wahungu *et al.*

5   2001; Pays *et al.* 2009). Red-necked wallabies are also sexually dimorphic but considerably

6   larger (males average 18.6 kg while females average 13.8 kg) (Strahan 2002). Like

7   pademelons, they forage on grasses and herbs in open habitats adjacent to forest cover.

8   Although they can sometimes forage in groups at night, they are mostly solitary.

9   The study was conducted at Cowan Field Station, 44-km north of Sydney and adjacent to

10 Muogamarra Nature Reserve (33º37'35"S, 151º09'20"E). Subjects were bred in captivity

11 and therefore can be considered predator naïve (Blumstein *et al.* 2000). However, wedge-

12 tailed eagles (*Aquila audax*) have been known to take animals from Cowan on occasion,

13 and domestic and wild dogs roam the adjacent reserve. Ten adult captive pademelons (4♂

14 6♀) and 14 adult wallabies (7♂ 7♀) were used in experiments. Subjects were tested

15 individually in one of two similarly-sized fenced enclosures (112 m^2 and 108 m^2, both

16 approximately 16 m by 7 m), each constructed of 2-m high chain-mesh fencing. To reduce

17 external stimuli, fences were covered with a 1-m high band of 60% Sarlon green shade

18 cloth. A viewing hide was placed at one end and covered with a 2-m high section of shade

19 cloth. Triangles of shade cloth were hung horizontally across three corners of each

20 enclosure to create cover, and a plastic shelter at one end provided additional cover. Food

21 and water were available *ad libitum*.

Acoustic recording and playback

Each subject was tested individually with six (pademelon) or seven (wallaby) different acoustic stimuli. We obtained six bioacoustic stimuli with different origins: two conspecific sounds (distress calls and foot-thumps), one heterospecific sound (distress call), two predator sounds (dingo howl, eagle call) and one benign control sound (magpie call). We obtained one novel sound (gunshot).

High-quality speakers (Behringer Truth B2031A) were placed at one end of the enclosure and stimuli were broadcast at amplitudes of 70-80 dB one meter in front of the speaker. Delivery was made using a Dell® notebook computer and a Tascam US122 USB Audio/MIDI interface. As the perception of sound by macropodids is poorly understood, all recording and broadcast equipment was chosen to maximise sound quality. An Audio Technica 835A microphone was used as it is sensitive to a broad frequency range (30-20,000 Hz) and has a flat frequency response. This means the microphone is equally sensitive to all frequencies, with no frequencies exaggerated or reduced, resulting in an accurate representation of the original sound. Likewise, the Behringer 2031A speakers used broadcast a broad frequency range (50-21,000 Hz), also with a flat response. Basic speakers designed for home entertainment tend to exaggerate low frequencies.

To reduce the loss of sound components that are undetectable by the human ear, acoustic stimuli were recorded and broadcast at a high sample rate and sample size. The sample rate is the number of samples of a sound that are taken per second, while the sample size is the precision with which a sample represents the actual amplitude of the sound (Charif *et al.*

1   1995). All recordings for this experiment were taken at a sample rate of 48 kHz and sample

2   size of 32-bit (compared with 44.1 kHz and 16-bit sample size for CD-quality audio).

3   In addition, amplitude was taken using a 'C' weighting rather than the more commonly

4   used 'A' weighting. Weighting functions are used to adjust the qualitative measurement of

5   sounds occurring in the real world to that which is perceived by the human ear (Aude

6   1998). A-weighted decibel measures compensate for the difference between perceived

7   performance and measured performance (Aude 1998). A C-weighted decibel measure has a

8   relatively flat response, so gives a measurement much closer to the actual loudness of a

9   sound and minimises assumptions about the acoustic capabilities of pademelons and

10   wallabies.

11   Dingo howls, foot thumps and distress calls were recorded using a digital Audio Technica

12   835A microphone attached to a Dell notebook computer via a Tascam US122 USB

13   Audio/Midi interface (48 kHz, 32-bit). Recordings of foot-thumps given by adult wallabies

14   were made at distances of 2-20 m. Dingo howls were recorded from captive animals at

15   Taronga Zoo, Sydney. Distress calls were obtained by either gently holding the tail of a

16   pademelon or by restraining it in a hessian sack. Adult wallabies did not elicit distress calls

17   despite many attempts without deliberately causing discomfort. However, a distress call of

18   a young-at-foot was obtained by gently holding the animal by the tail free of the ground for

19   a few seconds. Gunshot sounds were obtained online (22.05 kHz, 16-bit), and Australian

20   magpie and wedge-tailed eagle calls were obtained from commercial recordings

21   (Buckingham and Jackson 1985; Buckingham and Jackson 1999). All sounds were edited

22   to create a stimulus with a total duration of five seconds. Three individual gunshots and

1 foot thumps were included in each five-second stimulus, and a natural five-second sample

2 was taken from continuous recordings of distress calls, magpie calls, wedge-tailed eagle

3 calls and dingo howls. Sounds were edited using Adobe Audition 1.5 (Adobe Systems

4 Incorporated 2004). The order in which the different stimuli were given to each individual

5 was randomised. Two or three different exemplars of each stimulus sound were used during

6 playback.

7 Pademelons and wallabies were given at least 24 hours to acclimatise to their new

8 enclosure before commencing experiments. Each acoustic stimulus was broadcast over a

9 one-hour experimental period, either in the early morning (< 5 hours after sunrise) or late

10 afternoon (< 3.5 hours before sunset). During the one-hour experimental period a five

11 second recording of the stimulus sound was broadcast at five-minute intervals (i.e. 12

12 replicate broadcasts for each subject). Each individual was tested every morning and

13 afternoon (weather dependent) until all seven stimuli had been broadcast to the test subject.

14 Before playback commenced fresh grass was placed in the centre-rear of the enclosure to

15 encourage wallabies to move towards the middle of the enclosure. After placing the grass

16 within the enclosure the experimenter positioned themselves behind a hide overlooking the

17 enclosure and remained quiet for 20 minutes before commencing playback.

18 *Subject responses*

19 Behavioural responses to stimuli were captured using digital footage, recorded for 30

20 seconds prior to and following the sound broadcast. To simplify analyses, we quantified the

21 proportion of time allocated to (a) three different behaviours categories – alert (actively

22 monitoring its environment), other (feeding, hopping, walking, or grooming), and inactivity

1   and (b) two different vigilance levels – heightened vigilance (attentive, body rigid, upright,

2   eyes wide) and attention to the sound source (face oriented within 20° towards the speaker).

3   The proportion of time allocated to these behaviours was calculated for each 30 second

4   interval prior to and after the stimulus broadcast using the computer program Observer 5.0

5   (Noldus Information Technology 2003).

6   *Data analysis*

7   A mixed modelling approach was used to allow for nesting as individual subjects were

8   tested every five minutes over one hour. A generalised additive mixed model was run for

9   each behaviour category, with subject specified as a random variable and sound and time

10 (smoothed) as fixed variables. An autoregressive correlation structure of order one was

11 added to accommodate for the lack of temporal independence. Short-term habituation to

12 acoustic stimuli was examined by incorporating the time of the sound broadcast (in

13 minutes) as a dependent variable in the models. Sound was treated as a factor with the

14 Australian Magpie set as the reference level to ensure behavioural responses were

15 compared to the baseline response of a non-threatening natural sound. Models were run for

16 each species separately in R (version 2.12.1) using the 'mgcv' package (R Development

17 Core Team 2008). Models were run using the difference in the proportion of time spent per

18 30 seconds engaged in each behaviour type across trials before and after the sound

19 broadcast. As we were interested in whether the mean time allocated to a particular

20 behaviour change after the broadcast, we only included non-zero scores (i.e. we ignored

21 sample points where a behaviour type was not engaged in within either 30 second period).

1 **Results**

2 *Spectral analysis of stimuli*

3 Recorded foot thumps had very short durations (less than 0.2 seconds), encompassed a

4 broad frequency range, and exhibited energy greater than 1 kHz (Fig. 1). Lower limits of

5 foot thumps dropped below 50 Hz although the exact lower range is uncertain as the

6 microphone had a minimum frequency of 30 Hz and at this frequency there is overlap with

7 background noise. We were unable to detect infrasonic sound (lower than 20 Hz) with the

8 available equipment and it is plausible that the behavioural cue may come from sounds in

9 this range. Distress call recordings consisted of three to four separate distress 'grunts' (each

10 of duration 0.2 to 0.35 seconds), interspersed with four to six sharp breaths (0.15 to 0.2

11 seconds). They encompassed a broad frequency range with most of the energy between 200

12 Hz and 2 kHz.

13 Two types of call were included in the wedge-tailed eagle broadcast. The first was a shrill

14 disyllabic whistle (Marchant and Higgins 1993), approximately one second long with

15 complex harmonic structure and bands lying between 500 Hz and 7 kHz. The second was a

16 high wavering whistle (Marchant and Higgins 1993), with rapidly repeated elements of

17 total duration two seconds at 3 to 4 kHz. Dingo howls consisted of three to four dingoes

18 howling in unison, each howl approximately 1.8 to 3 seconds in duration, with complex

19 harmonic bands at 400 Hz gradually attenuating up to 15 kHz. Magpie song was a complex

20 combination of different elements of duration 0.1 to 0.7 seconds, most with distinct

21 harmonic bands between 500 Hz and 11 kHz.

1   Gunshots were of sudden onset, had short durations lasting approximately 0.3 seconds and

2   exhibited reverberation up to 0.5 seconds. Recordings encompassed a broad frequency

3   range but with much of the energy less than 2 kHz.

4   *Acoustic playback - red-necked pademelons*

5   Post-broadcast, there were increases in the mean time spent alert across all presented

6   acoustic stimuli, regardless of origin (mean response increases between 19 and 32%) (Fig.

7   2). This included the magpie broadcast (27%), which was intended to be a familiar and

8   non-threatening sound. Consequently, no other acoustic stimuli significantly differed in

9   their increase in alert response, although the greatest mean response (32%) was recorded in

10   response to the dingo call (Table 1a). When aggregated together, post-broadcast responses

11   to acoustic stimuli resulted in reductions of behaviours such as grooming, feeding and

12   movement. All stimuli resulted in some reduction, although the greatest reduction (-20%)

13   occurred in response to the distress call of a conspecific. Inactivity in response to acoustic

14   stimuli was observed to decline post-broadcast for all stimuli except the distress call by a

15   conspecific, where a 9% increase in mean response was recorded. Little response in activity

16   to the magpie broadcast occurred, while the greatest decline in inactivity occurred in

17   response to the dingo broadcast (-18%), significant at the 0.01 level.

18   The shift in alert behaviour was further examined by recording heightened levels of

19   vigilance (becoming upright) and attention (face towards the sound source). All acoustic

20   stimuli led to increases in vigilance state post-broadcast (mean responses between 19 and

21   27%), including a 23% increase to the magpie control stimulus (Fig. 3). The greatest mean

22   responses were recorded in response to the dingo call and foot thump stimuli. Likewise, all

1 stimuli resulted in increases in attention post-broadcast. The magpie broadcast elicited the

2 greatest change in mean response (17%), followed the dingo call (16%) and foot thumps

3 (13%). The change in response to eagle calls and gun shots were significantly lower than

4 that observed to the magpie broadcast.

5 Short-term habituation effects in the change in mean response post-broadcast were

6 experienced across each of the three behaviour and two vigilance categories, although alert

7 and vigilance were only significant at the 0.01 level (Table 1a). By examining the change in

8 mean response across subjects over time, rapid habituation to the dingo calls and foot

9 thumps was evident, with a 93% mean change in alert behaviour at first dingo broadcast

10 declining rapidly to a 13% mean increase in alert behaviour at the end of the hour of trials

11 (Fig. 4). Foot thump responses declined from over 50% increases after the first two

12 broadcasts to below 10% for the remaining broadcasts. No clear patterns were evident for

13 distress calls or magpie calls, with variability high, however, there were apparent increases

14 in responsiveness to eagle calls and gunshots.

15 *Acoustic playback - red-necked wallabies*

16 Unlike the red-necked pademelon, the magpie broadcast was relative benign to the red-

17 necked wallaby, resulting in little change in any form of behaviour (Fig. 2). Significant

18 increases in the mean time spent alert post-broadcast were therefore recorded for dingo

19 calls (10% mean increase), conspecific distress calls (19% mean increase) and gunshots

20 (9% mean increase), relative to the magpie broadcast (0% mean increase) (Table 1b).

21 Likewise, conspecific distress calls resulted in a significant mean decrease in non-alert

22 behaviours (-12%) relative to the magpie broadcast, although no other stimuli resulted in

significant declines. Inactivity also significantly declined post-broadcast for conspecific distress calls (-21%) and gun shots (-20%), although dingo and eagle calls also resulted in decreases (-10% and -9% respectively).

Heightened vigilance and attention were both relatively unaffected by the broadcast of the magpie call, the control stimulus (Fig. 3). The greatest mean increase in time spent vigilant occurred after eagle calls (10%) (significant at the 0.01 level), dingo calls and gun shots (both 8%), but the latter two were not significantly different from the magpie response (Table 1b). Changes in attention to the sound source occurred after the conspecific distress call (19%) which was significantly different from the magpie response. Other acoustic stimuli resulted in very similar increases in mean change in time allocated to attention post-broadcast (between 7% and 10%).

No short-term habituation was detected in alert, other or inactivity behaviour (Table 1b). Changes in mean response were lower than those exhibited by red-necked pademelons, hence variability in responses across time prevented the detection of any significant trends. However, suggestions of weak declines in alert response were observed for dingo, eagle, foot thump and gunshot broadcasts (Fig. 4). In contrast, mean responses to conspecific distress calls were constant across the sampling period, suggesting that habituation to these broadcasts did not occur and responses were stable. Declines in time allocated to heightened vigilance and attention behaviour were detected, although patterns were very similar to trends exhibited in alert response.

Discussion

Captive red-necked pademelons and red-necked wallabies responded to acoustic stimuli by increasing the time spent engaged in alert behaviour post-broadcast. Correspondingly, other behavioural activities, such as inactivity, declined. Pademelons were overall more responsive in eliciting alert behaviour than wallabies, although they appeared to not distinguish greatly among different acoustic stimuli. Despite not greatly altering responses post-broadcast, wallabies did distinguish among stimuli, responding greatest to conspecific distress calls. Along with recent findings for western grey kangaroos (*Macropus fulignosus*) (Biedenweg *et al.* 2011) and previously for tammar wallabies (*Macropus eugenii*) and red-necked pademelons (Blumstein *et al.* 2000; Blumstein *et al.* 2002), these findings confirm that species in the Macropodidae utilise acoustic stimuli to assess threat risk and that acoustic stimuli may therefore have some potential as part of deterrent measures in wildlife-human conflict situations. However, here we were further concerned with whether acoustic stimuli that were biological in origin, including from predators, conspecifics and heterospecific, would elicit different responses than novel or benign stimuli.

Red-necked pademelons have previously been shown to be non-selective in responding to a similar variety of acoustic stimuli (Blumstein *et al.* 2002), a finding confirmed in this study. Unlike wallabies who ignored the broadcast of the benign control stimulus, pademelons elicited similar responses to the magpie broadcast as for other acoustic stimuli. Surprisingly, the novel startle sound of the gun shot either did not result in a different response by pademelons to the magpie or responses were less (i.e. attention behaviour). The gun shot did, however, significantly increase alert behaviour (also observed in heightened

vigilance) and decrease inactivity in wallabies, when compared to the magpie control. Overall, under the conditions tested our novel sound did not elicit any change in response for either species that reflects suitability for use as a deterrent. In contrast, conspecific distress, dingo and eagle calls all resulted in significant changes in behaviour. Using responses to the Australian magpie as a baseline, pademelons similarly responded to all forms of acoustics presented, including the supposed benign control, while wallabies responded mostly to conspecific acoustics (although not heterospecific acoustics) and only mildly to predator and novel acoustics.

Blumstein *et al.* (2000) reported that tammar wallabies (*Macropus eugenii*) on Kangaroo Island were sensitive to sounds made by conspecifics but not those made by predators. Here we report that predator sounds, namely dingo calls, elicited strong alert responses in pademelons but not different from the control, and significant but weaker responses in wallabies. Predator calls are frequently employed to communicate to conspecifics and prey may eavesdrop on these vocalisations to provide them with information on the threat and location of predators (Ito and Mori 2010). Similarly, alarms signals are a fundamental process by which conspecifics communicate about dangers associated with potential predator attacks. Alarm call theory predicts several purposes for these signals, including communicating about dangers to individuals of the same species (conspecifics) or communicating to the predator that it has been seen such that successful capture is unlikely (Shelley and Blumstein 2005). For these reasons, non-lethal deterrents for macropodids based on bioacoustics provide considerable promise but will inevitably be species and situation specific, and directly influenced by grouping behaviour.

1   Both distress calls and foot-thumps are typically produced when macropodid individuals

2   are in danger, such as when confronted by a predator. Coughing as a sign of fear,

3   submission, or increased level of excitement has been documented in red kangaroos

4   (*Macropus rufus*) (Croft 1981), whip-tailed wallabies (*Macropus parryi*) (Kaufmann 1974),

5   and eastern grey kangaroos (*Macropus giganteus*) (Kaufmann 1975; Coulson 1997), and

6   alarm vocalisations have been recorded in two potoroids and two wallaroos (Coulson

7   1989). When startled, the rufous bettong (*Aepyprymnus rufescens*) was observed to utter a

8   low, short hissing sound combined with foot-thumping, which caused individuals nearby to

9   become alert, and when fleeing for cover made a long hissing sound, combined with foot-

10   thumping, which caused others also to flee (Johnson 1980). As a further example, isolation

11   calls from dependent young in eastern grey kangaroos can convey information such as the

12   caller's identity and location (Baker and Croft 1993). Such behavioural responses suggest

13   vocalisations such as these have the potential to be incorporated into a bioacoustic

14   deterrent. Use of distress vocalisations have produced similar results in species from other

15   families, such as eastern chipmunks (*Tamias striatus*) (Weary and Kramer 1995) and black-

16   crowned night herons (*Nycticorax nycticorax*) (Spanier 1980), in the latter case successfully

17   deterring animals from using a regular roost site.

18   A foot-thump is considered an acoustic signal as it is visually inconspicuous, created by

19   one or both feet striking the ground in the first couple of hops when taking flight (Coulson

20   1989). A review by Rose *et al.* (2006) found that foot-thumping was almost universal in the

21   Macropodidae, although whether it functions as a signal to conspecifics or to the predator

22   remains unclear. Regardless, conspecifics have been found to respond to foot-thumping.

Tammar wallabies became vigilant in response to foot-thumps (Blumstein *et al.* 2000), and foot-thumping by eastern grey kangaroos caused others present to become vigilant and often to take flight (Kaufmann 1975). A higher incidence of foot-thumping in conditions of low light or dense ground cover, or when individuals are not in visual contact lends support to the hypothesis that macropodids use other sensory modalities, in this case auditory cues, when visibility is compromised (Ramp *et al.* 2005; Rose *et al.* 2006). There are many benefits foot-thumping could have; such as warning conspecifics, confusing predators, the creation of havoc, creating social cohesion, pursuit-invitation, and as a pursuit-deterrent. Despite using sensitive audio equipment for the recording and playback of foot-thumps we were unable to detect any significant difference in response to foot-thumps from the baseline.

The ability to utilise foot-thumps as a deterrent hinges on the capacity to accurately replicate the conditions of a foot-thump, which is extremely difficult without incorporating the infrasonic element (i.e. the vibrations that travel through the ground when the hind legs of the macropodid are thumped on the ground). This would require the use of specialised recording and playback equipment that to date has not been attempted. Increased alertness and higher vigilance levels in experimental animals were observed in response to foot-thumps from other macropod species held captive in adjacent yards that they could not directly see. This anecdotal observation suggests that playback and/or recording of foot-thumps may not have been optimal despite the use of high-quality audio equipment; indeed, pilot research into recording foot-thumps has shown that making high quality recordings of foot-thumps frustratingly difficult. Proper investigation of mechanisms to artificially

1 reproduce foot-thumps accurately is warranted. It is likely, however, that distress calls

2 communicate a higher level of danger, and therefore risk, as they are usually only emitted

3 when an animal has been captured or restrained (Croft 1981), while foot-thumps are

4 typically given when an animal is fleeing from a disturbance (Rose *et al.* 2006).

5 *Management implications*

6 The trade-off between foraging and predation risk is a well-known concept that has

7 received considerable attention over the last few decades. Higher risk foraging patches

8 typically result in more time spent vigilant or scanning for predators, often at the expense of

9 foraging opportunities (Lima and Dill 1990; Maguire *et al.* 2005), and many animals avoid

10 areas where risks are high (Banks 2001; Wahungu *et al.* 2001). Additionally, animals feed

11 preferentially at sites that provide cover (Blumstein and Daniel 2003), spending more time

12 foraging close to shelter when predation risk is high (Johnson 1980; Banks 2001; While and

13 McArthur 2005). By increasing perceived predation risk these aversive responses can be

14 exploited to reduce damage due to macropod browsing damage and encourage animals to

15 seek alternative foraging sites. The success of distress calls in eliciting aversive behaviour

16 indicates that the successful manipulation of communicatory cues may have a place in

17 future wildlife management. To be effective in the long term the potential for habituation

18 must be examined *in situ*. To combat this effect, it may be possible to combine acoustic

19 deterrents, both bioacoustic and non-bioacoustic, with visual and olfactory methods to

20 implement a more holistic, effective, and humane approach to wildlife management.

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1 **Figures**

2 **Fig. 1**

3 Spectrograms of each acoustic stimulus used in experiments: (a) red-necked pademelon

4 foot thump; (b) red-necked wallaby foot-thump; (c) gunshot; (d) adult red-necked

5 pademelon distress call; (e) juvenile red-necked wallaby distress call; (f) wedge-tailed eagle

6 1; (g) wedge-tailed eagle 2; (h) dingo howls; (i) magpie song.

7 **Fig. 2**

8 Mean proportional difference in time allocated to three behavioural categories in response

9 to seven different sound broadcast types to red-necked pademelons and red-necked

10 wallabies. Error bars represent 95% confidence intervals.

11 **Fig. 3**

12 Mean proportional difference in time allocated to heightened vigilance and attention (face

13 towards the sound broadcast) behaviour after the broadcast of seven different sound types

14 to red-necked pademelons and red-necked wallabies. Error bars represent 95% confidence

15 intervals.

16 **Fig. 4**

17 Short-term habituation to acoustic stimuli expressed as the mean proportional difference in

18 time allocated to alert behaviour over the one hour trial period for both red-necked

19 pademelons and red-necked wallabies. Error bars represent 95% confidence intervals.

1   Tables

4   **Table 1. Responses of red-necked pademelons and red-necked wallabies to sound**
5   **broadcasts**

6   Generalised additive mixed models of the difference in time spent engaged in different

7   behaviours before and after presentation of acoustic stimuli relative to a control (magpie

8   call) for (a) red-necked pademelons and (b) red-necked wallabies. SE is the standard error

9   of the coefficient; DF is the degrees of freedom.

10   **(a) Red-necked pademelons**

Behaviour	Variable	Coefficient	SE	DF	t-value	p-value
Alert	Intercept	0.2788	0.0614	190	4.5431	*< 0.0001*
	Dingo	0.0411	0.0772	190	0.5324	0.5950
	Eagle	-0.0980	0.0791	190	-1.2382	0.2172
	Distress RNP	-0.0928	0.0907	190	-1.0236	0.3073
	Foot thump	-0.0589	0.0801	190	-0.7354	0.4630
	Gunshots	-0.0388	0.0846	190	-0.4589	0.6469
	s(Time)	-0.2221	0.1266	190	-1.7550	0.0809
Other	Intercept	-0.0949	0.0498	283	-1.9053	0.0578
	Dingo	0.0110	0.0688	283	0.1605	0.8726
	Eagle	0.0355	0.0701	283	0.5062	0.6131
	Distress RNP	-0.1013	0.0770	283	-1.3152	0.1895
	Foot thump	0.0252	0.0677	283	0.3728	0.7096
	Gunshots	0.0607	0.0713	283	0.8513	0.3953
	s(Time)	0.0421	0.0205	283	2.0558	*0.0407*
Inactive	Intercept	-0.0448	0.0543	269	-0.8263	0.4094
	Dingo	-0.1361	0.0718	269	-1.8954	0.0591
	Eagle	-0.0496	0.0747	269	-0.6635	0.5076
	Distress RNP	0.1343	0.0857	269	1.5673	0.1182
	Foot thump	-0.0075	0.0722	269	-0.1039	0.9173
	Gunshots	-0.0625	0.0735	269	-0.8505	0.3958
	s(Time)	0.0459	0.0214	269	2.1411	*0.0332*
Vigilance	Intercept	0.2254	0.0499	211	4.5206	*< 0.0001*
	Dingo	0.0535	0.0674	211	0.7940	0.4281

	Eagle	-0.0335	0.0744	211	-0.4509	0.6525
	Distress RNP	-0.0469	0.0814	211	-0.5765	0.5649
	Foot thump	0.0410	0.0773	211	0.5305	0.5964
	Gunshots	0.0110	0.0789	211	0.1398	0.8889
	s(Time)	-0.1090	0.0627	211	-1.7382	0.0836
Attention	Intercept	0.1638	0.0417	489	3.9258	*0.0001*
	Dingo	-0.0172	0.0557	489	-0.3086	0.7578
	Eagle	-0.1086	0.0548	489	-1.9803	*0.0482*
	Distress RNP	-0.0941	0.0558	489	-1.6857	0.0925
	Foot thump	-0.0339	0.0564	489	-0.6014	0.5479
	Gunshots	-0.1167	0.0559	489	-2.0879	*0.0373*
	s(Time)	-0.0568	0.0158	489	-3.5893	*0.0004*

1

2 **(b) Red-necked wallabies**

Behaviour	Variable	Coefficient	SE	DF	t-value	p-value
Alert	Intercept	0.0048	0.0272	751	0.1750	0.8611
	Dingo	0.0956	0.0382	751	2.5010	*0.0126*
	Eagle	0.0609	0.0377	751	1.6164	0.1064
	Distress RNP	0.0342	0.0381	751	0.8975	0.3697
	Distress RNW	0.1863	0.0379	751	4.9204	*< 0.0001*
	Foot thump	0.0236	0.0394	751	0.6002	0.5485
	Gunshots	0.0825	0.0389	751	2.1222	*0.0341*
	s(Time)	-0.0402	0.0337	751	-1.1944	0.2327
Other	Intercept	-0.0022	0.0246	743	-0.0906	0.9278
	Dingo	-0.0595	0.0331	743	-1.7966	0.0728
	Eagle	-0.0423	0.0327	743	-1.2916	0.1969
	Distress RNP	-0.0177	0.0329	743	-0.5386	0.5903
	Distress RNW	-0.1184	0.0328	743	-3.6062	*0.0003*
	Foot thump	-0.0014	0.0341	743	-0.0422	0.9663
	Gunshots	-0.0110	0.0337	743	-0.3278	0.7432
	s(Time)	0.0435	0.0270	743	1.6116	0.1075
Inactive	Intercept	-0.0014	0.0469	230	-0.0292	0.9767
	Dingo	-0.1019	0.0713	230	-1.4291	0.1543
	Eagle	-0.0918	0.0690	230	-1.3300	0.1848
	Distress RNP	-0.0410	0.0644	230	-0.6369	0.5248
	Distress RNW	-0.2171	0.0740	230	-2.9351	*0.0037*
	Foot thump	-0.0230	0.0817	230	-0.2819	0.7783

	Gunshots	-0.1984	0.0724	230	-2.7394	*0.0066*
	s(Time)	-0.0088	0.0204	230	-0.4287	0.6685
Vigilance	Intercept	0.0167	0.0369	757	0.4521	0.6513
	Dingo	0.0559	0.0451	757	1.2403	0.2152
	Eagle	0.0816	0.0459	757	1.7774	0.0759
	Distress RNP	0.0037	0.0465	757	0.0803	0.9361
	Distress RNW	0.0449	0.0449	757	1.0001	0.3176
	Foot thump	0.0125	0.0472	757	0.2651	0.7910
	Gunshots	0.0610	0.0456	757	1.3359	0.1820
	s(Time)	-0.0392	0.0118	757	-3.3366	*0.0009*
Attention	Intercept	0.0460	0.0342	928	1.3443	0.1792
	Dingo	0.0484	0.0420	928	1.1540	0.2488
	Eagle	0.0401	0.0421	928	0.9522	0.3413
	Distress RNP	0.0224	0.0414	928	0.5417	0.5882
	Distress RNW	0.1476	0.0414	928	3.5703	*0.0004*
	Foot thump	0.0394	0.0439	928	0.8968	0.3701
	Gunshots	0.0272	0.0418	928	0.6516	0.5148
	s(Time)	-0.0465	0.0111	928	-4.2038	*< 0.0001*

1

2