Ventilatory frequency as a measure of the response of tammar wallabies (*Macropus eugenii*) to the odour of potential predators

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Abstract

This study uses changes in ventilatory frequency to quantify the physiological response of an Australian terrestrial herbivore, the tammar wallaby (*Macropus eugenii*), to olfactory cues suggesting the presence of potential predators. Ventilatory frequency proved to be a quantifiable measure to assess the response of this macropod marsupial to olfactory cues. Ventilatory frequency increased from mean resting levels of 45 ± 5.1 breaths min^{-1} to 137 ± 11.2 breaths min^{-1} during the first minute of exposure to all odours. These physiological responses diminished over time, with ventilatory frequency in the first minute after introduction of the scents greater than that during the subsequent four, suggesting that the initial reaction was due to disturbance and was investigative in nature. However, the ratio of ventilatory frequency in the remaining 4 min after introduction of the odours compared to before was greater for fox (3.58 ± 0.918) and cat (2.44 ± 0.272) odours compared to snake (2.27 ± 0.370), distilled water (1.81 ± 0.463) and quoll (1.71 ± 0.245) odours, suggesting that fox and cat odour provoked a greater response. However, the wallabies' response to the odour of these introduced predators and horse odour (2.40 ± 0.492) did not differ. Our study indicates that a long period of co-history with particular predators is not a pre-requisite for detection of potentially threatening species. We do not find any support for the hypothesis that an inability to interpret olfactory cues to detect and respond to potential predation by introduced predators is responsible for the decline of these macropod marsupials.

Introduction

Olfactory cues are used by mammalian prey to recognise potential predators (Lima and Dill 1990; Kats and Dill 1998) and therefore odours derived from predator glands, hair, faeces and urine may represent an indication of the risk of predation for potential prey (Jedrzejewski *et al.* 1993). Field and laboratory studies have demonstrated that some prey species have the capacity to detect potential predators by their scent and that predator odours have immediate effects on prey behaviour (see review by Apfelbach *et al.* 2005).

The examination of physiological parameters of animals under the stress of predation risk may help to further understand their responses to predator scents. Perceiving the presence of a predator can represent a strong alerting stimulus that may elicit a physiological stress response in prey (Dell'omo *et al.* 1994). For this reason, a number of previous studies have used physiological reactions to predator scents to quantify animals' fear of predation (Monclús *et al.* 2005, 2006; Feoktistova *et al.* 2007). For example, hedgehogs (*Erinaceus europaeus*) exposed to badger (*Meles meles*) faecal suspension increased oxygen consumption as a consequence of increased alertness (Ward *et al.* 1996). Predator odour induced increased corticosterone in rodents (Vernet-Maury *et al.* 1984; Kavaliers *et al.* 2001), and adrenocorticotropic hormone increased in rats exposed to ferret (*Mustela putorius furo*) odour (Masini *et al.* 2005).

Changes in ventilatory frequency (f_R) in crayfish have been reported after exposure to stressful sensory stimuli (Schapker *et al.* 2002) but to our knowledge, f_R has not been used previously for quantifying a response to predators in mammals. f_R is likely to be a good indication of an animal's perception of predator odour, as it is known that animals alter their pattern of f_R when exposed to odours (Doty 1975, Engen 1982, Laska 1990), ventilatory parameters including f_R increase for animals which are not in a resting state e.g. during a period of stress such as during restraint (Bucher 1985; Chappell 1992; Larcombe 2002), and

ventilatory variables are highly correlated with metabolic rate (e.g. Chappell 1985, 1992; Chappell and Dawson 1994; Dawson *et al.* 2000; Larcombe 2002; Cooper and Withers 2004; Withers and Cooper 2009). Measurement of f_R has an advantage over metabolic rate as it is an instantaneous measure of the animal's physiological state, and is preferable to measuring heart rate or hormone levels, as it can be measured non-invasively on an un-instrumented animal, using whole-body plethysmography. We examine here the use of ventilatory frequency to investigate the response of a native Australian marsupial, the tammar wallaby (*Macropus eugenii*), to the scent of potential predators.

The tammar wallaby is a medium-sized Australian macropodid marsupial with disjunct populations in southern Western Australia and South Australia (Poole e*t al.* 1991; Hinds 2008). Its distribution has decreased significantly on the mainland since European settlement, and feral predators are believed to have made a significant contribution to the disappearance of many populations (Calaby and Gigg 1989; Johnson *et al.* 1989; Smith and Hinds 1995; Morris *et al.* 1998). Previous behavioural studies have provided an understanding of its anti-predator strategies and use of predator cues (Griffin *et al.* 2001; Blumstein *et al.* 2002, 2004). Tammars respond to the sight of predators by reducing feeding and increasing vigilance, but they do not respond to predator acoustic stimuli (Blumstein *et al.* 2000) and appear unresponsive to predator olfactory cues (Blumstein 2002). The potential inability of tammar wallabies, and possibly other marsupials, to respond to olfactory cues of predation risk may explain their particular vulnerability to feral animals and may have contributed to their rapid decline.

Here we use f_R as a measure of the physiological response of tammar wallabies to the odour of potential predators. We assess the use of this quantifiable, non-invasive physiological measure of response to predator and control odours, and compare our findings to previously published

behavioural responses of tammar wallabies to olfactory predator cues to resolve more clearly how this species responds to such stimuli.

Materials and methods

Study animals

Eight male tammar wallabies were caught at Tutanning Nature Reserve (32° 32' S; 117° 19' E), approximately 30 km east of Pingelly, Western Australia. They were housed in pairs for up to 9 months in predator-proof outdoor enclosures at the University of Western Australia, Perth, where they were exposed to natural weather and photoperiod. Kangaroo pellets (Glen Forrest Stockfeeders), lucerne chaff, fresh vegetables and water were available *ad libitum*.

Experimental procedures

Whole-body open-flow plethysmography (Malan 1973; Dawson *et al.* 2000; Larcombe 2002; Cooper and Withers 2004) was used to measure f_R (breaths min^{-1}) of tammar wallabies before and after exposure to a range of control and predator odours. Changes in pressure within the plethysmography chamber, resulting from the warming and humidifying of inspired air, were measured using a Sable System PT-100 pressure transducer. The analog voltage output from the transducer was converted to a digital signal using a Pico Technology ADC 11 data logger, and recorded on a personal computer every 15 msec^{-1} for approximately 20 sec using PicoScope. A custom-written Visual Basic (V6) program (P Withers) was used to calculate f_R. Experiments were conducted during the tammars' inactive phase (daytime) after the animals had been fasted for 24 hrs, to ensure that animals had baseline resting f_R during experiments, with sufficient scope to measure changes in f_R due to exposure to odours. A wallaby was removed from its enclosure, weighed to ± 1 g and placed in a 60 L Perspex plethysmography chamber located inside a controlled-temperature room, set to a thermoneutral temperature of 28 - 31 °C (Dawson *et al.* 1969). When the wallaby had attained a quiet resting state, as indicated by deep, regular ventilation and remote observation, f_R was measured immediately

before and then at 1 min intervals for 5 min after the introduction of a control or predator odour. Two mL of liquid or 2 cm x 6 cm of solid scent source were placed in the inlet airline of the chamber for 5 min. Separate tubes were used exclusively for each type of odour and only one scent was presented at a time, with a minimum of 1 hr between presentation of successive odours. During this time, ventilation was monitored until it became regular, and the wallaby was observed using a video camera to ensure it had returned to a resting state after the scent had flushed out of the chamber. Washout time of the plethysmography chamber was determined to be 20.4 min after Lasiewski *et al.* (1966). The wallaby was exposed to the different odours in random order and was in the chamber for up to 10 hours. At the conclusion of the experiment, the wallaby was weighed to ±1 g and returned to its enclosure. Body mass of a wallaby on an experimental day was calculated as the mean of masses before and after the experiment.

Odour sources

The presence of four predators (snake, quoll, fox and cat) was simulated during experiments by introducing either a fluid (urine) or solid (skin, faeces) odour into the chamber inlet air line. Predators were chosen to represent both Australian native and introduced predators. Skin was obtained from a black-headed python (*Aspidites melanocephalus*; donated by a private source) and a fox (collected from a fresh road kill), urine from a feral cat (donated by the Department of Environment and Conservation) and faeces from a northern quoll (*Dasyurus hallucatus*; housed in captivity at UWA and fed exclusively on meat). Horse (*Equus caballus*) urine (donated by a private source) and distilled water were used as control odours. Predator skin, faeces and urine have all elicited responses in prey species in previous studies (see review by Apfelbach *et al.* 2005), and although different sources of odour could lead to variability in the response, most studies have shown that prey react to predator odours independently of the source (Müller-Schwarze 1972; Melchiors and Leslie 1985; Swihart *et*

al. 1991; Epple *et al.* 1993). Although the geographic ranges of black-headed pythons and northern quolls do not overlap with those of tammar wallabies, these snake and quoll species were considered to be sufficiently closely related to sympatric carpet python (*Morelia spilota*) and chuditch (*Dasyurus geoffroii*) predators as to provide representative odours.

Data analysis

All values are presented as mean ± standard error (SE), with N = number of individuals and n = number of measurements; N and n = 8 unless stated otherwise. The effect of exposure to each odour was tested separately using paired t tests of f_R before (mean f_R over the 5 min preceding exposure) and after (f_R in the minute following exposure) introduction of the odour. Two-way analysis of variance (ANOVA; time and odour as factors) with Student-Newman-Keuls (SNK) *post hoc* tests was used to compare the after:before ratio of f_R for the different odours and to determine if there was a temporal effect on the response over the 5 minutes following exposure. Temporal effects were then quantified with linear regression. Statistical analyses were accomplished using StatistiXL Version 1.7.

Results

The mean body mass of all wallabies over all experiments was 5.08 ± 0.043 kg (N = 8, n = 48). While resting, the wallabies were observed to lie on their side with legs extended or crouch with hind legs and tail forward (Fig.1 A and B). After introduction of all the odours, wallabies would stand, rotate their ears and initially face the inlet airline (Fig.1 C). After exposure to fox and cats odours, four individuals were observed to move away from the inlet air connection and crouch in the furthest corner of the metabolic chamber (Fig. 1 D), but when exposed to the other odours, they would quickly go back to resting. Although the other four wallabies did not retreat in the back of the chamber after investigation of fox and cat odours, they did not return to a resting state until after these scents had been removed.

Mean resting f_R was 44.9 ± 5.12 breath min^{-1} for all wallabies over all experiments (N = 8, n = 48). Exposure to all odours significantly increased f_R (to 137 ± 11.2 breaths min^{-1}, N = 8, n = 48) compared to resting f_R ($t_7 \geq 3.04$, P ≤ 0.019; Fig. 2). For all odours, no significant difference in response (after:before f_R ratio) to the odours was detected when all 5 min post exposure were included in the model ($F_{5,210} = 1.989$; P = 0.082), although there was a significant effect of time ($F_{4,210} = 17.03$; P < 0.001). The after:before f_R ratio was significantly higher in the first minute after exposure to the odours than the subsequent four minutes (SNK P < 0.001). When the first minute after exposure was removed from the model, there was a significant effect of odour on the after:before f_R ratio ($F_{5,168} = 5.416$; P<0.001); the f_R response was greater for fox (SNK P ≤ 0.040) and feral cat (SNK P ≤ 0.029) odours than for quoll, snake and distilled water (Fig. 3). However, responses to fox, feral cat and horse scents did not differ (SNK P ≥ 0.101). The significant effect of time remained, with the after:before f_R ratio higher during the second minute post-exposure than for the subsequent three minutes (SNK P ≤ 0.014). Linear regressions of the after:before f_R ratio over the 5 minutes post-exposure were significant and negative for all odours ($F_{1,38} \geq 7.75$, P ≤ 0.008) except cat ($F_{1,38}$ = 3.44, P = 0.071), and ANOVA indicated that f_R during the first minute was significantly higher than each of the subsequent four for water, horse, quoll odours (SNK P < 0.012), and significantly higher than the fifth for fox odour (SNK P = 0.039; Figure 4).

Discussion

We demonstrate that f_R is a quantifiable measure of response to the odour of a potential predator, and is a useful tool to assess the response of macropod marsupials to olfactory cues. Tammar wallabies responded differently to various predatory and control odours, and had a greater physiological response to the odour of cats and foxes compared to quolls, snakes and water. Clearly tammar wallabies are able to detect and respond to the odour of potential predators, even non-native species. Our data do not support the hypothesis that an inability to

interpret olfactory cues of potential predation by introduced predators is responsible for the decline in distribution and abundance of macropod marsupials.

Resting f_R of 45 ± 5.1 breaths min^{-1} at thermoneutrality for tammar wallabies is consistent with the 48 ± 6.6 breaths min^{-1} reported by Dawson *et al.* (1969). This indicates that the tammar wallabies were calm and resting prior to introduction of the odours, providing scope for the wallabies to increase f_R as a response to the odours. The wallabies responded to the introduction of all odours with an immediate increase in f_R.

A change in ventilatory rate has been reported in a variety of animals as an index of response to sudden environmental changes, representing an animal's readiness for a consequent behavioural reaction (Wilkens 1976; McMahon and Wilkens 1983; Laska, 1990; Burmistrov and Shuranova 1996). We demonstrate here that macropod marsupials also increase f_R in response to exposure to olfactory stimuli, and that this response is mediated by different olfactory cues. A change in barometric pressure within the plethysmography chamber, due to a brief interruption of the incurrent air flow while the odour was introduced, presumably disturbed the resting wallabies. This initial disturbance accounts for the initial response to all odours, including distilled water, and highlights the need for appropriate controls in studies such as this. It is necessary to examine differences in the magnitude and time-course of the response to experimental and control odours, rather than just the before/after response to any given odour.

During the initial period of increased f_R the wallabies also orientated toward the stimulus, approached the inlet airline and appeared to investigate the odours, except distilled water. This exploratory behaviour is similar to that observed for other mammals exposed to predator olfactory stimuli (Caine and Weldon 1989; McGregor *et al.* 2002; Monclús *et al.* 2006). For example, rodents displayed similar odour assessment when presented with the scent of cat (Blanchard and Blanchard 1989; Williams *et al.* 1990) and stoat (*Mustela erminea*; Kemble

and Bolwahnn 1997), while black-tailed deer closely examined droppings of potential predators such as the snow leopard (*Panthera uncia*), coyote (*Canis latrans*) and mountain lion (*Felis concolor*; Müller-Schwarze 1972).

The initial exploratory increase in f_R by tammar wallabies generally decreased in the second minute. This is consistent with the hypothesis the initial reaction was investigative in nature. When this initial investigative phase was eliminated from the analysis (i.e. the response from min 2 to min 5 was examined), fox and cat odours elicited a greater response than the odour of quoll, snake and water. The response to cat odour was also maintained at initial levels throughout the duration of exposure, unlike responses to other odours.

An inability to recognise or react to the odour of introduced predators has been suggested to contribute to the impact of introduced foxes and cats on Australia's native fauna (Dickman and Doncaster 1984; Dickman 1992), and indeed introduced predators have a greater impact on prey populations than native predators (Salo *et al.* 2007). However, our results indicate that tammar wallabies reacted more strongly to the odour of introduced species, and therefore it seems unlikely that a lack of predator recognition contributes to the impact of introduced predators on this species. Various studies have demonstrated that prey may respond to predators even if they have not shared a long evolutionary history (Boag and Mlotkiewicz 1994; Engelhart and Müller-Schwarze, 1995; Rosell and Czech 2000). For example, alpine goats (*Capra hircus*) suppressed feeding in reaction to exotic predator scents (Weldon *et al.* 1993) and hare wallabies (*Lagorchestes hirsutus*) responded cautiously to visual contact with an unknown predator (McLean *et al.* 1996).

Predation risk varies with the predator type, and previous studies indicate that prey discriminate between more and less dangerous predators by responding to or avoiding cues which represent higher risks, which are usually more abundant or efficient predators (Helfman 1989; Licht 1989; Smith and Belk 2001; Stapley 2003). For example, bank voles

(*Clethrionomys glareolus*) showed discrimination and differential responses to seven species of predator, with the highest response for weasel and the lowest for raccoon dog (*Nyctereutes procyonoides*), reflecting the degree of specialisation of these predators in hunting for bank voles (Jedrzejewski *et al.* 1993). Water voles (*Arvicola terrestris*) reacted more to predators such as mink (*Mustela vison*), which have a greater impact on vole populations than to less significant predators such as rats (Barreto and Macdonald 1999). Some prey species need complex stimuli, not only in different sensory modalities, but also combinations of factors from both predator and prey, for full anti-predator behaviour to occur. For example, salamanders (*Plethodon cinereus*) only responded to the chemical stimuli of garter snakes (*Thamnophis sirtalis*) if the snakes had been feeding on salamanders, and not if they had been feeding on earthworms (Madison *et al.* 2002). It is likely that efficient placental predators such as foxes and cats represent a greater predation risk to tammar wallabies than native predators such as quolls and snakes. Indeed, *Macropus* marsupials can constitute a substantial proportion of the diet of feral cats (Catling 1988; Paltridge *et al.* 1997; Molsher *et al.* 1999; Paltridge 2002) and the fox is the most likely predator of macropods on mainland Australia (Kaufmann 1974), and is considered the principal cause for the decline of tammar wallabies in Western Australia (Kinnear *et al.* 1988). Although quolls and snakes presumably represent some degree of risk (Belcher 1995; Blumstein *et al.* 2004; Glen and Dickman 2006), the wallabies may not perceive these predators as representing a great or immediate threat. The specific native predators used in this study are not sympatric with the tammar wallabies, and it is possible that the wallabies were more familiar with the threat posed by cats and foxes than with the quoll and snake species tested. However, close ecological and phylogenetic analogues do exist at Tutanning Nature Reserve and therefore this explanation is unlikely. The wallabies' response to horse odour was surprising. However, large herbivores may also represent a significant risk to smaller ones. Changes in plant species composition have been

shown in areas grazed by large herbivores, with smaller species being negatively affected (Bakker *et al.* 2009). Therefore, horses may represent a threat in terms of competition for resources and although not potential predators for tammar wallabies, their large size may also represent a risk. However, as it is unlikely that the wallabies have previously encountered horses, the results obtained with horse odour may also be an example of neophobia; the wallabies may have been responding to horse scent because this was a novel odour (Boag and Mlotkiewicz 1994; Kemble and Bolwahnn 1997). The time course of the response, with a rapid decline in f_R over time, similar to that seen for water and quoll odours, supports this hypothesis. Another macropod, the red-necked pademelon (*Thylogale thetis*), also showed a neophobic response to an unknown herbivore, spending more time close to a potential predator (dog) scent, than to the unknown herbivore odour (Blumstein *et al.* 2002).

Past experience of a predator may result in greater responses to predator cues (see Apfelbach *et al.* 2005). McLean *et al.* (2000) showed that bettongs (*Aepyprymnus rufescens*) and quokkas (*Setonix brachyurus*) learned to be cautious of dogs and foxes after chase-training. Griffin *et al.* (2001) and Blumstein *et al.* (2002) demonstrated that visual and olfactory predator recognition may need to be learned by predator-naive tammar wallabies. Blumstein (2002) also suggested the existence of an experience-based mechanism for predator recognition in tammar wallabies. Tammars isolated from predators did not show visual, auditory or olfactory predator recognition (Blumstein 2002; Blumstein *et al.* 2004), while those which encountered predators regularly responded to visual or auditory cues of even unknown predators (Blumstein *et al.* 2000). The wallabies used in this experiment were wild caught and therefore there is no record of their previous experience with predators. However, it is likely that they had encountered some predation risk as both mammalian and avian predators are present at Tutanning Nature Reserve (Blumstein 2002; Blumstein and Daniel 2002) and indeed the presence of foxes is well documented (Kinnear *et al.* 2002). Prior

experience with predators may account for differences in response to predator odours between this study and that of Blumstein (2002), who found that predator-naive Tammar wallabies showed no behavioural response to predator odours. Presumably the wallabies used in this study have been previously confronted by predators, and recognise the high potential predation risk associated with the odours of fox and cat.

Whole-body plethysmography was found to be an effective technique for quantifying changes in f_R of a macropod marsupial in response to the odour of a potential predator. This non-invasive technique provides an instantaneous measure of the animal's physiological response in a controlled environment. It is straight forward and poses little imposition on the study species or risk to the welfare of the animals. The technique is sufficiently sensitive to detect differential responses to different predator odours and we suggest that it may be a suitable technique for examining the response of other mammalian species to olfactory cues, with particular value for assessing predator responses of endangered species, where more invasive physiological techniques are undesirable.

Acknowledgements

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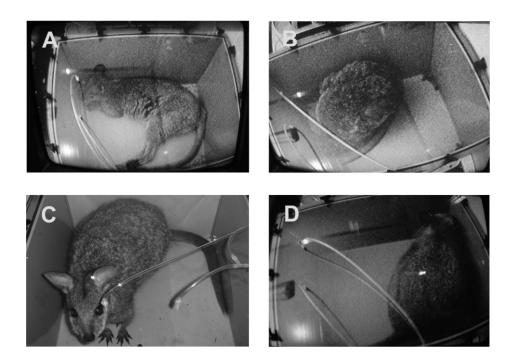
Figure 1 Behaviour of tammar wallabies (*Macropus eugenii*) in the plethysmography chamber A) and B) at rest before introduction of an odour, C) investigating an odour during the first minute after exposure and D) after exposure to fox odour (Photographs by V. Mella and S. Schmidt).
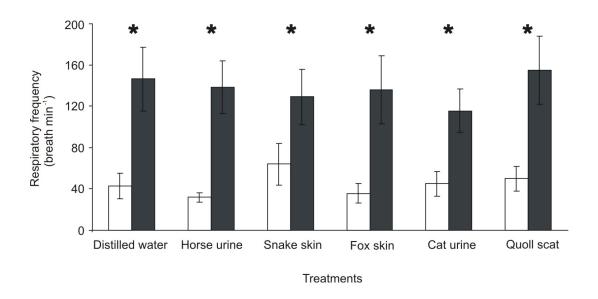
Figure 2 Effect of various odours on the ventilatory frequency (f_R) of tammar wallabies (*Macropus eugenii*) during the first minute of exposure to the odours. White bars represent f_R before and black bars after exposure. * indicates a significant difference between before and after exposure f_R. Values are mean ± SE, N = 8.
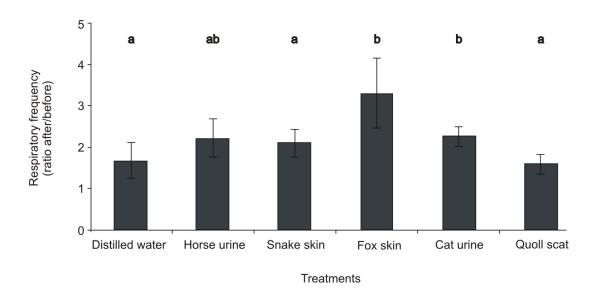
Figure 3 After/before ratio of tammar wallaby (*Macropus eugenii*) ventilatory frequency during the second minute of exposure to various odours. Different letters indicate a significant difference, values are mean ± SE, N = 8.
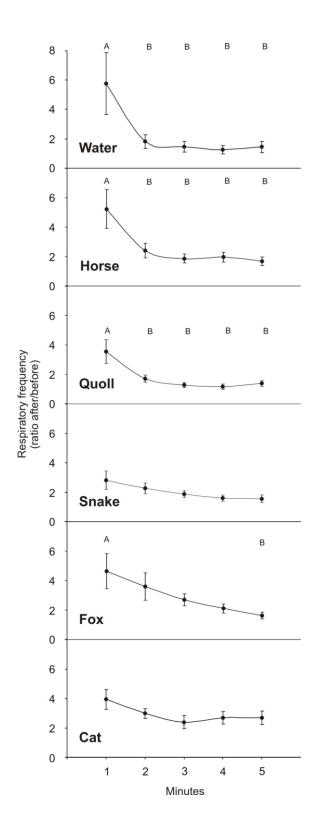
Figure 4: Temporal effects of different odours on the respiratory frequency of tammar wallabies. Different letters indicate significant differences between minutes after exposure to the odour, values are mean ratio of after/before exposure ± SE (N = 8).