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Effects of historically familiar and novel predator odors on the physiology of an introduced prey

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Abstract

Predator odors can elicit fear responses in prey and predator odor recognition is generally associated with physiological responses. Prey species are often more likely to respond to the odor of familiar rather than alien predators. However, predator naïvety in an introduced prey species has rarely been investigated. We examined the physiological response, as shown by changes in ventilatory variables, of an introduced terrestrial herbivore, the European rabbit *Oryctolagus cuniculus*, in Australia, to the odor of potential predators and to control odors (distilled water and horse), to explore if responses were limited to historical (cat and fox) predators, or extended to historically novel predators (snake and quoll). All odors except distilled water elicited a response, with rabbits showing long-term higher respiratory frequencies and lower tidal volumes after introduction of the odors, indicating an increase in alertness. However, the intensity of the rabbits' reaction could not be directly linked to any pattern of response with respect to the history of predator–prey relationships. Rabbits exhibited significantly stronger reactions in response to both cat and quoll odors than they did to distilled water, but responses to horse, fox, and snake odor were similar to that of water. Our results show that the introduced rabbit can respond to both historical and novel predators in Australia, and suggest that shared evolutionary history is not necessarily a prerequisite to predator odor recognition.

Key words: physiology, ventilation, predator odor, rabbit, introduced prey, predator naïvety.

Odor plays an important role in predator–prey interactions (Kats and Dill 1998). Prey may interpret olfactory cues derived from predator feces, urine, glands, and hair as an indication of the risk of predation (Apfelbach et al. 2005). Exposure to such olfactory cues generally elicits a behavioral response such as increased vigilance, spatial and temporal activity modification, or direct avoidance (Kats and Dill 1998), similar to situations of high predation risk (Jędrzejewski et al. 1993; Mella et al. 2014). Changes in parameters such as heart rate, metabolic rate, and corticosterone also indicate a physiological response of prey to predator cues, suggesting increased alertness, stress, or anxiety (Dell’Omo et al. 1994; Chabot et al. 1996; Blanchard et al. 1998). Therefore, physiological responses to predator odors have been used successfully to quantify animals' fear

of predation in various studies (e.g., Monclús et al. 2006a; Feoktistova et al. 2007; Mella et al. 2010).

The majority of the studies investigating the evolution of predator odor recognition have examined responses of native prey to historical and exotic predators (Apfelbach et al. 2005). We are aware of only two studies (Dickman 1992; Barrio et al. 2010) that have examined the effects of predators on an introduced prey species, despite the contribution of these studies to understanding the evolution of predator and prey interactions independent of phylogenetic and biogeographical influences. These studies focused on the behavioral consequences of olfactory predator cues for two prey species, the house mouse (*Mus domesticus*; Dickman 1992) and the European rabbit (*Oryctolagus cuniculus*; Barrio et al. 2010), introduced in

Australia after European settlement (Myers et al. 1994; Breed and Aplin 2008). Both studies found that the introduced prey species did not respond to Australian native predator odors. In contrast, the odor of natural coevolved predators, such as cats *Felis catus* and foxes *Vulpes vulpes*, also introduced in Australia by European settlers (Coman 1983; Abbott 2002), elicited antipredator behavioral responses in both prey (Dickman 1992; Barrio et al. 2010).

Naivety and the inability to respond appropriately to the threat of evolutionary unfamiliar predators may be a possible explanation for the lack of behavioral response to predator odors in prey species (Cox and Lima 2006; Carthey and Banks 2014). However, failing to behaviorally avoid an area characterized by predator odor does not necessarily mean that prey do not recognize these as potential predators (Banks and Dickman 2007), as avoiding such areas is a trade-off between mitigating the threat of predation and meeting other necessary life functions, such as feeding and reproduction (Lima 1998; Lima and Bednekoff 1999). Examining prey physiological responses to predator odors can help in determining whether prey are actually increasing their alertness, even in absence of a behavioral response, as expected in case of predator odor recognition (e.g., Mella et al. 2010).

Here, we investigate the physiological antipredator response of the introduced European rabbit to the odor of native and exotic predators in Australia. The rabbit has a long co-evolutionary association with foxes and cats in Europe (Delibes-Mateos et al., 2007; Malo et al., 2004), but it has only had a historically limited contact with native Australian predators, which represent comparatively novel threats. Therefore, the rabbit is an interesting model to examine the evolution and adaptation of prey physiological responses to predators. Rabbits have a well-developed olfactory system and use smell and scent marking for social communication and recognition of conspecifics (Mykytowycz 1968; Sneddon 1991; Hayes et al. 2002). They respond to odors of both sympatric and allopatric predators, when the predator archetype is familiar (Boag and Mlotkiewicz 1994; Bakker et al. 2005). Therefore, olfaction seems to play an important role in predator avoidance (Bakker et al. 2005; Monclús et al. 2005, 2006). However, in Australia, rabbits do not avoid areas treated with quoll *Dasyurus maculatus* odor during feeding trials (Barrio et al. 2010), suggesting that they do not behaviorally avoid historically novel predators. But do they recognize them as potential threats at all? Respiratory parameters such as respiratory frequency (f_R) and tidal volume (V_T) are particularly useful as noninvasive, instantaneous measures of physiological state that quantify the fear of potential prey to predator odors (Mella et al. 2010). Therefore, to overcome the potential discrepancy between predator recognition and behavioral response, we examine these physiological parameters to determine if rabbits in Australia increase their alertness toward historically novel (quoll, snake) or historically familiar (cat, fox) predators. If the physiological response of rabbits mirrors their behavioral response (Barrio et al. 2010) to novel Australian predators, we would expect little difference in their response to quoll and snake odor compared to control odors (distilled water, horse).

Materials and Methods

Study animals

Six adult rabbits (4 males, 2 females) were captured on the grounds of the Department of Agriculture and Food of Western Australia (DAFWA) in Forrestfield, Perth, WA during summer 2008, using wire mesh cage traps, baited with diced carrots following the procedure of

Twigg et al. (1996). Predators including cats, foxes, dogs, snakes, goannas, and raptors are likely to occur in the area where the rabbits were captured. Trapped rabbits were housed at Curtin University in indoor enclosures in pairs of the same sex. Rabbits were maintained on a 12:12 light:dark photoperiod at an ambient temperature of 21 °C and provided with food (rabbit pellets and fresh vegetables), water *ad libitum*, and environmental enrichment including sand, twigs, branches, and refuges.

Experimental procedure

Rabbits were removed from their enclosures in the morning during their inactive phase (daytime), weighed to ± 1 g and then placed into a 10 L plethymograph chamber that consisted of a Perspex box set in a temperature-controlled room. Air passed through the chamber at 2.5 L min⁻¹. After the rabbits had attained a quiet resting state, a treatment odor (see “Odor sources” section) was introduced into the inlet airline of the chamber for 5 min, by passing the air through a tube containing the odor source. A separate tube was used for each odor to prevent cross-contamination. The order of odor introduction was selected randomly. Only one odor was used at a time and there was at least 1 h between presentation of successive treatments to ensure that the previous odor had flushed out of the chamber (washout was calculated to be 18.4 min after Lasiewski et al. (1966)) and that rabbits had re-attained a resting state before introduction of a new odor (verified by a constant, regular ventilatory pattern). At the end of each experimental day, rabbits were removed from the chamber and their body temperature measured with an Omron MC-510 ear thermometer. The rabbits were again weighed to ± 1 g, before being returned to their enclosure. Body mass of a rabbit on a specific day was calculated to be the mean of masses obtained before and after the experiment.

Rabbits' f_R (breaths min⁻¹) and V_T (body temperature and pressure saturated, BTPS; mL) were measured for ventilatory measurements, using open-flow whole-body plethysmography (Withers 1977; Cooper and Withers 2004) with the system calibrated after Szewczak and Powell (2003). Warming and humidifying of inspired air caused pressure changes within the plethysmography chamber; these were detected by a custom-made pressure transducer with a Motorola MPX2010 sensor. The analog voltage outputs of the pressure transducer were converted to a digital signal using a Pico Technology ADC 11 data logger, and were recorded on a personal computer every 2 ms for approximately 20 s using PicoScope. Respiratory variables were measured immediately before and then after introduction of an odor at 1-min intervals for 5 min. Calculations were made using a custom-written Visual Basic (VB) program (Withers, P.) after Malan (1973), Szewczak and Powell (2003) and Cooper and Withers (2004). Minute volume was calculated as $f_R * V_T$.

Odor sources

Predator-based odors were obtained from different odor sources, such as urine, scats, and pelt/skin, with only one source to represent each predator treatment. All these odor types have been shown to elicit responses in prey species in previous studies (Apfelbach et al. 2005), but it is possible that different odor sources represent different information concerning predation risk (e.g., Blanchard et al. 2003; Masini et al. 2005). Although the use of different odor sources is not ideal, it was necessary here for logistical reasons, and can still reveal important information about prey recognition of predator olfactory cues (e.g., Mella et al. 2010). Urine, feces, and scent glands contain a

number of common sulfur compounds (Epple et al. 1995) and in most previous research, prey avoided predator odors regardless of the source (e.g., Dickman and Doncaster 1984; Gorman 1984; Dickman 1992). Fox and cat odor represented historical predators and northern quoll *Dasyurus hallucatus* and black-headed python *Aspidites melanocephalus* odor represented novel Australian predators. Horse *Equus caballus* odor and distilled water were controls. Fox pelt was obtained from fresh road kill victims, and shed python skin was donated by private owners (from snakes fed on a diet of rodents). Cat urine samples were provided by the Western Australian Department of Environment and Conservation (sampled from culled feral cats) and horse urine was provided by private owners. Quoll fecal samples were obtained from a captive individual maintained on a meat diet at the University of Western Australia, Perth. All samples were obtained shortly before experiments and kept refrigerated at $\sim 4^{\circ}\text{C}$ until used.

Data analysis

Values are presented as mean \pm standard error (SE; $N=6$), where N is the number of animals and n is the number of measurements. Statistical analyses were carried out using *StatistiXL* (www.statistiXL.com) and R (version 2.15; R Development Core Team, 2011).

Before and after exposure differences

Each odor used in the experiment was tested individually for its effect on respiratory values. Two-tailed paired t -tests (statistiXL) were used to determine if f_R and V_T of rabbits in the minute after exposure to each scent were significantly different than immediately before. Any change in f_R or V_T was considered as a response to the odor introduced to the chamber. Since the differences within the before and after values of each scent were tested individually and results were not combined to find a general difference in the response to the odors, it was not necessary to correct for multiple comparisons (Aickin and Gensler 1996; Perneger 1998; Bender and Lange 2001).

Odor differences and time effect

Effects of odor and time (e.g., each successive minute after exposure, for 5 min) on f_R and V_T before and after exposure to the odor were determined with linear mixed effect models in R using nlme (Bates et al. 2012) and language R (Baayen 2008) packages. Due to differences in respiratory variables before exposure to some odors, we also analyzed the ratio of after/before for each minute of exposure. Odor and time were fixed factors and individual rabbit was a random factor. Interaction terms for all fixed factors were included in the model. Overall significance of odor and time were determined by likelihood ratio tests (LRT) of the full model against the model with only odor as a fixed factor, and the model with no fixed factors (Crawley 2007).

Results

The mean body mass of the rabbits before and after the experiments was 1.1 ± 0.03 kg ($N=6$; $n=50$). When resting, rabbits remained inactive with a very regular breathing pattern, with f_R and V_T indicating slow and deep breaths (Figure 1A). When they were exposed to a scented treatment, rabbits would arouse from their resting state with an increase in f_R and a decrease in V_T (Figure 1B).

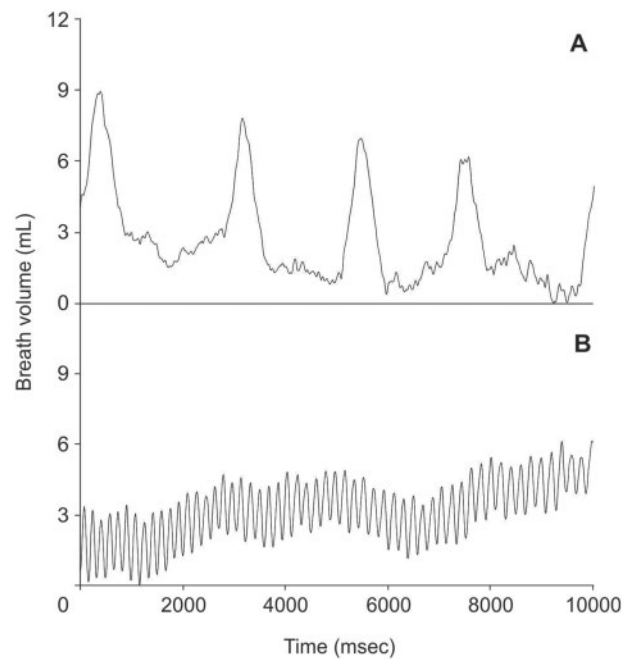


Figure 1. Typical breathing trace for rabbits. (A) At rest, before the introduction of an odor. (B) Alert, after the introduction of an odor.

Before and after exposure differences

Mean resting f_R (in the minute before exposure to the odors) ranged from 46.5 ± 10.9 breaths min^{-1} (before horse odor) to 74.5 ± 15.5 breaths min^{-1} (before quoll odor), and V_T from 4.9 ± 0.9 mL (before quoll odor) to 8.1 ± 1.3 mL (before horse odor). In the first minute after introduction of the odors mean f_R increased significantly ($t_5 \geq 2.84$; $P \leq 0.04$) compared to the minute before for all odors (range 129 ± 50.3 breaths min^{-1} to 253 ± 25.1 breaths min^{-1}) except distilled water (122.8 ± 50.48 breaths min^{-1} ; $t_5 = 1.64$; $P = 0.16$; Figure 2A). Mean V_T decreased significantly ($t_5 \geq 2.61$, $P \leq 0.04$) for all odors (range 2.4 ± 0.2 mL to 3.3 ± 0.6 mL) except distilled water (3.8 ± 0.6 ; $t_5 = 1.52$, $P = 0.18$) and fox (3.0 ± 0.5 ; $t_5 = 2.03$; $P = 0.09$; Figure 2B).

Odor and time effects

Odor had a significant effect on both f_R and V_T . The addition of odor as a fixed factor significantly improved mixed effects models for analyses of “before odour” (LRT = 8.00, $\chi_{5,8} = 16.0$, $P = 0.007$), “after odour” (LRT = 46.6, $\chi_{5,8} = 93.0$, $P < 0.001$), and “after/before ratio” (LRT = 15.2, $\chi_{5,8} = 30.3$, $P < 0.001$) data for f_R compared to a random intercept only model (i.e., with no fixed factors). Similar improvement in mixed effects models after the introduction of odor as a fixed factor was observed for V_T (“before odour” LRT = 27.8, $\chi_{5,8} = 55.6$, $P < 0.001$; “after odour” LRT = 20.5, $\chi_{5,8} = 41.1$, $P < 0.001$; “after/before ratio” LRT = 21.2, $\chi_{5,8} = 42.4$, $P < 0.001$) compared to a model with no fixed factors. The addition of time as a fixed factor did not further improve any of the “after odour” models (f_R LRT = 5.8, $\chi_{24,32} = 11.6$, $P = 0.98$; V_T LRT = 8.0, $\chi_{24,32} = 15.9$, $P = 0.89$) or “after/before” ratio models (f_R LRT = 9.8, $\chi_{24,32} = 19.6$, $P = 0.72$; V_T LRT = 8.1, $\chi_{24,32} = 16.1$, $P = 0.88$; Figure 3), and there were no significant interactions between odor and time. This indicated that the rabbits’ response to the various odors was maintained at a similar level throughout

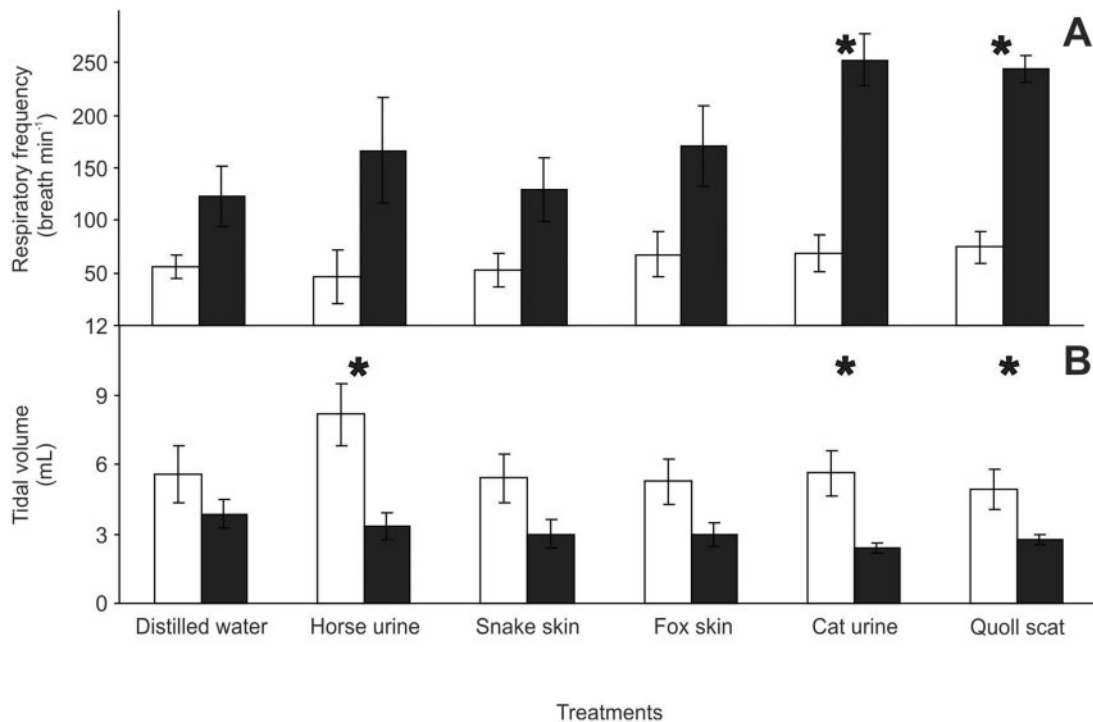


Figure 2. Respiratory frequency (A) and tidal volume (B) of rabbits before (white bars) and after (black bars) exposure to predator (fox, cat, quoll, and snake) and control (horse, distilled water) odors. Respiratory frequency increased significantly in response to all odors except distilled water and tidal volume decreased significantly in response to all odors except distilled water and fox. An asterisk indicates a significant difference in the after/before ratio compared to distilled water at $P < 0.05$. Values are mean \pm SE, $N = 6$.

the 5-min postexposure period, so time was not included in further analyses.

During the minute before the introduction of the odor, individual rabbit accounted for 36% of the variance for f_R and 45% of the variance for V_T . Rabbits had a significantly higher f_R before the introduction of quoll odor ($t = 2.17$, $P = 0.03$) compared to the water control, and a significantly higher V_T ($t = 5.64$, $P < 0.001$) before the introduction of horse odor compared to the water control. After the introduction of the odors, individual rabbit accounted for 19% of the total variation in f_R and 15% in V_T . f_R was significantly higher in response to the introduction of cat ($t = 7.11$, $P < 0.001$) and quoll ($t = 6.83$, $P < 0.001$) odors compared to the water control, and V_T was significantly lower in response to cat ($t = 4.30$, $P < 0.001$) and quoll ($t = 4.16$, $P < 0.001$) odors compared to the water control. Individual rabbit accounted for 39% of the “after/before ratio” variance for f_R , and 34% for V_T . Cat ($t = 3.77$, $P < 0.001$) and quoll odors ($t = 2.40$, $P = 0.02$) elicited significantly higher f_R after/before ratios than the water control (Figure 2A); there was no difference between the water control and the other odors ($t < 1.83$, $P > 0.07$). Cat ($t = 5.31$, $P < 0.001$), quoll ($t = 3.23$, $P = 0.001$), and horse ($t = 3.93$, $P < 0.001$; Figure 2B) odors elicited a significant reduction in V_T after/before ratios compared to the water control; there was no difference between the water control and fox ($t = 0.12$, $P = 0.91$) or snake ($t = 1.12$, $P = 0.26$) odors.

Discussion

Our study demonstrates that European rabbits, introduced to Australia by European settlers, have a physiological response to both a historically novel Australian marsupial predator (quoll), and

a placental predator with a longer evolutionary history (cat). Therefore, although rabbits did not behaviourally avoid quoll odor (Barrio et al. 2010), they did respond physiologically, by increasing their alertness. Hence, it appears that rabbits can detect historically novel marsupial predators, as well as more historically familiar felids. This study highlights the utility of physiological measures for examining predator-prey relationships, as behavioral measures of prey response may be more difficult to determine, particularly if there are conflicting demands such as a requirement to forage versus predator avoidance.

The rabbits' mean resting (before odor introduction) f_R was 60.9 breath min^{-1} and V_T was 319 mL min^{-1} over all experiments ($N = 6$, $n = 36$), similar to a predicted resting f_R of 60 – 70 breaths min^{-1} (Kleinman and Radford 1964) and V_I of 420 mL min^{-1} (Stahl 1967) for a rabbit-sized mammal. This indicates that rabbits were calm and resting before introduction of the treatments, so there was sufficient scope to detect a physiological response after exposure to the odors. There was substantial individual variability in f_R and V_T values among rabbits before introduction of the odors, presumably reflecting varying prior experiences (Vitale 1989) and/or differing “personality” of these wild-caught individuals (Careau and Garland 2012). An individual's prior experience may influence the response of prey species to predator odors (Blumstein 2002). Wild rabbits were used for this study, as the antipredator responses of captive individuals bred and housed in a predator-free environment may not be representative of those of wild individuals (Blumstein et al. 2002). However, this means that any previous predator encounters for our individual rabbits are unknown. It is likely that rabbits would be familiar with all the predator odors except quoll, and possibly horse, as cats, foxes, and snakes are almost certainly present in the area from where the rabbits were captured. However, individual

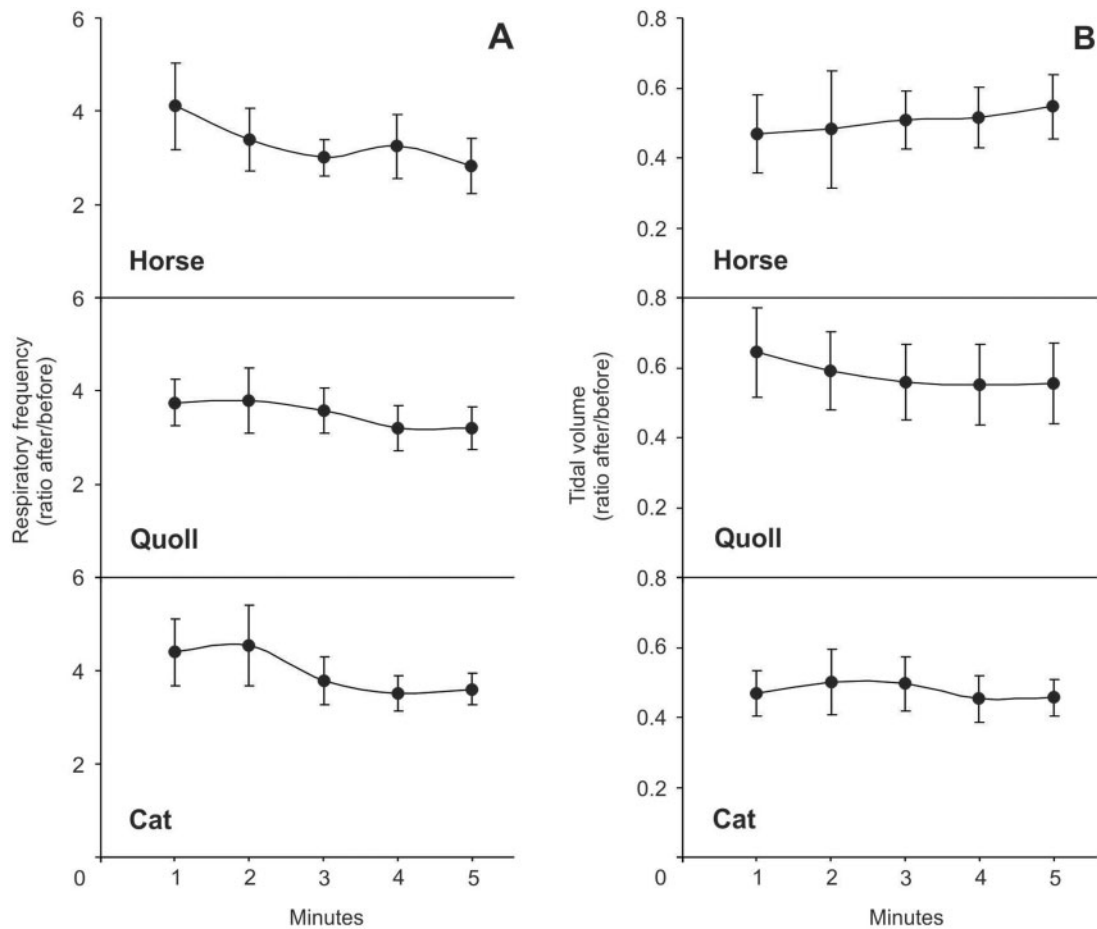


Figure 3. Time course of the rabbits' response to a herbivore (horse) and two predator (cat and quoll) odors. Respiratory frequency (A) and tidal volume (B) remained constant during the 5 min following exposure to the odors. Values are mean \pm SE, $N=6$.

variability in odor response was less after introduction of the odors, suggesting a common physiological response to olfactory cues, and there was no pattern of response intensity with the likelihood of previous predator encounters.

A ventilatory response (either increasing f_R , decreasing V_T or both) was observed for all odor treatments, but there was no significant response to the unscented control of distilled water, indicating that the rabbits were reacting to the odors and not to any disturbance resulting from the introduction of the treatments into the airstream. Modification of respiratory parameters can be considered an index of response to sudden environmental changes, representing an individual's readiness for a consequent behavioural reaction, such as physical exertion (Burmistrov and Shuranova 1996; Schapker et al. 2002). Therefore, the rabbits' responsiveness to the olfactory treatments may indicate high sensitivity to stimuli in their environment and quick reaction time (as suggested for rats, *Rattus rattus*; Burwash et al. 1998). Similar rapid increase in f_R in response to odors has also been associated with increased alertness for tamar wallabies (*Macropus eugenii*; Mella et al. 2010).

Despite an observed response to all odors, the intensity of the rabbits' physiological response varied for different predator odors relative to the unscented distilled water control. A significantly higher V_T for rabbits before introduction of horse odor makes interpretation of a significant after/before ratio for this odor difficult. However, a similar f_R after/before ratio for horse and distilled water, together with the same f_R and V_T after exposure for horse and water

suggest that this elevated after/before ratio is a consequence of the elevated V_T before exposure to horse odor, and not a response to the odor itself (Figure 2). Cat and quoll odor consistently elicited significant respiratory responses, but fox and snake did not. Rabbits have previously shown physiological and behavioral responses when exposed to fox odor (Monclús et al. 2005, 2006a, 2006b; Barrio et al. 2010), so similarity of response intensity to fox odor compared to control in our study was surprising.

One possible explanation for the unexpected lack of response to fox odor is that comparison between odors in our study is confounded by odor source (pelt/skin versus urine versus feces). It may be possible that the odor intensity of the pelt/skin sources used in the experiment did not resemble those normally encountered by prey in the presence of a real predator (Apfelbach et al. 2005; Bytheway et al. 2013). However, changes in ventilatory variables were greater in response to cat urine and quoll feces than they were to horse urine. We could also detect a strong odor from all samples, including the fox and snake skin, so presumably the rabbits could too. Hence, although we cannot discount the possibility that the moderate response of the rabbits to fox and snake odor may be related to low effectiveness of our pelt/skin samples compared to waste products, comparison of responses to cat, quoll, and horse, relative to the water control, suggest that the rabbits did indeed respond to two of the predatory species more intensely.

Cats share a considerable evolutionary history with European rabbits (Malo et al. 2004), are considered major predators for

rabbits in Australia (Jones and Coman 1981; Catlin 1988; Molsher et al. 1999) and rabbits behaviorally avoid cat odor cues (Barrio et al. 2010). Therefore, odor recognition for cats was expected. However, rabbits do not share a long period of sympatric evolution with quolls, but they also showed a strong reaction to their odor, despite the findings of Barrio et al. (2010) that rabbits do not behaviorally avoid quoll odor. Quolls are opportunistic predators with strongly scented body and feces and include rabbits in their diet (Pollock 1999; Glen and Dickman 2006; Oakwood 2008). Therefore, it is conceivable that rabbits may consider quoll odor a potential cue of predation risk, and our physiological data indicates that they certainly increase alertness and therefore respond to the odor, even if this does not translate into behavioural avoidance of quoll-scented areas (Barrio et al. 2010). Quolls commonly use latrines (Kruuk and Jarman 1995), but these may not necessarily coincide with foraging areas, so avoiding quoll fecal odor may be unnecessary for prey. Our results suggest that rabbits are indeed able to recognize quoll odor as a potential threat and are ready to react in case of danger. Other studies suggest that prey species do not necessarily completely avoid areas with detectable predator odors, if these odors do not contain information about immediate risk (e.g., Mella et al. 2014).

Our results indicate that rabbits do not only have a physiological response to predators with which they share a long period of coevolution, they also respond to historically novel marsupial predators. It has been suggested that rabbits can respond to novel predator odors (e.g., Boag and Mlotkiewicz 1994) because they show a generalized response to odors of well-known predator types (e.g., felids), rather than a specific response to predator species (Barrio et al. 2010). Our study is the first to demonstrate that rabbits increase alertness when faced with a novel predator archetype, with a very different evolutionary path from historically known or closely related predators.

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