

Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear

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Abstract Predators attack and plants defend, so herbivores face the dilemma of how to eat enough without being eaten. But do differences in the personality of herbivores affect the foraging choices of individuals? We explored the ecological impact of personality in a generalist herbivore, the brushtail possum (*Trichosurus vulpecula*). After quantifying personality traits in wild individuals brought temporarily into captivity, we tested how these traits altered foraging by individuals when free-ranging in their natural habitat. To measure their responses to the dual costs of predation risk and plant toxin, we varied the toxin concentration of food in *safe* foraging patches against paired, non-toxic *risky* patches, and used a novel synthesis of a manipulative Giving-Up-Density (GUD) experiment and video behavioural analysis. At the population level, the cost of *safe* patches pivoted around that of *risky* patches depending on food toxin concentration. At the individual level, boldness affected foraging at *risky* high-quality food patches (as behavioural differences between bold and shy), and at *safe* patches only when food toxin concentration was low (as differences in foraging outcome). Our results ecologically validate the personality trait of boldness, in brushtail possums. They also reveal, for the first time, a nuanced link between personality and the way in which individuals balance the costs of food and fear. Importantly, they suggest that high plant defence effectively attenuates differences in foraging behaviour arising from variation in personality, but poorly defended plants in safe areas should

be differentially subject to herbivory depending on the personality of the herbivore.

Keywords Boldness · Ecological validation · Plant toxins · Predation risk · Brushtail possum

Introduction

Most animals have to tackle the problem of finding food in a landscape of fear. But for herbivores, the problem is two-fold because they face costs associated not only with their predators but also from the plants they consume. Plants use defences such as toxins and digestibility reducers to lower food quality and hence decrease herbivory (McArthur et al. 1991). These defence compounds constrain the range of plants on which herbivores feed (Provenza and Malechek 1984; McArthur et al. 1993), reduce how much they eat (Lawler et al. 1998; Wiggins et al. 2003; Sorensen et al. 2005) and, ultimately, can influence herbivore fitness (DeGabriel et al. 2009). Plant toxin concentration varies across the landscape (Lawler et al. 2000; O'Reilly-Wapstra et al. 2004; Villalba and Provenza 2005; Andrew et al. 2007), forcing herbivores to search for high-quality food, and, as they do, they are exposed to different levels of predation risk.

The fear of predation is an influential modifier of prey behaviour (Lima and Dill 1990; Preisser et al. 2005; Creel and Christianson 2008), with many potential triggers including direct cues of predation, such as predator odours (e.g. Mella et al. 2010, 2014a; Banks et al. 2014) and indirect cues from the environment, such as habitat characteristics (Mella et al. 2014b). As these cues vary in space and time, so does the landscape of fear (Laundré et al. 2001; van der Merwe and Brown 2009). To avoid predation, prey

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can forgo foraging opportunities; yet to avoid starvation, they may sacrifice safety to access food.

The dual costs of food and fear together affect foraging decisions, and animals often trade-off the two (e.g. Hernández and Laundré 2009). Manipulative studies show an integrated influence of plant toxins and predation risk on foraging behaviour of free-ranging mammals (Schmidt 2000; Fedriani and Boulay 2006; Hochman and Kotler 2006; Shrader et al. 2008; Kirmani et al. 2010). With increasing dietary toxin, captive herbivores (e.g. common brushtail possums, *Trichosurus vulpecula*; Nersesian et al. 2011) and free-ranging frugivores (e.g. thick-tailed bushbabies, *Otol-emur crassicaudatus*; McArthur et al. 2012) shift from foraging in *safe* but toxic food patches to preferring *risky* but non-toxic ones.

However, individuals within a population may manage foraging costs in different ways, as a function of their personality (defined as the consistent difference in behaviour between individuals; Réale et al. 2007). Research with captive mammalian herbivores, such as sheep (*Ovis aries*; Michelena et al. 2009) and fallow deer (*Dama dama*; Bergvall et al. 2011) show that bold individuals (those with a greater propensity to take risks; van Oers et al. 2004; Wolf et al. 2007), are more likely to explore new foraging opportunities than shy individuals. Similarly, bold free-ranging grey mouse lemurs (*Microcebus murinus*) take less time to enter risky feeding stations than shy individuals (Dammhahn and Almeling 2012).

Studies on fish (e.g. Wilson and McLaughlin 2007; Pellegrini et al. 2010), birds (e.g. Dingemanse et al. 2003; Herborn et al. 2010; Minderman et al. 2010) and mammals (e.g. Dammhahn and Almeling 2012) have ecologically validated personality measured in captivity. This validation is important for comprehending how individual differences in behaviour arise and are maintained in a population and for understanding the fitness consequences of personality (Réale et al. 2007; Minderman et al. 2010).

To date, little is known of how personality affects responses of free-ranging herbivores to the dual costs of plant defense and predation risk, but this is important because herbivores are the key link between plants and higher trophic levels. Capturing how personality modifies foraging decisions should improve our understanding of plant-herbivore interactions, predator–prey dynamics and community ecology.

Our aim, therefore, was to determine how personality shapes the foraging responses of a generalist mammalian herbivore to plant toxins and perceived predation risk. We used the brushtail possum as a model because it confronts a toxic leaf diet daily (Freeland and Winter 1975), while also being vulnerable to predation (Kerle and How 2008). We quantified, in captivity, personality traits among individuals

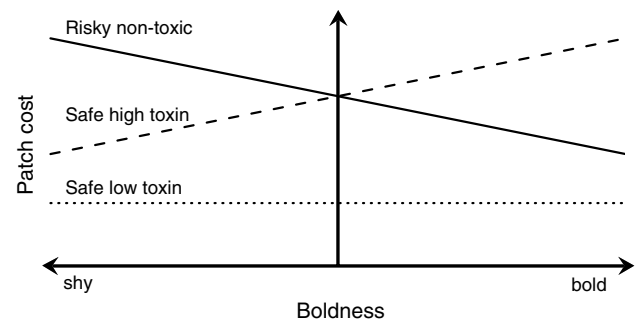


Fig. 1 Predicted influence of personality on herbivores perceived patch cost (e.g. GUD) at *risky* non-toxic food patches (solid line) and *safe* food patches varying in toxin concentration (dotted line for low cineole concentration and dashed line for high cineole concentration)

from a wild population and then validated the ecological significance of these traits in the field.

To do this, we tested how wild, free-ranging brushtail possums responded to the trade-off between food quality and predation risk at the population level, and how personality modified individual foraging responses. At the population level, we predicted that individuals would prefer safe non-toxic food patches over risky non-toxic patches, but that their preference would switch as the cost of safe patches rose with increasing toxin concentration of food (consistent with Nersesian et al. 2011; McArthur et al. 2012). At the individual level, our hypothesis was that personality differences among individuals would alter how much time they spent, how much food they harvested, and how they behaved at feeding stations differing in plant toxin concentration and perceived predation risk. Specifically, we predicted that bolder individuals would favour risky food patches, shy individuals would prefer safety at the expense of food quality, but that bold and shy animals would value safe, high-quality food patches (Fig. 1; McArthur et al. 2014).

Materials and methods

Study species and study site

Brushtail possums are small (2–5 kg), solitary, nocturnal, arboreal marsupials (Kerle and How 2008) that choose foraging patches based on food quality (Pietrzykowski et al. 2003; Wiggins et al. 2003) and safety (Le Mar and McArthur 2005b; Kirmani et al. 2010; Mella et al. 2014b). They can consume higher-quality food on the ground than in the trees (Freeland and Winter 1975), but perceive food patches on the ground as riskier than those above ground (Mella et al. 2014b).

We studied possums from Ku-ring-gai Chase National Park, New South Wales, Australia (33°41'16.24"S, 151°09'11.90"E). The Park is dominated by eucalypt woodland and inhabited by terrestrial predators, such as the invasive red fox (*Vulpes vulpes*; Kovacs et al. 2012) and the occasional domestic dog (*Canis lupus familiaris*; Banks et al. 2003), and avian predators of possums, such as the native powerful owl (*Ninox strenua*; Kavanagh 2003).

Personality tests

We trapped exhaustively in the park, over an area of ~50 ha for 12 weeks at night, using live cage traps (66 cm L × 24 cm W × 24 cm H; model 205; Tomahawk, USA) following standard operating procedures for marsupials (Petit and Waudby 2012). Trap success was low (5 %) but not unusual for small Australian mammals (e.g. Woinarski et al. 2001; Vernes and Pope 2006). Population density estimate was 0.3 possums ha⁻¹, similar to other studies in south/eastern Australia (Dunnet 1964; Le Mar and McArthur 2005a). We caught 13 adult brushtail possums (4 females, 9 males), suggesting a high proportion of the population in that area had been captured.

We measured consistency in individual behavioural traits relating to docility (sensu Réale et al. 2000; Korhonen et al. 2002) by using a handling bag test (i.e. measuring immobility; Martin and Réale 2008a, b). Captured individuals were released from the trap into a hessian bag and suspended in the bag for 1 min, while time spent static was quantified. In studies on other species, stressed animals (based on cortisol levels) were less mobile during human handling and consequently defined as docile (Koolhaas et al. 1999; Martin and Réale 2008a). During our handling bag test, we therefore considered less mobile (i.e. more static) possums as more docile. Each possum was then weighed, sexed, fur-marked and microchipped with uniquely numbered PIT tags (Bio-mark HPT12) inserted subcutaneously between the shoulder blades.

Captured possums were then brought into captivity for 10 days to run arena tests (modification of open-field tests; Walsh and Cummins 1976) under standard conditions, in a natural forest setting at Cowan Field Station (University of New South Wales, Muogamarra National Park, New South Wales, Australia), 10 km north of the study site. We chose to bring animals into captivity, because a pilot study indicated low repeat capture rates (~50 % of possums not re-caught) and we wished to avoid possible bias towards re-trappable animals (Biro and Dingemanse 2009). Possums were housed individually in outdoor pens (12 m L × 5 m W × 4 m H) made with wire netting, natural soil base, branches for climbing and a nest box. They were provided with ad libitum water and fresh food (fruit, eucalypt leaves and rabbit food pellets; Stockfeeds, Narellan, New

South Wales). Possums were left undisturbed in the pens for two nights to allow settling.

For the behavioural tests, an individual possum was moved to one of two large outdoor fenced arenas (wire netting, 70 m L × 2.5 m W × 5 m H) on its own for one night and tested during its active phase (night time). To ensure the possums experienced natural conditions during the quantification of personality (as recommended by Niemelä and Dingemanse 2014), arenas were set within the forested area of the field station. Each arena had very little ground cover, no trees or shrubs and only one refuge, the individual nest box. We avoided handling possums before the tests by shifting them to the arenas during the day, while they slept in their nest boxes. Each nest box was placed in the same location at one end of the arenas and the trial began when a possum first emerged from its refuge at dusk.

In each arena, three identical stations (27 cm L × 33 cm W × 100 cm H) were set at different distances from the nest box: 1, 35 and 70 m. We filmed the possums at the stations and at the nest box with motion-sensitive infra-red digital cameras (ScoutGuard model SG550) for the entire night (ca. 12 h). This provided a greater scope for individuals to demonstrate variation in behaviours and allowed time to visit all the stations. The time at the stations and at nest box (where behaviours were recorded) represented on average only 15 min (2 %) of the total time spent in the arenas. The remaining time was spent moving in the arena and sleeping in the nest box. We scored and quantified behaviours related to boldness and activity/exploration from video footage using JWatcher (Blumstein and Daniel 2007).

The next day, the possums were returned to their original pen, where they were housed for 1 week before repeating the tests in the same arena (on night 10 of captivity) to estimate behavioural consistency. This is a moderately short timeframe relative to the life span of the species, but it is similar to other studies (e.g. Kurvers et al. 2010; Sinn et al. 2014). We consider this interval adequate because we were not aiming to define lifetime consistency in behaviour and because longer timeframes in captivity alter behaviour of brushtail possums (Day and O'Connor 2000). After the tests were repeated, possums were returned to their enclosures. The following night, they were moved from the nest box into a hessian bag to perform a second handling bag test before being transported back and released at their site of capture in Ku-ring-gai Chase National Park.

The significance of the behaviours as personality traits was assessed using general linear mixed-effect models, log-likelihood ratio tests and calculating repeatability for the traits (after Dingemanse and Dochtermann 2013). We tested the significance of between-possum difference in behaviour (i.e. personality) by running two models with multiple fixed factors (*test-number*, *arena-number*, *sex* and *body weight*),

with and without *possum identity* as a random effect, using the REML method in SAS (PROC MIXED; SAS Institute, 2003). We followed statistical methods outlined in Dingemans et al. (2010) and Dochtermann and Jenkins (2011), appropriate for our small sample size. We chose not to use principal component analysis (PCA) to reduce the number of variables because we were interested in finding specific repeatable behaviours to quantify personality.

Food quality-predation risk experiment

After the possums were released at the site of capture, we chose six sites within the trapping area for our food quality–predation risk experiment. Sites were spaced at least 400 m apart to ensure different possums visited each site. At each site, we set up four pairs of feeding stations (eight feeding stations per site), each pair consisting of a 1.5 m high above-ground *safe* feeder and an on-ground *risky* feeder (based on Mella et al. 2014b). Each feeder was fitted with an infra-red motion sensitive digital camera (Scout-Guard SG550v) to film the behaviours of possums at the feeders.

We used the plant toxin 1,8-cineole, a volatile terpene commonly found in leaves from many *Eucalyptus* species consumed by possums (Moore et al. 2004; O'Reilly-Wapstra et al. 2004). Following McArthur et al. (2012) and Nersesian et al. (2011), we varied the concentration of the toxin in food placed in the *safe* feeders, while the food placed in *risky* feeders was always toxin-free. We prepared four different diets by grinding commercial rabbit pellets and adding one of four 1,8-cineole (purity 99 %; Felton Grimwade & Bickford, Oakleigh South, Victoria, Australia) concentrations (0, 1, 5, 10 %), 6 % water and 10 % raw sugar to each of the ground diets before repelleting them (size: 8 mm Ø × 2 cm L) in a stock feed pelleting machine (Buskirk Engineering, model PM605). The influence of these toxin concentrations on food intake resembles those of natural food (O'Reilly-Wapstra et al. 2004; Marsh et al. 2006b). Each diet was prepared in separate batches to avoid cross-contamination between cineole treatments. The food was placed in airtight containers, kept at 4 °C and used within a week, to prevent cineole evaporation.

We used the Giving-Up-Density (GUD) approach (Brown 1988), by daily counts of the number of food items remaining after the previous night of foraging. For the experiment, 20 pellets were mixed with an inedible matrix (1.2 kg sawdust), placed in plastic containers (12 cm H × 27 cm L × 33 cm W) attached to the feeding stations, and replaced daily. One pellet was always placed on top of the sawdust. If it remained untouched, we considered that the feeder had not been visited unless video evidence showed otherwise. The experiment ran for 4 consecutive days at each site over a total period of 2 weeks (some sites

were visited earlier than others). Cineole treatments were switched within a site, every day, in a cross-over design (Ratkowsky et al. 1993) until all treatments were presented at each *safe* feeder within each site.

How do free-ranging brushtail possums respond to food quality and predation risk?

We tested whether the GUD obtained from *safe* and *risky* feeders, and the difference in GUD between *safe* and *risky* patches was a function of the cineole treatment, following McArthur et al. (2012). The three dependent variables of *safe*-GUD, *risky*-GUD and *difference*-GUD, were each tested using the mixed model procedure in SAS (PROC MIXED). The *difference*-GUD model was run to incorporate the paired nature of the *safe* and *risky* feeders in the experimental design. *Cineole concentration* (continuous) and *experimental day* were fixed effects. *Site*, *feeder number* and the interactions between *site* × *experimental day* and *site* × *cineole concentration* were included in the model as random factors.

Does personality influence individual foraging response to food and fear?

To test the effect of personality on GUD, we determined which individual possum was responsible for the final GUD at each feeding station throughout the experiment using video identification. Four of the six sites were visited only by marked (known) individuals, but two sites were visited by both marked and unmarked (unknown) individuals. Data from any unmarked possum responsible for the GUD at the patches (based on video footage of the last forager) were excluded from the personality analyses (16 % of all data). There was no bias across treatments in excluded data.

The available sample size for quantifying foraging responses depended on population density, on trappability of possums for the personality evaluation, and on the willingness of free-ranging individuals to visit feeding stations in the wild. Despite extensive efforts, sample size of individuals at feeding stations was low ($n = 6$ of the 13 individuals with quantified personality traits). However, we observed each individual multiple times (19–38 samples per individual), and, by using a cross-over experimental design (described later), each was observed under a range of different treatment levels across several nights and feeders (total $n = 192$ feeder-nights), essentially acting as its own control. Sample size and design was therefore similar to many captive animal studies of diet, diet selection and ecophysiology (e.g. Marsh et al. 2005, 2006a; Shipley et al. 2006, 2012; Nersesian et al. 2011, 2012) and, we argue, sufficient to test for strong (but not weak) linear relationships between foraging response variables and personality.

For statistical analysis, we grouped cineole treatments at the *safe* feeders into *low* (0 and 1 %) and *high* (5 and 10 %) cineole concentration, to increase power for testing the effect of personality on GUD. The effects of *personality* (i.e. boldness, exploration/activity or docility), *sex* and *body weight* were tested together in three separate models on (1) *safe*-GUD at *low* cineole concentration, (2) *safe*-GUD at *high* cineole concentration, and (3) *risky*-GUD using the mixed model procedure in SAS (PROC MIXED).

We used JWatcher (Blumstein and Daniel 2007) to quantify individual foraging (time spent searching for food through the sawdust and eating) and vigilance behaviour (as proportion of time spent standing immobile with head and ears raised) during the focal time. We used proportion of time spent vigilant because as total time spent at the feeder increases, the total time spent vigilant may also increase simply because animals spend more time there. Proportional vigilance should therefore reveal more informative patterns of alertness. We tested the effects of *personality* (i.e. boldness, exploration/activity or docility), *sex* and *body weight* on these behaviours as above.

One of the possums foraged for over 8 min at the *safe* patches with 0 % cineole concentration. We therefore tested data with and without this outlier and the significance of the results was not affected.

Results

Personality tests

Possum identity had a significant effect on three behaviours (Fig. 2): time spent static in the handling bag test (i.e. docility, LRT = 43.3; $P < 0.001$), number of times possums emerged from the next box to explore the arena (i.e. activity/exploration, LRT = 9.3, $P = 0.002$) and propensity to forage in an unfamiliar environment (Wilson et al. 1993, 1994; Rekilä et al. 1997), calculated as time spent foraging (i.e. boldness, LRT = 9.2, $P = 0.002$). Other behaviours recorded during the arena tests were not consistent within individuals and were therefore discarded. *Test-number*, *arena-number*, *sex* and *body weight* did not have a significant effect on any of the traits ($F_{1,10} \leq 3.06$, $P \geq 0.11$). Repeatability was high for all traits (0.98 for docility, 0.96 for exploration/activity and 0.67 for boldness).

How do free-ranging brushtail possums respond to food quality and predation risk?

Possums visited on 83 % of 192 feeder-nights and at least one feeder for each *safe*-*risky* pair was always visited. *Risky*-GUD was not a function of the *cineole concentration* in the *safe* patch ($F_{1,89} = 1.91$, $P = 0.17$; Fig. 3). In

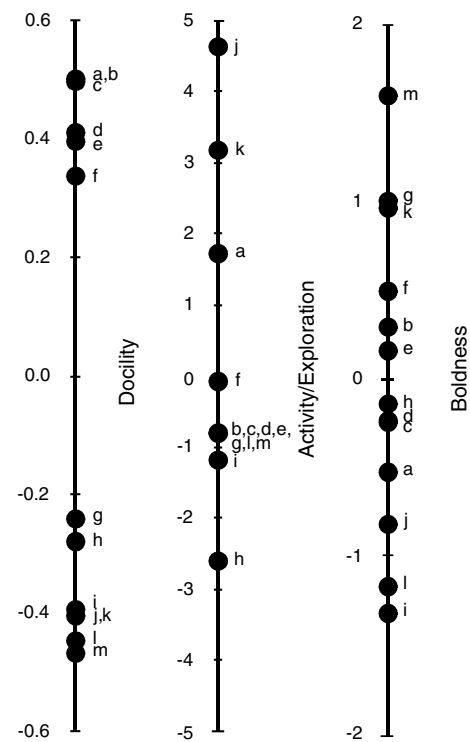


Fig. 2 Best linear unbiased predictors from univariate models of docility, activity/exploration and boldness are used to illustrate the relative value of each personality trait for individual possums. Each individual is represented by a different letter ($n = 13$)

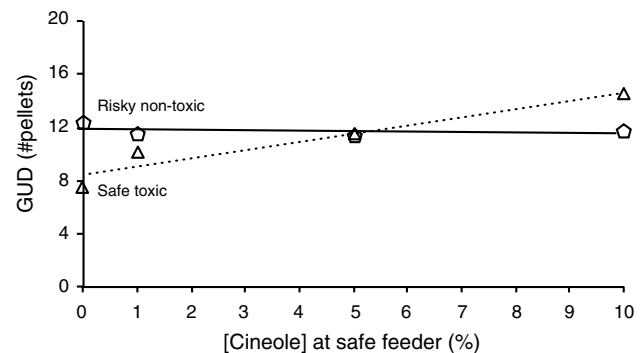


Fig. 3 Giving-up-density at *risky* non-toxic feeders (open pentagon) and *safe* variably toxic feeders (open triangle) as a function of toxin concentration at *safe* feeders. Values are least-square means

contrast, *safe*-GUD significantly increased ($F_{1,89} = 6.95$, $P = 0.009$; Fig. 3) with increasing toxin concentration at *safe* feeders, hence *difference*-GUD ($F_{1,89} = 4.41$, $P = 0.04$) was also affected. The point where *safe* and *risky* feeders were equivalent (equivalence point; sensu McArthur et al. 2012) occurred at cineole concentration of 5 %. At the highest cineole concentration, possums preferred to feed at *risky* rather than *safe* feeders (Fig. 3). *Experimental day* ($P \geq 0.418$), *site* ($P \geq 0.288$), *feeder number*

($P \geq 0.323$), *site* \times *experimental day* ($P \geq 0.136$) and *site* \times *cineole concentration* ($P \geq 0.574$) were not significant for any of the variables tested and were therefore removed from the final models.

Does personality influence individual foraging response to food and fear?

Six (3 females and 3 males) of the possums with quantified personality traits visited the feeding stations during the experiment and were responsible for the final GUD at the patches. This subsample of individuals showed a similar range in values for the three personality traits to that of the total sample tested (see Fig. 2, $n = 13$ vs. Fig. 4, $n = 6$). There was no effect of *boldness* on GUD at *risky* feeders ($F_{1,4} < 0.01$, $P = 0.97$; Fig. 4a), but GUD increased with boldness at *safe* feeders with *low* cineole concentration ($F_{1,4} = 10.92$, $P = 0.03$; Fig. 4a). In contrast, at *safe* feeders with *high* cineole concentration the effect of boldness on GUD was not significant ($F_{1,4} = 0.06$, $P = 0.82$; Fig. 4a). Neither *docility* ($F_{1,4} \leq 2.76$, $P \geq 0.17$) nor *activity/exploration* ($F_{1,4} \leq 5.13$, $P \geq 0.09$) had a significant effect on GUD. *Sex* ($P \geq 0.07$) and *body weight* ($P \geq 0.09$) were removed from the final models as they had no significant effect on GUD.

The dominant behaviours at feeders were foraging (average 30–38 %) and vigilance (20–23 %). The rest of the time possums spent investigating (sniffing and inspecting the feeders), moving (approaching/leaving the feeders), self-grooming/scratching and interacting with other individuals. Possums normally visited the feeders alone but we occasionally recorded aggressive interactions between two individuals. This resulted in a brief confrontation with one possum leaving the site, but most of these individuals (hence personality traits) were unidentified.

At *risky* feeders, *boldness* had a significant effect on time spent foraging ($F_{1,4} = 20.25$, $P = 0.006$; Fig. 4b). At *safe* feeders with *low* cineole concentration, time spent foraging also depended on *boldness* ($F_{1,4} = 7.33$, $P = 0.05$; Fig. 4b), but it did not at *safe* feeders with *high* cineole concentration ($F_{1,4} = 0.65$, $P = 0.46$; Fig. 4b). Bolder possums spent significantly more time foraging at the *risky* and at the *safe* feeders with *low* cineole concentration than did the shy. At *safe* feeders with *high* cineole concentration possums spent little time foraging irrespectively of their personality. There was no significant effect of *boldness* on proportional time spent vigilant at *risky* feeders ($F_{1,4} = 0.99$, $P = 0.36$; Fig. 4c), at *safe* feeders with *low* cineole concentration ($F_{1,4} = 0.61$, $P = 0.48$; Fig. 4c) or at *safe* feeders with *high* cineole concentration ($F_{1,4} = 5.08$, $P = 0.09$; Fig. 4c). Neither *docility* ($F_{1,4} \leq 2.94$, $P \geq 0.16$) nor *activity/exploration* ($F_{1,4} \leq 1.29$, $P \geq 0.32$) had a significant effect on any behaviour at the feeders. *Body*

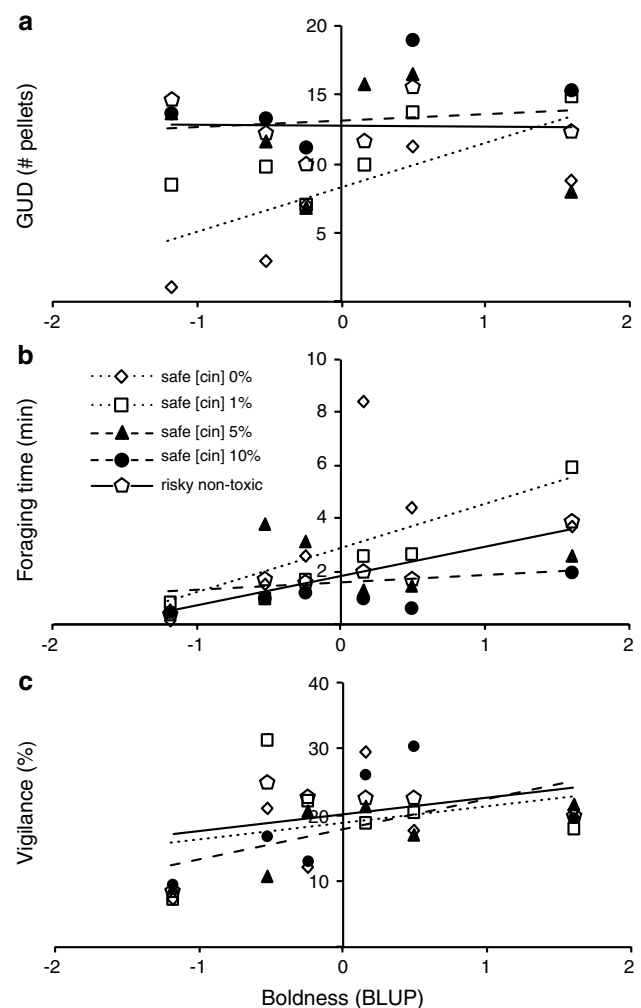


Fig. 4 Effect of boldness on Giving-Up-Density (a); time spent foraging (b); vigilance as a percentage of total focal time at the feeder (c) for possums ($n = 6$) at *risky* non-toxic feeders (*compact* line) and *safe* feeders at *low* (open symbols, dotted line) and *high* (closed symbols, dashed line) cineole concentration. Values are least-square means per individual possum

weight ($P \geq 0.15$) and *sex* ($P \geq 0.16$) had no significant effect on time spent foraging or vigilant so were removed from the final model.

Discussion

We found consistent, highly repeatable between-individual differences in three behavioural traits—docility, activity/exploration and boldness—in brushtail possums tested in captivity. The relatively short interval between repeat tests means that the consistency we quantified may reflect short-term rather than longer-term behavioural traits (Dingemanse et al. 2012), since personality may change as individuals age (Petelle et al. 2013). Nevertheless, we were able to

demonstrate the relevance of these traits to differences in individual foraging patterns over a similar, short timeframe.

Population level response to food and fear

Our results demonstrate that free-ranging possums responded to the dual influence of plant toxin and predation risk at food patches in their natural environment. At the population level, toxin-free *safe* feeders were preferred (i.e. lower GUD) to toxin-free *risky* feeders, indicating that possums perceived them as higher-quality patches, as predicted (based on Mella et al. 2014b). The cost of plant toxin pivoted around the cost of predation risk as a function of its concentration (Fig. 3), consistent with previous studies (Nersesian et al. 2011; McArthur et al. 2012). GUD remained unchanged at *risky* but non-toxic patches, as with free-ranging thick-tailed bushbabies (McArthur et al. 2012). Hence, it seems that, in the wild, foraging possums do not compensate for low-quality safe food by shifting their feeding to risky locations, in contrast to those in captivity, which have no other alternatives (Nersesian et al. 2011), presumably because they can feed elsewhere.

Individual level response to food and fear as a function of personality

Importantly, we found that the personality trait of boldness (quantified in captivity) shaped the foraging response (in the wild) of individuals to the costs of food (specifically plant toxin) and fear (Fig. 4a, b; as predicted by McArthur et al. 2014). The influence of boldness was manifest at *risky* patches, and at *safe* patches when food was relatively low in toxin or toxin-free. The cost of high toxin concentration in food at *safe* patches swamped any influence of individual personality on foraging. Interestingly, our results did not support the specifics of our conceptual model (Fig. 1), but, rather, demonstrated an unexpected and more nuanced influence of animal personality on how herbivores behave and consume food at patches.

Specifically, shy and bold possums foraged differently at *risky* feeders. Shy possums were more efficient (foraging time per food consumed), yet achieved the same foraging outcome (as GUD) as bold possums, contrary to our predictions (Fig. 1). Shy individuals often have a higher perception of predation risk because they are more fearful (Koolhaas et al. 1999) and, if so, shy possums may have harvested food quickly to reduce the time spent at *risky* feeders. This suggests that herbivores with different personalities perceive the same food patch as differing in foraging opportunity and predation risk.

At *safe* feeders with low cineole concentration, bold and shy possums also varied in their foraging, but here they achieved different foraging outcomes. Contrary to

our expectations, shy possums foraged more efficiently, spending less time yet harvesting more (lower GUD), than bold individuals. This result contradicts the view that boldness is necessarily positively correlated with intake (e.g. Voisinet et al. 1997; Biro and Stamps 2008; Kurvers et al. 2010; Bergvall et al. 2011), and suggests that future studies should ensure intake is quantified along with foraging time.

A possible mechanistic explanation relating foraging strategy to boldness is that shy individuals search for food more methodically and pay greater attention to the environment than bold ones, which, in contrast, sample more superficially and haphazardly (Verbeek et al. 1994; Marchetti and Drent 2000; Guillette et al. 2011; Sih and Del Giudice 2012). An ecological explanation is that shy individuals explore foraging patches quickly to avoid competition with bolder conspecifics, which often outcompete them for access to feeding sites (e.g. Ward et al. 2004; David et al. 2011; Cole and Quinn 2012). If bold individuals spend more time at food patches (e.g. this study; Kurvers et al. 2010; Cole and Quinn 2012), they may actively limit access to feeding sites by shy individuals. In fact, dominant possums tend to exclude other individuals from their territories (Biggins and Overstreet 1978). If shy possums can only access feeding areas briefly, they may compensate by exploiting them efficiently. Consistent with this, poor competitive ability drives individual chub (*Leuciscus cephalus*) to acquire food at elevated rates (Krause 1994).

We conclude that the foraging strategy of shy possums is to limit time spent at the feeders by eating as much as possible (to avoid potential exclusion by competitors) and as fast as possible (to reduce exposure to predators), resulting in better immediate foraging efficiency. Conversely, the bold strategy is to forage slowly because these individuals are more willing to assume the risk of predation and to devote time to unproductive foraging (resulting in higher GUD), because they have a lower perception of starvation risk. As boldness had no effect on vigilance (Fig. 4c), lower foraging efficiency by bold individuals could not be explained by a shift in time allocation from foraging to food defence (i.e. monitoring the food area).

There may be other links between foraging behaviour and animal characteristics, including other personality traits, which we were not able to reveal with our low sample size, but that can be tested in future. For example, some weak patterns (e.g. between exploration and GUD at *risky* feeders) need to be further explored as part of a larger study.

Plant toxins attenuate personality effects

Our results show that plant toxins can represent an overwhelming foraging constraint, one that could not be overridden by individuals with different personality. Bold and

shy individuals foraged in the same way and achieved the same foraging outcome (high GUD) at *safe* feeders with *high* toxin concentration, contrary to our prediction (Fig. 1). High toxin concentration reduces feeding bout size, feeding rate (Wiggins et al. 2003) and total intake due to physiological constraints (Boyle and McLean 2004; Marsh et al. 2006b) and clearly presented an impenetrable physiological barrier irrespective of personality. This supports the concept that environmental stressors (here, as plant toxin) may attenuate or even mask behavioural variation and their links to physiology (Killen et al. 2013).

Taken together, our results show that the difference in GUD observed between toxin-free *safe* feeders and toxin-free *risky* feeders at the population level (Fig. 3) was largely driven by shy animals. The trade-off between food and predation risk is therefore perceived differently by individuals with different personalities, but this only occurs when the toxin concentration is low. In fact, shy possums took advantage of the *low* toxin concentration at *safe* feeders by reducing GUD more than bold individuals, which in contrast fed similarly at *safe* and *risky* patches. Shy animals concentrate their foraging at *safe* non-toxic patches and feed more here, while bold individuals spread their foraging activities among feeders, without perceiving *risky* feeders as more dangerous than *safe* non-toxic ones.

Conclusions and implications for plant-herbivore interactions

From the herbivore perspective, our results are consistent with the view that, within a population, there may be multiple alternative adaptive ways to succeed (Sih et al. 2004; Sih and Del Giudice 2012; Wolf and Weissing 2012). The next step is to determine whether these different foraging strategies are linked to differences in life history strategies and/or fitness.

If we view GUD as a surrogate for herbivory, our results indicate that risky (for herbivores) areas provide plants with relative safety, irrespective of the personality of the herbivore. Similarly, highly defended plants should be less susceptible to consumption from herbivores across the boldness spectrum, and independent of where they grow, because of the significant and over-riding physiological constraint that they impose. In contrast, poorly defended plants should not only be more subject to herbivory in safe (for herbivores) patches in the landscape but also be differentially subject to herbivory depending on the personality of the herbivore. Incorporating personality can therefore enhance our understanding of plant-herbivore interactions, because of its fundamental impact on how individual herbivores perceive habitat quality (in terms of food and fear) and forage within it. This in turn could have far-reaching impacts on ecological communities.

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Conflict of interest The authors declare that they have no conflict of interest.

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