Functional Ecology

British Ecological Society

Functional Ecology 2011 doi: 10.1111/j.1365-2435.2011.01930.x

The foraging tightrope between predation risk and plant toxins: a matter of concentration

Clare McArthur*[,1], Paul Orlando[2], Peter B. Banks[1] and Joel S. Brown[2]

[1]*School of Biological Sciences, The University of Sydney, Heydon-Laurence Building (A08), Sydney, New South Wales, 2006, Australia; and* [2]*Biological Sciences, University of Illinois at Chicago, Chicago, Illinois, USA*

Summary

1. Plants defend and predators attack, provoking the foraging dilemma faced by herbivores and frugivores of how to eat enough without being eaten. High toxin concentration in leaves and fruits inhibits consumption, while predation risk reduces feeding opportunities, as prey forage to avoid encountering predators. Thus, both factors vary and define the quality of the landscape. How foraging animals directly quantify, compare and respond to these two costs has rarely been tested.

2. We show that free-ranging bushbabies – small, frugivorous primates – change their behaviour and use of artificial food patches based on the interplay between toxin concentration in food and patch safety. Using a titration experiment, we demonstrate that bushbabies quantify the relative costs of toxin and fear. We pinpoint where these costs are equivalent and show that animals seek food patches with the lower net cost.

3. We conclude that the ecological effectiveness of plant toxins as defence against consumers needs to be considered in the context of a landscape of fear – and the relative impact of anti-predator tactics and plant defence is strongly shaped by the concentration of these defences.

4. A corollary is that plants may benefit from fear as a substitute for their own chemical defence, adding a new dimension to the concept of indirect plant defence. Whether, from the plant's perspective, the benefits derived from fear can be considered evolutionarily adaptive rather than simply ecologically serendipitous remains to be tested.

Key-words: associational refuge, bushbaby, foraging behaviour, frugivore, herbivore, phenolic, plant defence, predation risk, primate, terpene

Introduction

Herbivores and frugivores face a never-ending daily dilemma of how to eat enough without being eaten. The risk of being eaten forces them, as prey, to make foraging decisions in response to predators (Lima & Dill 1990), while plant defences, such as toxins and digestibility reducers (McArthur, Hagerman & Robbins 1991), ensure that the plant community is not a free feed. Consumers of plants therefore forage in a landscape of both fear and food defences. Understanding how animals respond jointly to predation risk and to food characteristics provides a vital link for using responses of individuals to help explain population- and community-level dynamics.

Plant defences can reduce the fitness of consumers (Degabriel *et al.* 2009) by imposing metabolic, nutritional and foraging costs (Foley & McArthur 1994). The higher the toxin concentration in leaves, for example, the less herbivores can eat (Boyle & McLean 2004; Marsh *et al.* 2006) and the greater the change in their feeding patterns; they are forced to eat more slowly and in shorter feeding bouts (Sorensen, Heward & Dearing 2005; Wiggins *et al.* 2006; Marsh, Wallis & Foley 2007). Plants benefit from fruit consumption through seed dispersal, but many fruits, particularly when unripe, contain toxins as defence against consumers (Cipollini & Levey 1997a). Fruit toxins inhibit intake by frugivores (Cipollini & Levey 1997b; Iaconelli & Simmen 2002), decreasing the rate of fruit removal in a given feeding bout (Cipollini & Levey 1997b; Iaconelli & Simmen 2002; Schaefer, Schmidt & Winkler 2003). As toxin concentration in leaves and fruits varies over time and space, both among and within plants (Cipollini & Levey 1997b; Lawler, Foley & Eschler 2000; Schaefer, Schmidt & Winkler 2003; Boege & Marquis 2005; Moore & Foley 2005; Loney *et al.* 2006), consumers can select plants or plant parts that are low in toxins. To select high-quality (low toxin) food, however, the price may be to forage in risky areas

*Correspondence author. E-mail: clare.mcarthur@sydney.edu.au

where few dare to go. Such a trade-off between food quality and fear is real. Elk *Cervus elaphus*, for example, feed on lower quality food closer to the safety of the forest when wolves *Canis lupus* are in the landscape (Hernandez & Laundre 2005). Vervet monkeys *Cercopithecus aethiops* forage in a landscape of fear, and this landscape has a greater influence on ranging patterns than habitat quality, as defined by food availability (Willems & Hill 2009).

Prey assess the foraging costs of predation against the risk of catastrophic loss of life (Brown & Kotler 2004), the ultimate cost on fitness. The fear of predation is therefore a powerful modifier of prey behaviour that carries significant physiological, foraging and fitness costs. The sublethal effect of fear is at least as influential on overall prey dynamics as mortality (Lima & Dill 1990; Preisser, Bolnick & Benard 2005; Creel & Christianson 2008). In response to predation risk, prey may alter their foraging patterns in time and space, remain closer to refugia, become more vigilant, form larger groups and harvest less food from food patches (Lima & Dill 1990; Preisser & Bolnick 2008). In short, fearful animals forego feeding opportunities and harvest less food in the hope of avoiding attack.

The individual and interactive effects of predation risk and plant toxins on foraging have been tested recently in field experiments with fox squirrels *Sciurus niger* (Schmidt 2000), goats *Capra hircus* (Shrader *et al.* 2008), wood mice *Apodemus sylvaticus* (Fedriani & Boulay 2006) and brushtail possums *Trichosurus vulpecula* (Kirmani, Banks & McArthur 2010). Each of these studies demonstrates a change in where and how much food is consumed and all treat plant toxins as simply present/absent or high/low. But to paraphrase Paracelsus, from the 16th century, 'dose makes the poison'. A fine-grained exploration of the consequences of toxin concentration gradients that occur within and among plants can reveal important and realistic nuances that define the quality of the landscapes in which consumers of plants forage.

One powerful way to evaluate the relative influence of predation risk and plant toxin is to titrate the two, as in a chemistry experiment, by varying toxin concentration in a safe food patch and comparing its effect to that of fear in a risky food patch (Nersesian, Banks & McArthur 2011). The tipping – or equivalence – point is defined when foraging, measured, for example, as food intake, is equal across patches. Here, we apply these foraging concepts to free-ranging consumers of plants for the first time, using the thick-tailed bushbaby, *Otolemur crassicaudatus*, also known as the brown greater galago (Fig. 1a) as a model. These are small (1·2–1·4 kg) primates that consume fruits as a large part of their omnivorous diet (Ejidike & Osokodo 1997) and that are common in forested and wooded habitats in parts of Eastern and Southern Africa (Estes 1992). They are mainly arboreal, but are, nevertheless, vulnerable to terrestrial carnivores (Estes 1992). Our aim was to test the hypothesis that these animals quantify and compare the dual costs of plant toxins and perceived predation risk. We tested this by measuring foraging behaviour and food-patch depletion as a function of toxin concentration and fear. We consider the implications of our results for multi-trophic ecological interactions.

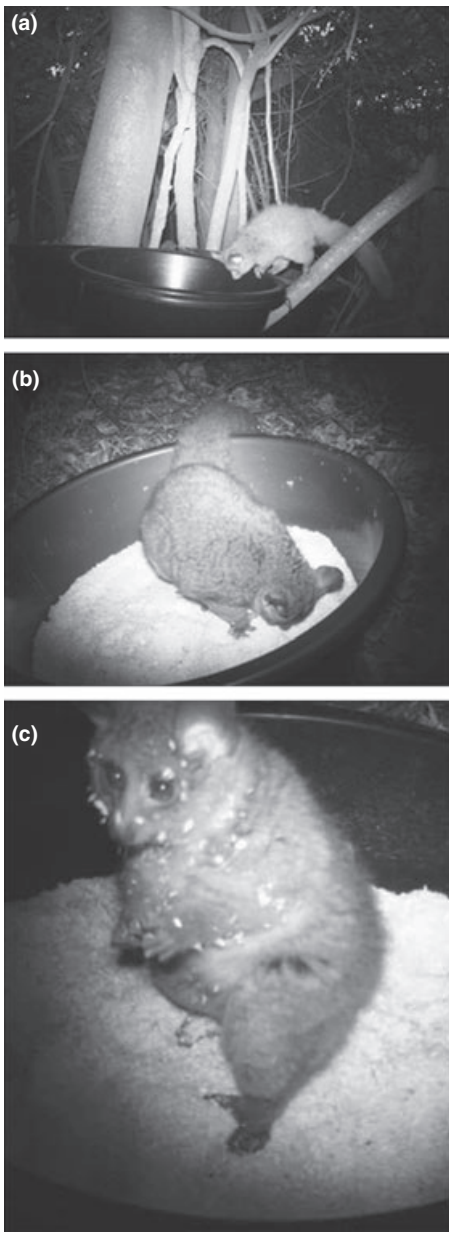

Fig. 1. Bushbaby (a) approaching the tree feeder, (b) foraging by scraping within the inedible sawdust matrix for food items and (c) in an alarmed state of vigilance.

Materials and methods

STUDY AREA AND SYSTEM

The research was conducted at the Lajuma Nature Reserve in the Soutpansberg Mountains, Limpopo Province, South Africa (29°26 E, 23°01 S). This preserve possesses diverse habitats in terms of topography (flat, to vertical cliffs) and vegetation (savanna grassland to cloud forest). The thick-tailed bushbaby occupies several forest habitats at Lajuma, but we restricted our work to medium-height upland scrub forest [7 m mean canopy height (Hahn 2006)]. Most of

these south-facing forests occur on moderate to steep slopes (3–20% grade) that receive greater precipitation (as cloud mist and rainfall) than the surrounding flatlands. We used four sites within this forest type, spaced at least 320 m apart, to maximize the chances that different bushbabies would be found at each.

Bushbabies are semi-social, often feeding alone in the wild or in maternal groups (Estes 1992). They have been known to follow the same routes nightly while foraging and to continue to return to fruiting trees while ripe fruits are available (Estes 1992). There is little dietary information for bushbabies within our particular study area, but there are well over forty species of trees and shrubs with flowers, fruit or pods that could be eaten by primates. These include various *Ficus* species (known bushbaby food (Estes 1992); including *F. sur*, *F. craterostoma and F. burkei*), *Mimusops zeyheri*, *Englerophytum mogalismontanum*, *Croton sylvaticus*, *Hyperacanthus amoenus*, *Syzygium cordatum*, *Rhus chirindensis*, *Ekebergia capensis* (known to be consumed by bushbabies; Ian Gaigher, pers. comm.) and *Ziziphus mucronata* plus the large-seeded *Acacia ataxacantha*. It has been suggested that fruit plays such an important role in the diet of bushbabies that its availability may limit their distribution (Estes 1992). The ready adaptability of bushbabies to unfamiliar and artificial habitats with toxin-rich plants (in the form of pine, *Eucalyptus* and coffee plantations; Estes 1992) suggests they have some capacity to deal with a range of plant toxins.

Arboreal predators, such as the large-spotted genet (*Genetta tigrina*) were observed in the study area, but adult bushbabies appear to be at little risk from them (Estes 1992). In contrast, when bushbabies spend time on the ground, they are prone to predation by carnivores such as leopard (*Panthera pardus*) and hyena (such as *Hyaena brunnea*) (Estes 1992), both of which occur in the area.

GENERAL EXPERIMENTAL APPROACH

We ran two experiments, the first (14–19 July, 2009) using the terpene toxin, 1,8-cineole (purity 99%, Sigma Product No. C80601; Sigma-Aldrich Pty. Ltd. Johannesburg, South Africa) and the second (23–28 July, 2009), which began 4 days after the first was complete, using the phenolic toxin, gallic acid (Sigma Product No. G7384, Sigma-Aldrich Pty. Ltd.). Cineole is a volatile, relatively nonpolar, strong-smelling compound (MW 154·25). It is common to many trees and shrubs globally, such as *Eucalyptus* in Australia (O'Reilly-Wapstra, McArthur & Potts 2004), *Pteronia* in Southern Africa (Hulley *et al.* 2010) and *Juniperus* in Europe (Hadaruga *et al.* 2011). Gallic acid (3,4,5-trihydroxybenzoic acid) is a nonvolatile, relatively polar, low-molecular weight (MW 170·12) phenolic that also occurs in many plants, including *Eucalyptus* (Hillis 1966), *Betula* (Lempa *et al.* 2000) and *Acacia* (Tung *et al.* 2011). Given that both compounds are widespread and, further, that mammalian detoxification mechanisms [such as the cytochrome P450 enzyme system (Pass & McLean 2001)] metabolise a diverse range rather than single toxins, we considered them to be both ecologically and pharmacologically relevant. Their contrasting characteristics allowed us to test whether foraging responses to toxin concentration were relatively general.

In both experiments, we used the giving-up-density (GUD) approach, in which food pellets were mixed into an inedible matrix of sawdust (Fig. 1b). The inedible matrix dilutes the food as more is found and consumed, forcing a progressive reduction in harvest rate (Brown 1988). We also used motion-sensitive infrared cameras to film the feeding stations at one of the four sites in the cineole experiment to quantify the behavioural responses underlying the ultimate GUD response.

TRIAL DESIGN

Within each of the four sites, we set up five feeding stations (mean 30 m apart, min. 14 m, max. 59 m), and at each of these stations, we placed one ('safe') feeder within a large tree at 1–2 m height and a second ('risky') feeder on the open ground below, at least 2 m from the tree. Although there are gradients of predation risk across the landscape, producing contours of fear (van der Merwe & Brown 2008), we chose a dichotomous safe/risky system here to provide a simple but clear test of our hypothesis using the titration methodology. We made the assumption that the tree feeder was relatively safer for bushbabies than the ground feeder. This seemed reasonable given that they are hunted by a suite of terrestrial predators, and they quickly seek refuge in trees when startled (Estes 1992). A portion (∼4 cm long, ∼3 cm diam.) of a relatively fresh leopard scat (found within the study region, frozen for no more than 1 week before use) was placed in an open plastic bag beside the ground feeder for the duration of each experiment to exacerbate the perceived predation risk at this feeder location.

Each experiment ran for 5 days. Each evening (just before dusk) at each feeder, we mixed 40 cat food pellets (∼7 g 'KiteKat' cat food) into the inedible matrix comprising 9·6 L of sawdust. We placed one extra pellet on top. If this pellet remained untouched and there were no signs of bushbabies (indicated by disturbances and impressions in the sawdust), then we considered that the feeder had not been visited. Within each site, the tree feeder at each station received one of five toxin concentrations (outlined later) on any particular day, subject to a Latin Square design, where each feeder received all five treatments over the 5 days and, no treatment was repeated across feeders on any given day. Feeders on the ground always contained toxin-free food.

TOXIN TREATMENTS APPLIED TO FEEDERS

As titration experiments, we varied the toxin concentration of the food placed in feeders in trees against their paired (toxin-free) feeder on the ground. The concentrations were chosen to mirror the effect on intake of many plant toxins in fruits and leaves, i.e. to reduce intake at high concentrations (Wiggins *et al.* 2003). Thus, the compounds, and their concentrations, were used as relevant and realist toxin models. The method retained the important ecological characteristic of real plants and their toxins (i.e. the effect on intake) while simplifying the system (using a single toxin); rather than attempting to represent any particular toxin or suite of toxins necessarily found in the fruits consumed by bushbabies.

For the cineole experiment, we prepared food at five toxin concentrations; 0, 0·025, 0·05, 0·10 and 0·02 g cineole per gram of cat food pellets. Pellets were first soaked for 1–2 min in water (to make the surface amenable to absorbing the toxin solution) then patted dry with paper towels. Next, the appropriate amount of cineole was mixed with sunflower oil (at 10% of the pellet dry mass) to reduce evaporation and to ensure even mixing among the individual pellets even at low concentration. Each batch of 40 pellets was prepared separately. Here, as with the gallic acid experiment, there was some loss of toxin from the food during the preparation and/or in the feeders, but this was not quantified. In a similar system, we have estimated that ∼50% of the cineole may be leached or evaporated from the food overnight, but the ranking and relative concentrations of the treatments remain the same.

For the gallic acid experiment, we prepared food at 0, 0·010, 0·025, 0·05 and 0·10 g gallic acid per gram of cat food pellets. The appropriate amount of gallic acid was dissolved in 90% ethanol (at 50% of the

pellet dry mass) and then mixed with the pellets (pre-soaked in water as for cineole). Pellets were dried in sunlight to evaporate the ethanol.

GIVING-UP-DENSITY

Giving-up-density (GUD) was measured as the number of food items remaining after a night of foraging. At dawn, the content of feeders was sieved to separate sawdust from the remaining food, and the number of food pellets counted. If neither feeder at a station was visited on a given night, the pair was treated as missing data (nine of 100 and eight of 100 for the cineole and gallic acid experiments, respectively).

VISITS TO FEEDERS AND CUMULATIVE TIME AT FEEDERS

We filmed the cineole trial at one of the four sites, using 10 infrared Scout Guard SG550 motion-sensitive cameras. Cameras were set on high sensitivity level, 20 s duration (trigger/re-trigger after 1–2 s) video-mode, 3M pixel image size (640 × 480). Battery problems during days four and five prevented us from taking data from two tree and two ground feeders, hence $n = 46$ camera nights instead of 50.

We quantified when and for how long bushbabies visited the feeders throughout the night, in total and for each visit, using the file information from the SD cards. All images were checked for nontarget species, but these were rare (~2·5% of all visits), and so their data ignored. For determining the cumulative time at feeders, we again used the SD card details to check and record the presence of bushbabies each night at each feeder at each station at every 5-min time interval starting from Time 0 (which was 17:40, near dusk and ~10 min before the earliest visit). We then pooled the data across nights for each treatment; giving up to 5 pooled tree nights per cineole concentration and 25 pooled ground nights (apart from missing data). We considered it acceptable to pool all of the ground data, because the GUDs on the ground were unaffected by the tree treatment (see Results). For each time interval, we then summed the number of times bushbabies were present at the feeder (up to 5 for tree-treatment feeders, and up to 25 for ground feeders). Values were then summed across time and divided by the maximum possible sum to provide percent cumulative time at feeder for each treatment.

BEHAVIOUR DURING THE FIRST VISIT TO EACH FEEDER

We investigated the first visit to each feeder in more detail (one 1st visit only lasted several seconds and was ignored), as it represented the greatest contribution to all the time spent at the patches (see Results). We used JWatcher™ V1.0 (http://www.jwatcher.ucla.edu/) to quantify: (i) the proportion of time at the feeder spent foraging as distinct from being vigilant (no other behaviours took up more than a few seconds), (ii) the proportion of time with either one (*alone*) or more (*with others*) bushbabies in the feeder, (iii) when vigilant, the proportion of time in each of three states: *aware*, *alert* or *alarmed* (Fig. 1c). We considered an animal to be *aware* when it was scanning with its head up, yet still on all four paws and chewing. We defined *alert* as an animal scanning with body semi-erect, often with one or both paws on the edge of the feeder, and rarely chewing. We defined *alarmed* as body upright, erect on hind legs, heavy breathing and no chewing. For the behavioural details at the first visit, $n = 34$ instead of 50 because of battery problems that limited the infrared image to just the first moment of many files (allowing us to see the animal, but not quantify its behaviour), but the data set was relatively balanced across treatments (at both tree and ground feeders: $n = 3$ instead of five for cineole concentrations 0·000, 0·050 and 0·200 g.g DM^{-1}; $n = 4$ for cineole concentrations 0·025 and 0·010 g.g DM^{-1}).

STATISTICAL ANALYSES

For the GUD data from both the cineole and the gallic acid experiment, we considered three questions: (i) was the Tree GUD a function of the toxin treatment? (ii) was the Ground GUD a function of the toxin treatment? and (iii) was the difference in GUD between Tree and Ground a function of the toxin treatment? This last variable enabled us to statistically incorporate the paired nature of the tree–ground data. We tested the three dependent variables (Tree GUD, Ground GUD, difference in GUD) using the mixed-model procedure in SAS (PROC MIXED; SAS Institute Inc., 2003). The full model was as follows:

$$\text{Dependent variable} = Day + Toxin + Site + Station(Site) + Site * Day + Site * Toxin$$

where *Day* (day 1–5 of the trial) and *Toxin* (i.e. the concentration of the toxin) were fixed effects and *Site*, *Station* nested within *Site* and interactions with *Site* were random effects. We removed the *Site* interaction terms (both trials) from the final models, because they were not significant. In our models, we allowed the variance component estimates to be unbounded by zero and used the Kenward–Roger correction for standard errors and *F*-statistics (Littell *et al.* 2006). Normal probability and residual plots were used to check for homoscedasticity, and the Shapiro–Wilk test was used to check for normality. No transformations were needed. We first ran the models with *Toxin* as a class variable to obtain and plot the GUD values as least-squares means. However, as it was clear that the relationships were linear, we then ran the models with *Toxin* as a continuous variable, so that we could define the slopes. We plotted the predicted relationship between GUDs and toxin concentration using the *Intercept*, *Toxin* and average *Day* parameter estimates. Results were essentially the same using both methods, but the use of *Toxin* as a continuous variable was more powerful.

For visits to feeders, we tested three dependent variables (Total time at feeders throughout the night, Starting time of the first visit, Length of the first visit) using the mixed-model procedure in SAS [PROC MIXED (SAS Institute Inc., 2003)]. The full model was as follows:

$$\text{Dependent variable} = Feeder + Toxin + Feeder * Toxin + Day + Station$$

where *Feeder* (tree or ground), *Toxin* (i.e. cineole concentration as a class variable, because we did not necessarily expect a linear relationship) and *Day* (day 1–5 of the trial) were fixed effects, and *Station* was a random effect.

We modelled the % cumulative time (C) at feeders as a function of *Time* (t) from the start and the six *Treatments* (i.e. five cineole concentrations in the tree feeders, and the toxin-free ground treatment) using the nonlinear procedure in SAS [PROC NLIN (SAS Institute Inc., 2003)]. We fitted the cumulative Weibull function, conditioned to pass through 100 (%) by the end of the night (i.e. after 12 hours):

$$C = 100(1 - e^{-zt})/(1 - e^{-12z})$$

where $z = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots$ with β_0 representing the intercept followed by a dummy variable for each treatment (β_1 for tree cineole treatment 0·000 g.g DM^{-1}, β_2 for tree cineole treatment 0·025 g.g DM^{-1},… β_6 for ground treatment). Initial parameter

estimates were set at 0·006 for the intercept, 0·004 for tree treatment 0·000 g.g DM^{-1}, −0·0002 for tree treatment 0·025 g.g DM^{-1} and zero for the other treatment parameters, with no boundaries. We tried raising *Time* to the power of a new parameter, but it made little difference to the results, and so it was entered as $Time^1$. We compared 95% confidence intervals to determine whether the parameter estimates for the six treatments were significantly different from one another; lack of overlap between the treatments CI's was interpreted as statistically significant. From the modelled parameter estimates, we calculated $Time_{50}$ (h), representing the time, from Time 0 [which was at 17:40 (dusk) and about 10 min before the earliest visit], taken to reach 50% of the cumulative total time spent at the feeders.

For behaviours during the first visit to the feeder, we tested just three proportional dependent variables, thus avoiding problems of lack of independence between associated variables: (i) proportion of time spent foraging at the feeder, (ii) proportion of foraging time spent *alone* in the patch and (iii) proportion of vigilance time *aware* (i.e. not *alert* or *alarmed*). We used the mixed-model procedure, and the final model for each was as follows:

$$\text{Dependent variable} = Feeder + Toxin + Day + Station$$

with independent variables as described earlier, again with *Toxin* included as a class variable and excluding the Feeder*Toxin interaction (not significant at $P \geq 0{\cdot}7$). Normal probability and residual plots were used to check for homoscedasticity, and the Shapiro–Wilk test was used to check for normality. Proportion of foraging time spent alone was square-root arcsine transformed for analysis; no other data needed transforming.

Results

GIVING-UP-DENSITY

When cineole was titrated against predation risk, GUD in the tree feeders increased significantly (Table 1a for cineole) and substantially with cineole concentration, while GUDs in the (toxin-free) ground feeders remained relatively constant (Table 1b for cineole; Fig. 2a). Bushbabies fed more (lower GUD) in the tree feeders than on the ground at zero cineole. The tipping point, where tree and ground GUDs were equivalent, occurred at a cineole concentration of ∼0·05 g.g DM^{-1}; and tree GUD was substantially higher than the ground GUD at the highest cineole concentration (Fig. 2a). The net result was a significant, negative relationship between the difference in GUD between the two locations (tree vs. ground) and the cineole concentration of the tree feeder (Table 1c for cineole).

When gallic acid was titrated against predation risk (Fig. 2b), GUD similarly increased with toxin concentration in the tree feeders (Table 1a for gallic acid). Again, GUD in the (toxin-free) ground feeders remained relatively constant (Table 1b for gallic acid), but in this case, there was no crossover (Fig. 2b): the ground no longer appeared riskier than the tree feeders. As with the cineole experiment, there was a significant, negative relationship for the difference in GUD between the two locations and the toxin (gallic acid) concentration in the tree feeder (Table 1c for gallic acid).

VISITS TO FEEDERS AND CUMULATIVE TIME AT FEEDERS

In the cineole experiment, bushbabies spent on average 21·0 min (SD 9·26, $n = 46$) over 3·83 visits (SD 1·57, $n = 46$) at each feeder, but the total time at both the tree and ground feeders decreased with increasing cineole concentration in the tree food (Table 2a; Fig. 3). The first visit (12·5 min, SE 1·32, $n = 46$) comprised nearly 60% of the total time at feeders and began about the same time (18:20 hours, SD 25 min) irrespective of feeder (tree vs. ground), cineole concentration,

Table 1. Results of the mixed-model analysis in the cineole and gallic acid experiments, testing the fixed effects of Toxin (i.e. cineole or gallic acid) concentration in food in the tree feeders (as a continuous variable) and Day on (a) the giving-up-density (GUD) at the tree feeders, (b) the GUD at the ground feeders and (c) the difference in GUD between the tree and ground feeders

	Cineole experiment				Gallic acid experiment			
Factor	d.f.	*F* value	*P*	Parameter estimate	d.f.	*F* value	*P*	Parameter estimate
(a)								
Intercept				10·52				9·63
Toxin	1	52·85	**< 0·01**	76·34	1	16·43	**< 0·01**	74·94
Day	4	5·43	**< 0·01**	3·69	4	15·29	**< 0·01**	3·42
Residual	69				69			
(b)								
Intercept				16·19				8·72
Toxin	1	0·01	0·91	−1·06	1	1·36	0·25	23·84
Day	4	5·73	**< 0·01**	2·48	4	7·78	**< 0·01**	3·67
Residual	69				69			
(c)								
Intercept				5·58				−0·97
Toxin	1	32·75	**< 0·01**	−76·91	1	5·31	**< 0·01**	−49·49
Day	4	0·19	0·94	−1·32	4	1·68	0·16	0·37
Residual	69				70			

Significant effects are in bold. Parameter estimates for the relationship are given, using the mean of days 1–5 for the Day estimate.

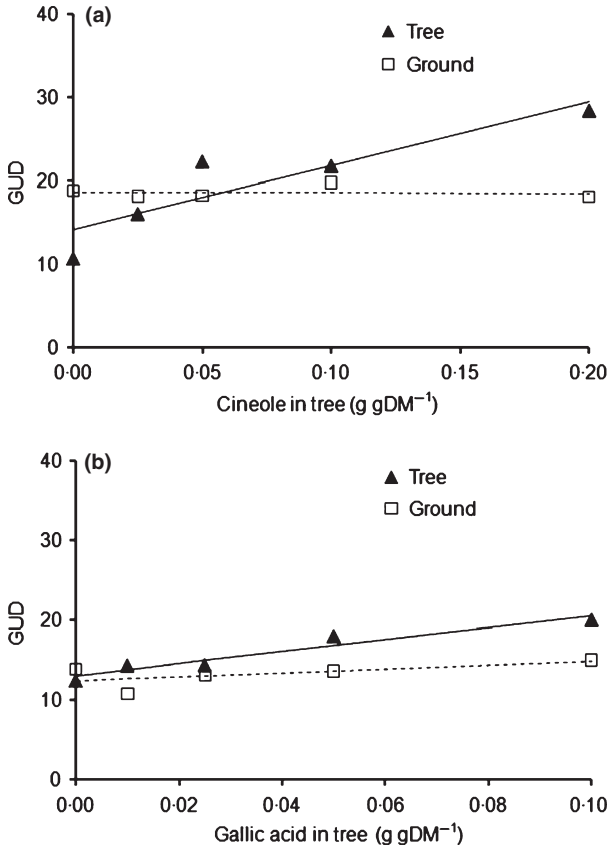

Fig. 2. Giving-up-density (GUD, number of pellets remaining) in tree (▲) and ground feeders (□) as least-squares means and as a linear regression as a function of (a) cineole or (b) gallic acid concentration (g.g DM^{-1}) of food in the tree feeder.

Table 2. Results of the mixed-model analysis in the cineole experiment, testing the fixed effects of Feeder (tree vs. ground), Toxin (i.e. cineole) treatment in the tree, the interaction between Feeder and Toxin, and Day on (a) the total time bushbabies spent at a feeder throughout the night, (b) the starting time of the first visit to the feeders and (c) the length of the first visit to the feeders

Factor	d.f.	*F* value	*P*
(a)			
Feeder	1	0·83	0·37
Toxin	4	2·86	**0·04**
Feeder*Toxin	4	0·72	0·59
Day	4	3·99	**0·01**
Residual	28		
(b)			
Feeder	1	0·26	0·62
Toxin	4	0·43	0·78
Feeder*Toxin	4	0·23	0·92
Day	4	1·84	0·15
Residual	28		
(c)			
Feeder	1	2·79	0·11
Toxin	4	1·57	0·21
Feeder*Toxin	4	2·25	0·09
Day	4	5·44	**< 0·01**
Residual	29		

Significant effects are in bold.

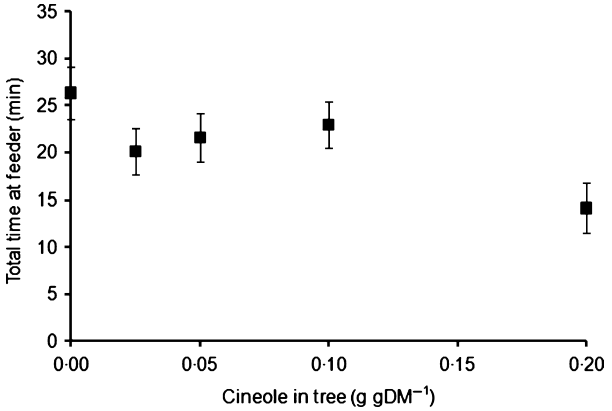

Fig. 3. Total time at feeder throughout the night in relation to cineole concentration (g.g DM^{-1}) of food in the tree feeder. Values are least-squares means (±SE).

their interaction or day (Table 2b). The length of this first visit was also unaffected by feeder, cineole concentration or their interaction but fluctuated significantly across days (Table 2c; daily pattern not shown).

The cumulative time at feeders (Fig. 4a,b) shifted significantly with treatment (Table 3). Bushbabies foraged earliest in the tree feeders in the absence of cineole [Tree (0·000)], followed by the toxin-free ground feeder, shifting progressively later in the evening for the two lowest tree cineole concentrations [Tree (0·025) and Tree (0·050)] then back earlier again at the highest two cineole concentrations. This resulted in a hump-shaped pattern in the 50% cumulative time spent at the feeders ($Time_{50}$) as a function of cineole concentration, and $Time_{50}$ varied by more than 1·5 h (Fig. 4c).

BEHAVIOUR DURING THE FIRST VISIT TO EACH FEEDER

Bushbabies spent 77·1% (SD 7·8, $n = 34$) of their time during the first visit to each feeder foraging and the rest of the time (22·9%) was spent vigilant. This percent foraging time did not vary with feeder (tree vs. ground) or cineole concentration in the tree food (Table 4a). The proportion of time spent foraging fluctuated over time (Table 4a), but generally decreased over the 5 days of the experiment (mean 82·4% on Day 1 to 75·5% on Day 5).

On the ground, bushbabies spent proportionally more time foraging alone than when in the tree, irrespective of cineole concentration in the tree food (Table 4b; Fig. 5a). When on the ground, they also spent proportionally more time in heightened states of vigilance (i.e. alert and alarmed combined) than when in the tree, irrespective of cineole concentration in the tree food (Table 4c; Fig. 5b).

Discussion

Our results demonstrate the complex and sophisticated ecological balancing act that free-ranging animals use when foraging. In doing so, they weigh up and respond to the two very

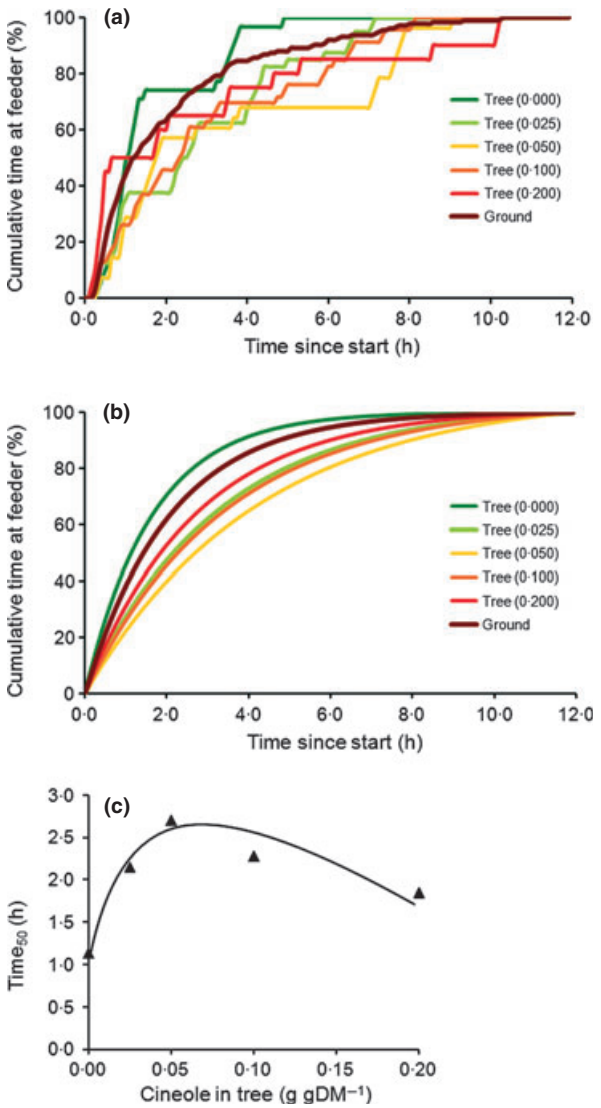

Fig. 4. (a) Actual and (b) modelled cumulative time and (c) the 50% cumulative time at feeders throughout the night, starting at dusk (i.e. Time 0 at 17:40) as a function of the cineole concentration (g.g DM^{-1}) in food in the tree feeder (a-c), or in the ground feeder (a, b). 'Tree (0·000)', for example, indicates the tree feeder at cineole concentration of 0·000 g.g DM^{-1}. In (a), the greater step sizes in tree treatments, compared with the ground, reflect the size of the data sets (five tree nights per treatment vs. 25 ground nights).

Table 3. The influence of the five tree cineole concentration treatments and the ground treatment on % cumulative time at feeders, shown as parameter estimates (with SE) modelled using the cumulative Weibull function and predicted $Time_{50}$ (time to reach 50% of the cumulative total time spent at the feeders). Tree (0·025) refers to the tree feeder with cineole at concentration of 0·025 g.g DM^{-1}

Variable	Parameter estimates	SE	$Time_{50}$ (h)
Intercept (β_0)	0·3023	0·0062	
Tree (0·000) (β_1)	$0·3076^{a}$	0·0175	1·14
Tree (0·025) (β_2)	$0·0086^{d}$	0·0097	2·15
Tree (0·050) (β_3)	$-0·0671^{e}$	0·0175	2·70
Tree (0·100) (β_4)	$-0·0109^{d}$	0·0094	2·28
Tree (0·200) (β_5)	$0·0652^{c}$	0·0107	1·85
Ground (β_6)	$0·1817^{b}$	0·0135	1·43

For the tree and ground treatments, superscripts that differ are significantly different based on non-overlap of 95% confidence intervals.

Table 4. Results of the mixed-model analysis in the cineole experiment, testing the fixed effects of Feeder (Tree vs. Ground), Toxin (i.e. cineole) treatment in the tree, and Day on (a) the proportion of time bushbabies spent *foraging* (as distinct from being vigilant) at the feeder, (b) the arcsine square-root transformed proportion of time bushbabies spent *alone* (as distinct from being with one or two others) when foraging and (c) the proportion of vigilance time in the state of being *aware*, i.e. not *alert* or *alarmed*, all during the 1st visit

Factor	d.f.	*F* value	*P*
(a)			
Feeder	1	2·01	0·17
Toxin	4	1·38	0·27
Day	4	3·28	**0·03**
Residual	23		
(b)			
Feeder	1	7·71	**0·01**
Toxin	4	0·72	0·59
Day	4	2·74	0·05
Residual	22		
(c)			
Feeder	1	4·59	**0·04**
Toxin	4	1·14	0·36
Day	4	2·39	0·08
Residual	23		

Significant effects are in bold.

different proximate costs associated with fear and food defences. The shifting relative impact of these two costs as animals are confronted with a gradient in plant defence has, to date, been demonstrated only with captive animals (the herbivorous common brushtail possum *Trichosurus vulpecula*) under tightly controlled conditions (Nersesian, Banks & McArthur 2011).

The increase in GUD as the concentration of both cineole and gallic acid increased confirms our expectation that toxin concentration plays a critical role in modifying foraging. We can understand this dose-dependent response from a physiological basis, i.e. the metabolism and excretion (hence subsequent intake) of toxins by animals is rate limited (Foley, Iason & McArthur 1999; Torregrossa & Dearing 2009). The cost of increasing toxin concentration is further demonstrated by the behavioural changes we quantified in the cineole experiment. The lower cineole concentrations delayed feeding by the bushbabies, pushing out their feeding time budget by 1·5 h (as measured by $Time_{50}$), thus imposing a substantial penalty to any further reward from these food patches. Again, such a delay in feeding is expected with the accumulated absorption of ingested toxins (Boyle *et al.* 2005), and a similar response is seen in the behaviour of captive ringtail possums (*Pseudocheirus peregrinus*) feeding on toxic eucalyptus leaves (Wiggins *et al.* 2006). At the two highest cineole concentrations,

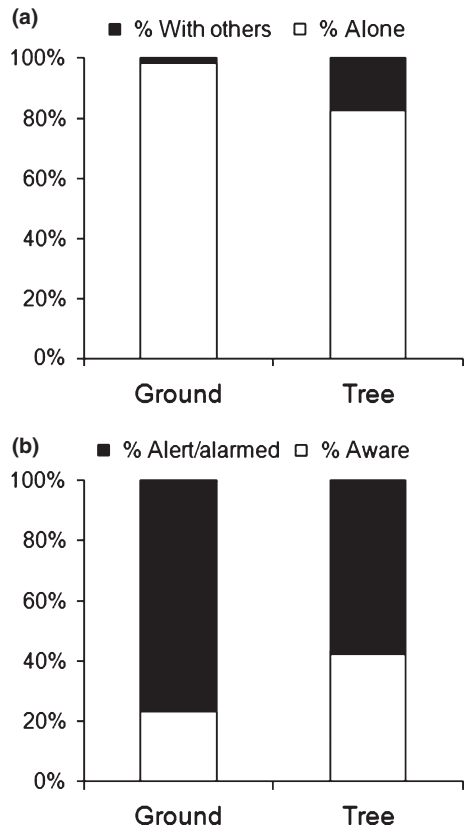

Fig. 5. Behaviours during the first visit to the tree and ground feeders, as (a) proportion of foraging time at feeder either alone or with others (combined total of two or three animals together in the feeder) and (b) proportion of vigilance time being either aware or alert/alarmed.

however, bushbabies simply abandoned their feeding early, thus incurring the greatest cost on foraging.

In the cineole experiment, the cost of the toxin pivoted around the cost of fear, seen by the shift in GUD and in the temporal changes to foraging patterns throughout the night. Bushbabies perceived the toxin-free ground feeders as riskier than the toxin-free tree feeders, shown by higher GUD. Animals also responded behaviourally to fear, with slightly delayed feeding (toxin-free ground $Time_{50}$ > toxin-free tree $Time_{50}$), heightened state of vigilance and reduced group foraging. While bushbabies often feed alone or in maternal groups (Estes 1992), our high-quality food source in artificial food patches may have led to more group feeding than usual in the safety of trees, but less so on the ground. Reduced foraging (higher GUD) at increasingly toxic tree feeders did not lead to increased harvesting (lower GUD) at the risky ground feeders. Presumably, bushbabies simply foraged elsewhere. Captive brushtail possums, with no other alternatives, do shift feeding to the risky food patch (Nersesian, Banks & McArthur 2011), highlighting how trade-offs depend on the availability of options. By the time we ran the gallic acid trial, bushbabies no longer perceived the ground feeders as riskier than the trees, despite the vulnerable location for this arboreal species and the presence of a predator cue (leopard scat). As large benefits must be outweighed by even larger costs to reduce net patch quality, the highly nutritious food we used may have induced greater feeding on the ground over time, as bushbabies recognized the nutritional benefits derived from feeding in a risky place. Our results also confirm the ephemeral nature of pulses of perceived predation risk, which can diminish over time (Lima & Bednekoff 1999; Kirmani, Banks & McArthur 2010) unless reinforced by actual risk.

There was a spill-over effect of increasing cineole concentration, decreasing total time at both tree and ground feeders. As the ground GUD remained unchanged, animals must have foraged increasingly effectively to compensate. At the highest cineole concentration, bushbabies must have been harvesting at a slower rate on the cineole diet in the tree than on the cineole-free diet on the ground, while the converse is true when cineole was absent from both feeders. Reduced feeding rate is a typical response to toxins such as cineole (Torregrossa & Dearing 2009), but it has interesting ecological implications. It exacerbates the metabolic cost of the toxin by reducing the harvesting rate, which in turn may interact with perceived predation risk to force patch quitting.

Our results, combined with the known variation in plant toxin concentration and predation risk that occurs throughout the landscape, highlight that the ecological effectiveness of plant toxins as defence against consumers needs to be considered in the context of a landscape of fear – and the relative impact of anti-predator tactics and plant defence is strongly shaped by the concentration of these defences. High toxin concentrations in plants in safe locations can make risky locations relatively less costly, and hence have the potential to drive animals to forage in such locations. For frugivores, such a shift in foraging may occur when availability of low-toxin (often ripe) fruit in safe areas diminishes towards the end of a fruiting season or when the low-toxin fruits have been consumed. Frugivorous birds in the rainforest of Venezuela, for example, collectively remove fruits in a dose–response manner related negatively to phenolic concentration and positively to energy, lipid and nitrogen (Schaefer, Schmidt & Winkler 2003), leaving fruits that are better defended. Whether these birds, or other frugivores in similar situations, then move to riskier foraging grounds to harvest low-toxin fruit there is unknown. For herbivores, a shift in foraging may be instigated once low-toxin leaves are consumed in safe areas or where previous herbivory has induced higher levels of plant defences (Karban & Baldwin 1997) in such areas. Areas of high predation risk, however, may simply be impenetrable, as neither the bushbabies in our study nor wood mice (Fedriani & Boulay 2006) foraged more in risky patches to compensate for reduced food quality (as toxin concentration increased or ripe fruit diminished) in safe patches. In both cases, however, the availability of alternative foraging locations meant that animals were free to avoid areas of high risk. Demonstrating the complexity of trade-offs in natural environments will depend on mapping fine-grained variation in both predation risk and food quality

across landscapes, and quantifying their integrated influence on foraging patterns.

A corollary of our findings – that bushbabies harvest most from the least costly patch irrespective of whether the cost is incurred from fear or toxins – is that these costs can be substitutable, at least ultimately, to foraging herbivores/frugivores. As both these factors affect a plant's vulnerability to being consumed, both can in turn be viewed as components of a plant's defence. This is similar to the concept of indirect defence, originally applied to plants that attract enemies of insect herbivores (Price *et al*. 1980). In that seminal paper, it was suggested that such enemies were mutualists with plants. The adaptive function of this 'mutualism', when it involves information-mediated resistance, has been debated (Kessler & Heil 2011), largely because there is little direct evidence for a fitness benefit to plants of enemy (particularly parasitoid) attractants (van der Meijden & Klinkhamer 2000). Nevertheless, there is evidence that plants benefit from growing in places that impose a high risk of predation to their mammalian herbivores. The growth of aspen *Populus tremuloides* in parts of Yellowstone National Park, for example, is greater in areas used more by wolves, and hence used less by browsing elk *Cervus elaphus* (Ripple *et al*. 2001). Thus, we suggest that fear is an additional dimension of indirect plant defence, different to both resource-mediated and information-mediated defence, but with some conceptual overlap with that of associational (plant) refuges or defence guilds (Atsatt & O'Dowd 1976) in that plant vulnerability can be modified by the surrounding biotic (and abiotic) landscape. As with associational refuges, however, it is unclear whether the benefits derived from fear are too diffuse and too uncontrollable, from the plant's perspective, to be evolutionarily adaptive rather than simply ecologically serendipitous.

Acknowledgements

We thank Ian and Retha Gaigher, Oldrich van Schalkwyk and others at Lajuma Nature Reserve for assistance at the field site; and Adrian N Goodwin for advice on the nonlinear modelling. This research was partly funded by an Australian Research Discovery Grant to CM and PBB (DP0877585), approved by the Animal Care and Ethics Committee, University of New South Wales (Approval # 08/75B) and conforms to the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes.

Author contributions

CMcA, PBB and JSB contributed to the conceptual basis of the research; CMcA, PO and JSB designed and ran the experiments; CMcA analysed the results and wrote the original draft; CMcA, PO, PBB and JSB all provided input into the final manuscript.

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Received 30 June 2011; accepted 26 September 2011
Handling Editor: Dan Hare