



# Limited influence of experimentally induced predation risk on granivory in a tropical forest

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## Short Communication

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### Abstract

Seed predation by rodents can strongly influence plant recruitment and establishment. The extent to which predation risk indirectly alters plant survival in tropical forests via impacts on granivory is unclear, making it difficult to assess the cascading impacts of widespread predator loss on tree recruitment and species composition. Experimental field studies that manipulate predation risk can help address these knowledge gaps and reveal whether antipredator responses among small mammals influence plant survival. We used camera traps and seed predation experiments to test the effects of perceived predation risk (via predator urine gel) on foraging behaviour of and seed removal by murid rodents in an unlogged and un hunted rainforest in Malaysian Borneo. We also explored the influence of seed traits (e.g., seed size) on removal by granivores and assessed whether granivore preferences for particular species were affected by predator urine. Murid visits to seed plots were positively related to overall seed removal, but were not affected by predator scent. Granivory was the lowest for the largest-seeded (>6 g) plant in our study, but was not influenced by predation risk. Predator urine significantly affected removal of one seed taxon (*Dimoocarpus*, ~0.8 g), suggesting that removal by granivores may be affected by predation risk for some seed species but not others. This could have implications for plant species composition but may not affect the overall level of granivory.

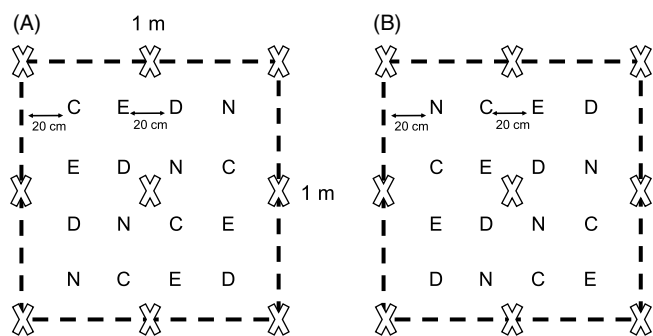
## Introduction

Murid rodents are among the most abundant granivores in tropical forests and can influence seed fate by consuming or destroying seeds and by dispersing them to different microhabitats (Wells & Bagchi 2005). Murids can influence species-specific seed survival (Hautier *et al.* 2010) if foraging decisions are associated with dietary preferences based on seed morphology (Dirzo & Mendoza 2007, Cramer 2014). Predator-induced changes in granivory could therefore affect seed survival (Laundré *et al.* 2014, Bestion *et al.* 2015) with disproportionate effects on seeds with particular morphological traits (Xiao *et al.* 2006, Forget & Jansen 2007, Bricker *et al.* 2010). Most of what we know about these processes, however, comes from temperate systems; the indirect effects of predators on seed survival via impact on granivorous rodents in tropical forests are much less well known.

Predator scent can elicit physiological and behavioural changes in prey (Apfelbach *et al.* 2005, Takahashi *et al.* 2005, Sündermann *et al.* 2008). Rodents often use scents (e.g., from urine) to gauge predation risk (Rosell 2001, Apfelbach *et al.* 2005, Ferrero *et al.* 2011, Bytheway *et al.* 2013) and may spend less time eating seeds or exhibit increased vigilance in riskier microhabitats (Lima & Dill 1990). In some cases, the indirect effects of predation risk may be as strong as direct reductions in prey abundance for plant survival (Hernández & Laundré 2005, Preisser *et al.* 2005). Though the effects of predator scent on prey foraging behaviour have been documented, whether predator-induced changes in foraging translate into altered seed removal, and survival has not been well explored in tropical systems.

## Methods

We used motion-triggered, infrared cameras (Reconyx HC500) and field experiments to test whether simulated predator presence affected visitation and seed removal rates of murid rodents in Danum Valley Conservation Area (DVCA; N5.10189°, E117.688°), Sabah, Malaysian Borneo. DVCA (438 km<sup>2</sup>) is the largest primary dipterocarp forested area in Sabah and is a Class 1 ('Totally protected') Forest Reserve with prohibited resource extraction (Hazebroek *et al.* 2012). Murid rodents (> 27 species) are the main mammal granivores, mostly from the genera *Rattus* and *Maxomys* (Phillips & Phillips 2016). Bearded pigs (*Sus barbatus*), lesser (*Tragulus napu*) and greater (*T. javanicus*) chevrotains, and red (*Muntiacus muntjac*) and Bornean yellow (*M. atherodes*) muntjac also occur in the system and eat seeds. All vertebrate species detected in our study area are listed in Supplementary Material Figure S1.



**Figure 1.** Experimental design used to test the effect of predator olfactory cues on murid rodent foraging behaviour. Each site consisted of one camera station with urine gel placed on the edges and corners of the quadrat ('treatment'; A), and another camera station ~ 50 m away with no urine-gel ('control'; B). Four seeds from each of four plant taxa were placed in each plot: *Elaeis* (E), *Cucurbita* (C), *Dimocarpus* (D), and *Nephelium* (N). 'X' denotes the locations where the urine gel was applied in the experimental quadrat.

We simulated predator presence using bobcat (*Lynx rufus*) urine gel (Bobcat P-Gel, PMart, Sandy Point, ME) at 10 paired experimental stations *ca.* 500 m apart (> the average daily movement of rodents in our site; Wells *et al.* 2006). Each station contained two 1 × 1 m quadrats (treatment and control) spaced 50 m apart (i.e., within broadly similar microhabitat conditions), with one camera trap overlooking each quadrat. We placed 5 g of urine gel in the treatment quadrats at several locations (Figure 1) and left the control quadrats unmodified. Cameras were active 24 hours per day and set to take 10 photos in rapid-fire succession upon triggering, with high trigger sensitivity and no quiet period between triggers.

At each quadrat, we placed four seeds from each of four plant species, for a total of 16 seeds, ~ 20 cm from plot edges and from adjacent seeds. Seed order was random, but conspecifics were not placed next to each other. Seeds were set out for four days, after which removal was determined by our field team counting the number of seeds missing from each plant taxon, with removal attributed to all granivores. We used camera trap photograph to determine seed removal by rodents in particular, with removal events considered independent when a photograph showed a rodent handling or removing seed and subsequent photographs showed a rodent with no seeds in its feet or mouth.

We used seeds from four plant genera varying in seed size: pumpkin (*Cucurbita pepo*; mean seed mass = 0.25 g), longan (*Dimocarpus longan*; 0.78 g), rambutan (*Nephelium lappaceum*; 1.00 g), and oil palm (*Elaeis guineensis*; 6.61 g). *E. guineensis* is native to Africa, but rodents are known to prey on seeds of this species in Southeast Asia (Buckle *et al.* 1997). *C. pepo* is native to North America, but *Cucurbita* spp. are known to be eaten by murids including *Rattus* spp. and *Mus* spp., both of which occur in our system (de Guia & Quibod 2014). *Dimocarpus* and *Nephelium* are in the Sapindaceae family, whose seeds are eaten by murid rodents in Borneo (Blackham & Corlett 2015).

### Data analysis

We used a generalised linear mixed-effects models (GLMM) with Poisson error distributions to compare the number of independent murid detections between treatment and control sites. We used *camera trap station ID* as a random intercept (a factor with 10 levels representing each treatment and control pair) to account for microhabitat differences among camera trap stations that may

have affected small-scale habitat selection (Bowers & Dooley 1993, Mayor *et al.* 2009). The number of independent murid detections was estimated from camera trap photos; detections were considered independent if they were separated by any non-murid species or were >5 minutes apart.

Next, we used a GLMM with binomial error distributions to model overall seed removal (by all granivorous taxa) as a function of two explanatory variables: the number of murid rodent detections and *treatment*. Here, the fate of each seed at the end of our study period was categorised as present or absent (i.e. seed removal, determined by our field team), and paired *camera station ID* was modelled as the random intercept.

To determine if seed removal by rodents in particular was influenced by predator scent, we used GLMMs with a binomial error distribution to model the overall proportion of seeds removed by rodents as a function of experimental treatment. We assessed overall removal as we could not distinguish between seed species being removed or handled by rodents in camera trap photographs. As before, *camera station ID* was used as the random effect. The presence of large-bodied granivores (i.e., bearded pigs) could have affected murid visitation to seed quadrats and seed removal (Keasing 1998), so we also ran a separate GLMM with the same model structure but excluded data from all quadrats visited by bearded pigs.

Finally, we examined if seed removal varied among seed species. We tested whether removal (by all granivores) differed among seed taxa (*Cucurbita*, *Dimocarpus*, *Nephelium*, and *Elaeis*) and whether predator scent had any effect on removal. First, we assessed seed removal (a binary response: seed present or missing from the quadrat at the end of the study) as a function of *seed species* and *treatment*. We used a post hoc Tukey test to compare seed removal between seed species. Finally, we ran separate GLMMs for each plant taxon, modeling individual seed removal caused by any animal (missing versus present) for each species, as a function of *treatment* and of *murid rodent detections*. For all models using species-specific removal as the response, we modelled overall removal (i.e., due to murids or non-murids), rather than seed removal by rodents *per se* because we were unable to distinguish seed species in the camera trap photos. For both types of analysis of species-specific seed removal, paired *camera station ID* was included in models as the random intercept.

All regression models were run using the *lme4* package (Bates & Maechler 2011) in R 3.3.2 (R Core Team 2018). The R package *Performance* was used to check for multicollinearity (Lüdecke *et al.* 2021). Only covariates with low or moderate correlation were retained in analyses. Comparisons of seed removal between species were performed using the *emmeans* package in R (Lenth 2020).

Though our model, predator species is not native to the study region, bobcats are potent predators of rodents elsewhere (Neale & Sacks 2001, Thornton *et al.* 2004), and their urine is a valid proxy for rodent predation risk for several reasons. Rather than responses conditioned to specific predators, prey species typically have innate, generalized responses towards predators in general (Hayes *et al.* 2006). Predator scent recognition is innate in murid rodents, and bobcat urine has been used in experiments measuring changes in rodent foraging (Orrock *et al.* 2004) and behaviour (Fendt 2006). Completely predator-naive laboratory rats (which, like the species we studied, are from the Muridae family but not sympatric with bobcats anywhere) have been shown to respond defensively to bobcat urine despite having spent their whole lives in captivity (Fendt 2006). Lab rat responses may differ somewhat from those of murids in nature, but studies with captive animals

suggest they exhibit broadly similar responses to those under natural conditions (Apfelbach *et al.* 2005). Non-sympatric predator scents elicit behavioural changes in other murid species as well (Bramley & Waas 2001, Dielenberg & McGregor 2001, Carthey & Banks 2016). Therefore, we were satisfied that bobcat urine could serve as a valid 'model predator' scent cue, given that urine from predators native to the study area (e.g., leopard cats, *Prionailurus bengalensis*) was not available.

## Results

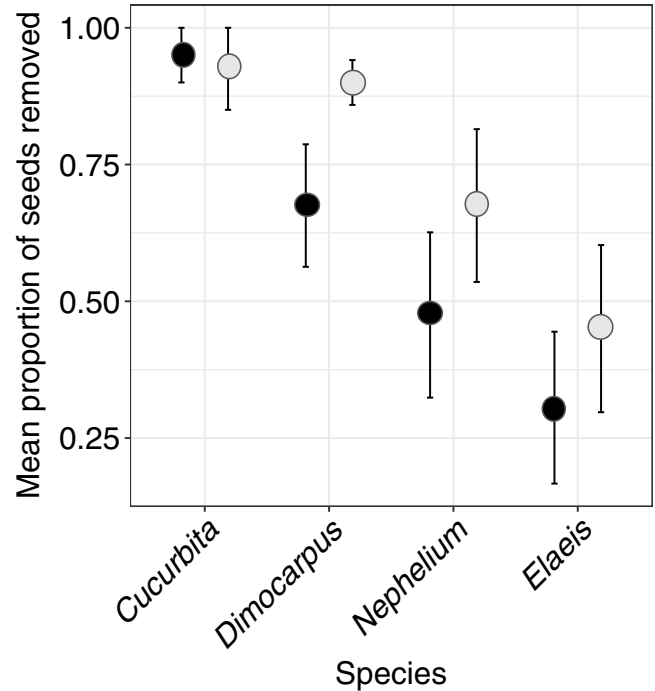
Murid visits to seed plots were similar between control and treatment sites ( $\beta_{\text{treatment}} = 0.270$ ,  $SE = 0.247$ ,  $df = 17$ ,  $P = 0.261$ ). Overall, seed removal by all granivores (i.e., murids and non-murids) was higher in predator urine quadrats ( $\beta_{\text{treatment}} = 0.662$ ,  $SE = 0.263$ ,  $df = 317$ ,  $P = 0.036$ ).

On average, murids removed 1.7 seeds ( $SD = 2.70$ ) across all quadrats, but the proportion of seeds removed was not significantly influenced by predator scent ( $\beta_{\text{treatment}} = 0.652$ ,  $SE = 0.411$ ,  $df = 17$ ,  $P = 0.113$ ; Figure S2). In the absence of bearded pigs, average seed removal (by all other taxa, not just rodents) was 2.54 seeds ( $SD = 3.33$ ) per site and removal by murids did not differ between treatment and control sites ( $\beta = 0.690$ ,  $SE = 0.475$ ,  $df = 8$ ,  $P = 0.146$ ).

Seed removal by all granivores (including camera sites visited by bearded pigs) varied across plant taxa. Removal of seeds of all other plant taxa was more frequent than that of *Elaeis* ( $\beta_{\text{Cucurbita}} = 5.298$ ,  $SE = 0.752$ ,  $df = 313$ ,  $P < 0.001$ ;  $\beta_{\text{Dimocarpus}} = 3.177$ ,  $SE = 0.517$ ,  $df = 313$ ,  $P < 0.001$ ;  $\beta_{\text{Nephelium}} = 1.973$ ,  $SE = 0.467$ ,  $df = 313$ ,  $P < 0.001$ ). Results for comparisons of removal between species are shown in Table S1. Removal of *Cucurbita* seeds was higher than that of all other species (Figure 2). Rodent visits were not significantly related to removal rates in any of the genera ( $P > 0.06$ ; Table S1). Seed removal in *Elaeis* was marginally significantly associated with rodent visits ( $\beta_{\text{Murid}} = 0.512$ ,  $SE = 0.264$ ,  $df = 76$ ,  $P = 0.052$ , Table S2) but, after excluding an outlier, there was no apparent effect ( $\beta_{\text{Murid}} = 0.269$ ,  $SE = 0.375$ ,  $df = 72$ ,  $P = 0.474$ ). *Dimocarpus* was the only taxon for which seed removal was affected by predator scent; removal was higher at sites with predator urine ( $\beta_{\text{treatment}} = 2.002$ ,  $SE = 0.878$ ,  $df = 76$ ,  $P = 0.023$ , Table S2).

## Discussion

Predator scent did not influence murid rodent visits to camera stations. The lack of difference in rodent visitation between treatments suggests that the perceived level of predation risk associated with our deployment of bobcat urine gel was insufficient to cause granivores to avoid the sites. Other studies have demonstrated murid foraging responses to predator scent, including from non-native predators (Wolff 2004, Apfelbach *et al.* 2005, Ramp *et al.* 2005, Carthey & Banks 2016). The lack of treatment effects that we observed could simply demonstrate that the perceived level of predation risk was not sufficient to alter foraging behaviour, such that food rewards outweighed potential risks of foraging in 'predator' plots. Trait-mediated predation effects are known in some systems (Schmitz *et al.* 2004, Preisser *et al.* 2005) but may be far from ubiquitous. Indeed, predators often have no detectable influence on prey distributions (Brodie & Giordano 2013). Even when prey do avoid predators spatially, avoidance movements are often very temporary, rendering changes in overall foraging patterns negligible (Kauffman *et al.* 2013, Brodie *et al.* 2014). It



**Figure 2.** Mean ( $\pm$ SE) proportion of seeds removed from treatment (predator urine gel) and control (no gel) plots in Danum Valley, Sabah, Malaysia. Removal was by all granivorous species combined. Seed removal was the lowest and the highest for the largest-seeded (*Elaeis*) and smallest-seed (*Cucurbita*) plants, respectively, in our study.

is possible that rodents only respond to predator scent immediately after application and that the perceived risk decreases as the urine is masked by other scents in the environment (McFrederick *et al.* 2009, Bytheway *et al.* 2013). However, rodents visited our stations throughout the study period (including immediately after gel application), suggesting that any temporal changes in urine gel potency did not influence rodent behaviour. Changes in granivore responses to predator odors could be context-dependent, varying with extrinsic factors such as temperature and weather (Herman & Valone 2000, Orrock & Danielson 2009). Finally, food availability (i.e., seed density) could influence animal willingness to forage as well as how much food they would consume in habitats perceived as risky (Brown *et al.* 1992). Overall, rodent food availability in our system may have been high as our study took place during a dipterocarp tree masting event providing known rodent food (Phillips & Phillips 2016).

Seed removal by rodents was unaffected by predator urine, but removal by all granivores combined varied with seed species and may have been influenced by seed traits. Granivores may prefer certain seed types depending on energy content (Xiao *et al.* 2006), handling time, body-to-seed-size ratio (Muñoz & Bonal 2008), toxicity, or morphology (Myser & Pickett 1993, Hulme & Benkman 2002). We found that removal rates varied among plant genera, suggesting that seed traits might influence granivore dietary preference. Although larger seeds provide more energy (Charnov 1976, Mack 1998, Brewer 2001), the largest seeds in our experiment (*Elaeis*) were removed least often, while the smallest (*Cucurbita*) were removed most often. Therefore, granivores in DVCA might prefer smaller seeds because of reduced handling times (Dirzo & Mendoza 2007, Muñoz & Bonal 2008, Wang *et al.* 2013). If removal was driven by seed size, low *Elaeis* removal could point to a dietary size threshold for seed predators, whereby

granivory has a greater negative effect on seeds below a certain weight (Dirzo & Mendoza 2007, Perez-Ramos *et al.* 2017). Also, granivores may have perceived the added time spent handling large *Elaeis* seeds in high-risk treatment quadrats as too high relative to energetic gains (Lima & Bednekoff 1999, Dirzo & Mendoza 2007). Foraging for small seeds may be perceived as less risky, even in the presence of predators.

## Conclusion

The use of predator scent to simulate predation risk can reveal how prey species perceive risk in the environment and how any subsequent changes in foraging behaviour might affect plants. Large-scale experiments could provide more insight into how widespread loss of top predators might indirectly affect plant communities. Future studies should use experimental enclosures to identify prey-specific changes in foraging behaviour. We also recommend placing seeds at a range of densities to investigate the influence of food availability on foraging decisions in high risk areas. Finally, evaluating prey responses towards a range of predator species could help determine whether rodents show similar responses towards other non-native predators.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S0266467422000050>

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**Data Availability Statement.** Data are available on Figshare.com ([https://figshare.com/authors/Alys\\_Granados/4108249](https://figshare.com/authors/Alys_Granados/4108249)).

**Competing Interests.** The authors have none to declare.

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