Animal Behaviour 224 (2025) 123195

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

The effect of competitor presence on the foraging decisions of small mammals

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ARTICLE INFO

Article history:
Received 23 June 2024
Initial acceptance 19 September 2024
Final acceptance 13 February 2025
Available online 8 May 2025
MS. number: 24-00393

Keywords:
Bush rats
common brushtail possum
competition
foraging behaviour
Rattus fuscipes
supplementary bait
Trichosurus vulpecula

Competitive interactions between species can have marked effects on the diets and foraging behaviours of the interactants. Dominant competitors can constrain the foraging decisions of subordinate competitors, reducing the individual fitness of subordinates and potentially driving their populations to low levels. Following a sustained population decline of the bush rat, *Rattus fuscipes*, in the presence of the competitively dominant common brushtail possum, *Trichosurus vulpecula*, at Booderee National Park in south-eastern Australia, we investigated whether possums affected the foraging decisions of bush rats. Using a manipulative feeding experiment, we predicted that bush rats would (1) increase visits to baited sites where possums had restricted access to the bait and (2) restrict visits to baited sites where possums had free access. We used camera traps to investigate visit patterns and time spent foraging at 40 baited sites with two treatments, one that allowed full access by both species (full access) and the other that attempted to prevent possum access (restricted access). We also measured additional covariate factors that may influence visits. Bush rats visited both treatments less when there were more possum visits. We also found that bush rats spent less time eating bait at sites regularly visited by possums, regardless of possums' access level. Our results indicate that negative interactions, such as competition, can restrict the ability of subordinate species to successfully forage, contributing to species declines.

The foraging strategies of animals influence how they interact with their living and nonliving environments (Corman et al., 2016; Denny et al., 2018). Foraging strategies include the decisions that individuals must make regularly about what to eat, when and where to locate food, the time spent foraging and when to depart from a food source (Corman et al., 2016; Denny et al., 2018; Searle et al., 2005). These decisions can, therefore, influence habitat use and the local distributions of animals, as well as how foragers interact with co-occurring species (Barabás et al., 2016; Godsoe et al., 2015; Halliday & Morris, 2013). The influence of predation risk on foraging has been well studied. Predators seek prey at times and in places where hunting is most likely to be successful (Denny et al., 2021; Pays et al., 2012). Prey species similarly anticipate and reduce the risk of encountering predators by selecting and departing from foraging patches when they perceive it to be safest to do so (Denny et al., 2021; Pays et al., 2012). If the foraging decisions of prey are constrained markedly by the presence of predators, individual fitness can be compromised and this can translate to declines at the population level (Preisser et al., 2005).

Competition between species may have similarly large effects on individual foraging strategies and their outcomes. Although individuals of a prey species may preferentially choose habitats with denser vegetation to avoid predation, this choice may also result in suboptimal foraging due to the presence of a dominant competitor (Halliday & Morris, 2013). For example, honeybees, *Apis mellifera*, readily forage on energetically profitable lavender flowers when on their own but forego this food source in the presence of bumble bees, *Bombus* spp., to avoid aggressive encounters with this larger competitor (Balfour et al., 2015). Aggressive, or interfering, competitors often attack or chase other species from shared resources

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https://doi.org/10.1016/j.anbehav.2025.123195

(King & Moors, 1979). An example is the Australian noisy miner, *Manorina melanocephala*, which chases other native birds away from flowers and other profitable food resources (Beggs et al., 2020). Physical characteristics, such as body size, can influence the success of competitors (Rayan & Linkie, 2016). This is evident in many carnivore guilds, such as that comprising tigers, *Panthera tigris*, dholes, *Cuon alpinus*, and leopards, *Panthera pardus*, with the latter two species showing temporal avoidance of the larger, more aggressive tiger (Rayan & Linkie, 2016). Similarly, the dingo, *Canis dingo/familiaris*, may constrain the place and time of foraging by smaller-bodied domestic cats, *Felis catus,* and red foxes, *Vulpes vulpes*, in Australia, through aggressive competition and, in extreme cases, by intraguild killing (Burrows et al., 2003; Moseby et al., 2012).

Avoidance behaviours are a common response to aggressive interactions (Astete et al., 2017; Barrull et al., 2014), especially by individuals of smaller or subordinate species. In situations where predation is unlikely, avoidance is often used as an indicator of interference (Périquet et al., 2016). For example, despite sharing many prey species, snow leopards, *Panthera uncia,* and common leopards, *Panthera pardus*, segregate their use of habitats to avoid aggressive encounters (Lovari et al., 2013). These avoidance behaviours reduce the risks of interspecific aggression but can be detrimental, driving increased vulnerability of individuals to other predators or reducing the quantity or quality of available food resources (Liu et al., 2020; Périquet et al., 2016). For instance, giant pandas, *Ailuropoda melanoleuca*, use poor-quality habitat and food to avoid exploitative competition with cattle (Liu et al., 2020). Avoidance can be either spatial or temporal or a combination of both (Wereszczuk & Zalewski, 2015). For example, long-legged buzzards, *Buteo rufinus,* and short-toed eagles, *Circaetus gallicus*, in Israel partition shared habitat on multiple scales, including by spatial and temporal segregation of their foraging activity (Friedemann et al., 2016).

Interactions between species and how these affect the decisions made by individual foragers can be studied by direct observation in large or conspicuous species, such as noisy miners (Beggs et al., 2020; Lindenmayer et al., 2023), but for smaller or more cryptic species other methods are needed. The giving-up density technique, which measures how long individuals spend at a food resource given certain conditions, is particularly useful in this respect (Brown, 1988; Denny et al., 2021; Hagy et al., 2017). Alternatively, carefully controlled experiments, such as laboratory-based studies or complete removal or addition experiments, can be used to investigate interactions, like competition, around manipulated resource availability (Dickman, 2011; Karlsson et al., 2018). Many of these experiments require known or precisely measured levels of resource scarcity or restriction of access by one or more interactants to an abundant food resource. We use this latter approach here.

In Booderee National Park, in south-eastern Australia, successful control of fox populations has contributed to changes in prey species abundance and composition, including considerable population growth of common brushtail possums, *Trichosurus vulpecula*, hereafter 'possum' (Dexter et al., 2013; Lindenmayer et al., 2018). Possum foraging behaviour changes in response to how risky food sources are perceived to be, including the risk of predation and quality of food, and possum foraging activity in Booderee is therefore likely to have expanded in response to fox control (Mella et al., 2015). Research into the impacts of possum population growth has uncovered a link with declines in small mammals, such as bush rats, *Rattus fuscipes* (Kanishka et al., 2023; Lindenmayer et al., 2018). As both possums and bush rats are dietary generalists and often forage in similar habitats, we predict that food competition may be a mechanism that shapes this relationship. Here, we expect that bush rats will alter their activity in response to changes in possum activity. This expectation is based on research that some rodents will change their foraging behaviours when co-foraging with competitors for limited resources (Cordero et al., 2024). Possum aggression and behavioural dominance have also been recorded at bait stations elsewhere, with possums exerting dominance over much larger species (Hickling & Day, 2024).

Using a manipulative experimental design, we investigated the potential influence of competition in shaping the foraging activity of these two native mammal species in Booderee National Park. In our proposed scenario, bush rats are the subordinate competitor, whereas possums are the dominant competitor. Our experiment was designed to investigate avoidance between this putatively dominant and subordinate pairs of mammal species and reveal foraging decisions made by the subordinate species in the presence and absence of the dominant species. We asked the overarching question: Does the presence of common brushtail possums reduce bush rats' access to and foraging activity at sites with shared food resources? We predicted that bush rats would access food resources (bait) less at sites where possums have access, compared with sites where possums do not have access. We tested this prediction by investigating visit patterns of the species, which we quantified as the number of times individuals visited baited sites and the time length of those visits. We conducted this investigation based on the following predictions. (1) Bush rats will increase visits to sites where possums have restricted bait-access, whereas possums will decrease visits to these sites. (2) Bush rats will make fewer, shorter visits with increasing possum presence at full bait-access sites, but not at restricted bait-access sites. (3) Bush rats will spend less time eating with increasing possum presence at full bait-access sites, but not at restricted bait-access sites. (4) Both possums and bush rats will increase the number and length of visits with increasing time since the other species has visited.

METHODS

Ethical Note

This study was conducted in strict accordance with the recommendations in the Australian Code for the Care and Use of Animals for Scientific Purposes. The protocol was approved by the Animal Experimentation Ethics Committee at the Australian National University (Protocol Number: A2021_52). To ensure ethical standards, we performed a pilot study in 2020 to ensure the type of bait used, the rubbish bins placed at each site and wildlife cameras would cause no harm or distress to the animals within the environment. The holes cut out of the rubbish bins were additionally inspected to ensure there were no sharp points on which animals could injure themselves. Cameras were set with no flash to avoid startling animals.

Study Location

Our experiment was conducted in March and April 2022 in Booderee National Park (BNP), a 6000 ha protected area on the south coast of New South Wales, Australia (Fig. 1). The park is owned by the Wreck Bay Indigenous Community and is jointly managed by them and Parks Australia. The park has a temperate climate, with an average rainfall of 1213 mm (Bureau of Meteorology, 2022). However, due to the La Niña weather system occurring at the time of data collection, the park experienced higher-than-average rainfall, including partial flooding, which occurred in the weeks prior to the experiment. The temperatures at the time of the experiment ranged from 13.5 °C to 26.6 °C (Bureau of Meteorology, 2022). The park has a heterogeneous environment, with vegetation types ranging from forests and woodlands to

Figure 1. Satellite map of Booderee National Park, Jervis Bay Territory, Australia. The blue circles identify the locations of the 40 supplementary feeding (bait) sites used in our experiment, with an identifying name in white next to each location (Esri, 2022).

sedgelands and heathlands (Taws, 1998). The park has experienced several wildfires in the last decades, with the most recent large fire occurring in 2017 (Lindenmayer et al., 2023).

Experimental Setup

We established our experiment at 40 sites across BNP, selecting these by referring to trapping records from the immediately previous 5 years (Lindenmayer et al., 2008, 2016). The 40 sites were established in places selected from a long-term monitoring programme established in 2002 and had annual mammal trapping records, with trapping occurring at each site every other year (Kanishka et al., 2023; Lindenmayer et al., 2008). The criteria for site selection were records of both bush rats and possums being trapped at the same site within the last 5 years, with preference given to the most recent trapping sessions or sites where both species had been trapped most regularly. We selected only those sites within woodland and forest vegetation types, as both species were caught consistently within these vegetation types.

We placed 60 litre black rubbish bins upside down at 40 sites, with an entrance at the base that was modified to create two site conditions: full-access (entrance: 10 × 10 cm), where both species could easily gain access to bait placed inside the bin, and restricted-access (entrance: 5 × 5 cm), where only bush rats could gain easy access to bait. Specifically, the restricted-access sites were designed to prevent possums from accessing bait. To attract animals to enter the bins, we used 100 g of rodent pellets as bait, placed on a ceramic dish in the centre of the bin. We placed remote cameras facing the entrance to each bin on the bottom of a star picket (1–2 m above the ground depending on the slope of the ground) 2 m away from the bin.

Cameras recorded animal activity for 28 days and we collected data on the amount of bait taken at each site every other day (depending on site accessibility due to weather conditions). We measured the amount of bait taken by both weight (in grams) and visual assessment (as an estimate of percentage taken or spilled) to confirm visits to the sites. We replenished the baits at least once a week, or if more than 20 g was taken, or if there was evidence of the bait going mouldy.

Camera Data Collection

We collected data on bin visits from the remote cameras. We used two brands of cameras: Boly ScoutGuard Trail Cameras (Boly Media Communications, California, U.S.A.) and Bushnell Core DS No Glow Trail Cameras (Bushnell Outdoor Products, Kansas, U.S.A.). We set the cameras to take photos only at night when both species were active and take three photos in succession upon detecting movement, with a minimum of a 10 s gap between sets of photos.

We recorded information for periods when an animal was visible on camera, which we refer to as 'visits'. A visit began when the animal was visible on camera and ended when it was seen exiting the site or there was more than 5 min between photos. During visits, we recorded the species' identity, time of arrival and exits, and a brief description of the activities the animal was performing during this time. We recorded the time lengths of visits by subtracting the time of entrance from the time of exit. We categorized this description into one of three broad activities (Fig. 2): the species was (1) within the site (that is, visible on camera, but not interacting with the bait or bin), (2) interacting with the bin (that is, sniffing/touching it, trying to move it, climbing on top or entering/exiting the bin) or (3) eating the bait. We identified the activity 'eating the bait' in possums when they visibly had their torso in the bin or head in the dish, and in bush rats when they had their head in the dish or they were facing the camera and visibly holding/chewing on bait (Fig. 2).

Figure 2. Example camera trap images of the categorized activities. (a) Bush rat within bait site, but not interacting with the bins. (b) Possum within site, but not interacting with the bins. (c) Bush rat interacting with the bin (specifically entering the bin). (d) Possum interacting with the bin (specifically jumping on top of the bin). (e) Bush rat eating bait, categorized by bush rat being inside the bin, visibly holding bait. (f) Possum eating bait, categorized by torso within bin, and dish visibly being empty in subsequent photos. Images (a) and (c) show examples of restricted-access bins, and images (d) and (e) show examples of full-access bins.

To quantify factors in addition to species presence that could affect foraging by bush rats, we collected information on topographic wetness, years since fire and the broad vegetation type at each site, as well as estimated illumination from moonlight and rainfall each night. We used fire, rainfall and illumination measures as covariates based on previous research demonstrating their effects on small and medium-sized mammals in Australia (Kanishka et al., 2023; Taylor et al., 2023). We also used the covariates topographical wetness and broad vegetation type as 'stand-in', easily measured variables to represent the environmental heterogeneity of the park (Kopecký et al., 2021; MacGregor et al., 2020). Topographic wetness is an estimate of the relative wetness of a catchment and is used as a proxy of soil moisture and habitat productivity (Kopecký et al., 2021). We calculated a topographic wetness index (TWI) across the park for all sites from raster grids using GROCLIM (site productivity; Xu & Hutchinson, 2011) and extracted using R (R Core Team, 2021). We categorized the broad vegetation type based on semi-annual vegetation surveys (MacGregor et al., 2020). The broad vegetation classifications come from long-used definitions within BNP to describe variations in the

heterogeneous environment and model their effects (Taws, 1998). We calculated the number of years since the last fire at each site based on historical and on-ground records. We estimated illumination from moonlight, based on the moon phase, from fishing/tide records for the coast of BNP (Tides4Fishing, 2023). We extracted the daily rainfall data from the nearby Point Perpendicular weather station (Bureau of Meteorology, 2022).

Statistical Analysis

To examine the effect of common brushtail possums on bush rat foraging activity, we constructed generalized linear mixed models (GLMMs) using the glmmTMB packager ver. 1.0.1 (Brooks et al., 2017) in R (R Core Team, 2021). Generalized linear mixed models quantify how continuous variables, such as count data, change in response to predictor variables, which can be either categorical or continuous, while taking random and predicted effects into account (Brooks et al., 2017). We used five different response variables (number of bush rat, *Rattus fuscipes* [RF_count] and possum, *Trichosurus vulpecula* [TV_count] visits within a night, length of time of bush rat [RF_time] and possum [TV_time] visits and length of time bush rats ate bait [RF_eat]; Table 1). We included TWI, years since fire, broad vegetation type, illumination and rainfall as covariates and included sites as a random intercept effect to account for the correlation between repeated measures at the same sites. There was no animal activity at some sites on many nights, yielding zero-count data that could bias our models (Welsh et al., 1996). Therefore, we used zero-inflated models, which address excess zeros by calculating a probability of absence (Welsh et al., 1996) when modelling the number of visits. Zero-inflated models consist of two model components: the zero-inflation component, which models the probability of a zero, and conditional component which models the count provided that the response is one or above. The zero-inflation component is inversely related to the count component: when the zero-inflation component predicts a higher probability of a zero, it reduces the likelihood of observing a positive count. In other words, a positive effect in the zero-inflation component (e.g. a higher probability of a zero) corresponds to a negative effect on the overall count outcome, as it shifts the distribution towards more zeros and fewer positive counts. We also used the response variables as explanatory variables in the other models to test associations between foraging activities between the species. We also used the access condition for the sites (either full- or restricted-access) as an explanatory variable. In order to compare model effects, we scaled all continuous variables to have a mean of 0 and a SD of 1.

To select the most important variables for each model, we used Akaike's information criterion for small sample sizes (AICc;

Table 1
Variables used in the five GLMMs examining the effect of common brushtail possums, *Trichosurus vulpecula* (TV), on bush rat, *Rattus fuscipes* (RF), foraging activity, including which models the variables were used in

Name	Description	Category	M1	M2	M3	M4	M5	Variation	Type	Details
RF_count	No. of bush rat visits	Explanatory	Response		✓	✓		Temporal	Continuous	Count of the no. of visits over a night. Rescaled. Interaction with bin.type.
RF_time	Time length of bush rat visits	Explanatory		Response	✓	✓		Temporal	Continuous	Length of bush rat visits. Rescaled. Interaction with bin.type.
TV_count	No. of possum visits	Explanatory	✓	✓	Response		✓	Temporal	Continuous	Count of the no. of visits over a night. Rescaled. Interaction with bin.type.
TV_time	Time length of possum visits	Explanatory	✓	✓		Response	✓	Temporal	Continuous	Length of possum visits. Rescaled. Interaction with bin.type.
RF_eat_time	Time length of visits where bush rat eats bait	Response					Response	Temporal	Continuous	Time length of a visit where main activity is bush rat eating bait. Rescaled. Only as a response variable in model 5
Time.Since.Rat	Time since the visit of a bush rat	Explanatory			✓	✓		Temporal	Continuous	Time since the last time the site was visited by a bush rat. Rescaled. Interaction with bin.type.
Time.Since.Possum	Time since the visit of a possum	Explanatory	✓	✓			✓	Temporal	Continuous	Time since the last time the site was visited by a possum. Rescaled. Interaction with bin.type
Bin.Type	The access type of the site	Explanatory	✓	✓	✓	✓	✓	Spatial	Categorical	Access type of site. Two categories: 1. Full-access 2. Restricted-access Interaction with all explanatory variables (except first.visit).
First.visit	Species ID of first animal that visits the bin	Explanatory	✓	✓	✓	✓	✓	Spatial	Categorical	Species ID of first visit: possum, bush rat, macropod, antechinus, etc.
Broad.Veg.Type	The main type of vegetation within the site	Fixed effect	✓	✓	✓	✓	✓	Spatial	Categorical	Two categories: 1. Forest 2. Woodland
Years.since.fire	No. of years since fire	Fixed effect	✓	✓	✓	✓	✓	Spatial	Continuous	One value per site, calculated from the date of the last fire. Rescaled
Twi_twi	Topographical wetness index	Fixed effect	✓	✓	✓	✓	✓	Spatial	Continuous	One value per site, calculated from spatial raster. Rescaled
Illumination	The nightly estimated level of light across the park	Fixed effect	✓	✓	✓	✓	✓	Temporal	Continuous	One record for each night. Rescaled
Rainfall	Nightly rainfall amount	Fixed effect	✓	✓	✓	✓	✓	Temporal	Continuous	Recorded amount of rainfall for each night. Rescaled

M1 to M5 represent the model numbers and variable with 'response' is the response variable within the corresponding model in that column. The category column explains whether we expected the variable to have a predicted effect on the response variable ('explanatory'), or if the variable was an indicator of site variation ('covariate'). Only explanatory variables were also used as response variables. The check marks within the model columns represent what variables are present in the full versions of the models, before model selection. The variation and type columns explain the data structure of the variable. Models 1 and 3 contain an additional zero-inflated step.

Burnham & Anderson, 2002) on all subsets of the five models (Table 1) using the dredge function in the MuMIn package ver. 1.43.17 (Bartoń, 2023). We chose the simplest model within two ΔAICc scores of the top-ranked model (Bartoń, 2023; Burnham & Anderson, 2002).

Prediction one: visit differences in bush rats versus possums at restricted versus full-access sites

We evaluated differences in the number and length of visits of bush rats and possums between the two site conditions (full- and restricted-access to food). We assumed a zero-inflated negative binomial error distribution for the zero-inflated models (number of visits, models 1 and 3) and a Gaussian error distribution for the other models (time length of visits, models 2 and 4). To do this, we measured the response in the visit patterns of both species in the first four models, separately (number of visits and time lengths of visits for each species as response variables, models 1–4, Table 1) to the access condition and the covariates (TWI, broad vegetation type, years since fire, illumination and rainfall).

Prediction two: bush rat responses to possum presence

We evaluated the number and time length of bush rat visits in response to the number and time length of visits by possums between the two site conditions. For this, we used the models with bush rat numbers and bush rat visit time lengths as the response variables. We included two interactions: between the number of possum visits and site-access condition and between the lengths of time of possum visits and site-access condition.

Prediction three: the effect of possums on bush rats eating bait

We evaluated the time that bush rats spent at sites when their main activity was eating bait, and how this varied in response to the number and time length of possum visits. To do this, we constructed a GLMM where the response variable was the length of time of bush rat visits when eating bait (model 5, Table 1). This response variable was calculated as a subset of the RF_time variable (Table 1) by subsetting to visits when bush rat activity was identified as 'eating the bait'. We assumed a Gaussian error distribution for this model. The explanatory variables were the number and time lengths of possum visits, with an interaction with the site-access condition for both variables.

Prediction four: time since the last visit

We evaluated the number and time length of bush rats and possums at bait stations in response to the time since the last visit by the other species. To do so, we used the four models used in the first prediction but focused on a new explanatory variable (models 1–4, Table 1). This variable was the time since the last visit by a possum for the bush rat models and the time since the last visit by a bush rat for the possum models. We included an interaction with the access condition.

RESULTS

Our sites were visited by bush rats 1904 times and by possums 1045 times over the 28 days of the experiment. The next most common visitors were macropods ($N = 173$), such as eastern grey kangaroos, *Macropus giganteus* and swamp wallabies, *Wallabia bicolor*. We also recorded visits from southern long-nosed bandicoots, *Perameles nasuta* ($N = 41$) and antechinuses, *Antechinus* spp. ($N = 38$), and occasional visits from birds of various species ($N = 5$). There were single visits from an echidna, *Tachyglossus aculeatus*, a diamond python, *Morelia spilota spilota*, and a red fox, *Vulpes vulpes*. We were unable to identify 32 of the visitors because they were obscured by vegetation or we only had a partial view of them (e.g. some fur visible, but no distinct features). Overall, we experienced six camera malfunctions; five of these issues were fixed immediately (with only two nights of information lost per incident). One camera stopped recording after day 11.

Prediction One: Visit Differences in Bush Rats versus Possums at Restricted versus Full-Access Sites

Based on the model selection, the most parsimonious versions of models 1–4 included the covariates rainfall and moonlight, but not years since fire, TWI, and the broad vegetation type (Fig. 3; Table S1; Fig. S2). We found no difference in the number or length of visits by either bush rats or possums in response to whether the sites offer full- or restricted-access to the food resource (bait; Fig. 3; Tables S2–S5). There was no significant difference between the restricted and full-access sites in any of the visit metrics (number of visits and time length of visits) for either bush rats or possums (Fig. 3; Tables S2–S5). High rainfall was negatively associated with the number of visits (bush rat: $m = -0.185$, $P < 0.001$, Possum: $m = -0.052$, $P < 0.001$) and the length of these visits (bush rat: $m = -18.561$, $P < 0.001$, Possum: $m = -45.256$, $P < 0.001$). We also found a positive association between rainfall and the probability of species absence for both bush rats and possums, based on the zero-inflation model (bush rat: $m = 0.531$, $P < 0.001$, Possum: $m = 1.175$, $P < 0.001$). High illumination from moonlight was negatively associated with the number of bush rat visits ($m = -0.185$, $P < 0.001$) and the probability that rats were present ($m = 0.096$, $P = 0.011$). However, this variable was positively associated with the amount of time bush rats spent at the site ($m = 7.621$, $P < 0.001$; Fig. 3). The number of possum visits was positively associated with increasing illumination ($m = 0.075$, $P < 0.001$). However, high illumination was also associated with a higher probability of absence, based on the zero-inflation model ($m = -0.524$, $P < 0.001$). Possums also decreased the amount of time spent at sites with increasing illumination ($m = -68.393$, $P < 0.001$; Fig. 3).

Prediction Two: Bush Rat Responses to Possum Presence

Based on model selection for models 1 and 2, the most parsimonious versions of both models included the possum variables TV_time and Time.Since.Visit with an interaction with the Bin.Type variable (Fig. 3, Table S1). In model one (RF_count), the possum variable TV_count was included as an independent variable, with no interaction. In model two (RF_time), the possum variable TV_count was included with an interaction with Bin.Type (Fig. 3). The number of bush rat visits was negatively associated with increasing numbers of possum visits, with no effect of access condition ($m = -0.186$, $P < 0.001$; Fig. 4a). The zero-inflation model showed that the probability of bush rat absence decreased with increasing possum visits ($m = -1.262$, $P < 0.001$; Fig. 3a). The number of bush rat visits also decreased when possum visits were longer, especially at full-access sites (Fig. 4b).

Bush rats spent longer at restricted-access bait sites that were visited by many possums and less time at full-access bait sites that were visited by many possums (Fig. 4c). The length of time bush rats and possums spent at sites was positively associated, with a more pronounced association at full-access sites (Fig. 4d).

Prediction Three: the Effect of Possums on Bush Rats Eating Bait

Based on the model selection results for model 5 (RF_eat), the covariates rainfall and illumination were found to have an effect, while Broad.Vegetation.Type, years.since.fire and TWI were excluded (Fig. S1; Table S1). The model also included the possum variables TV_time and Time.Since.Possum with an interaction with

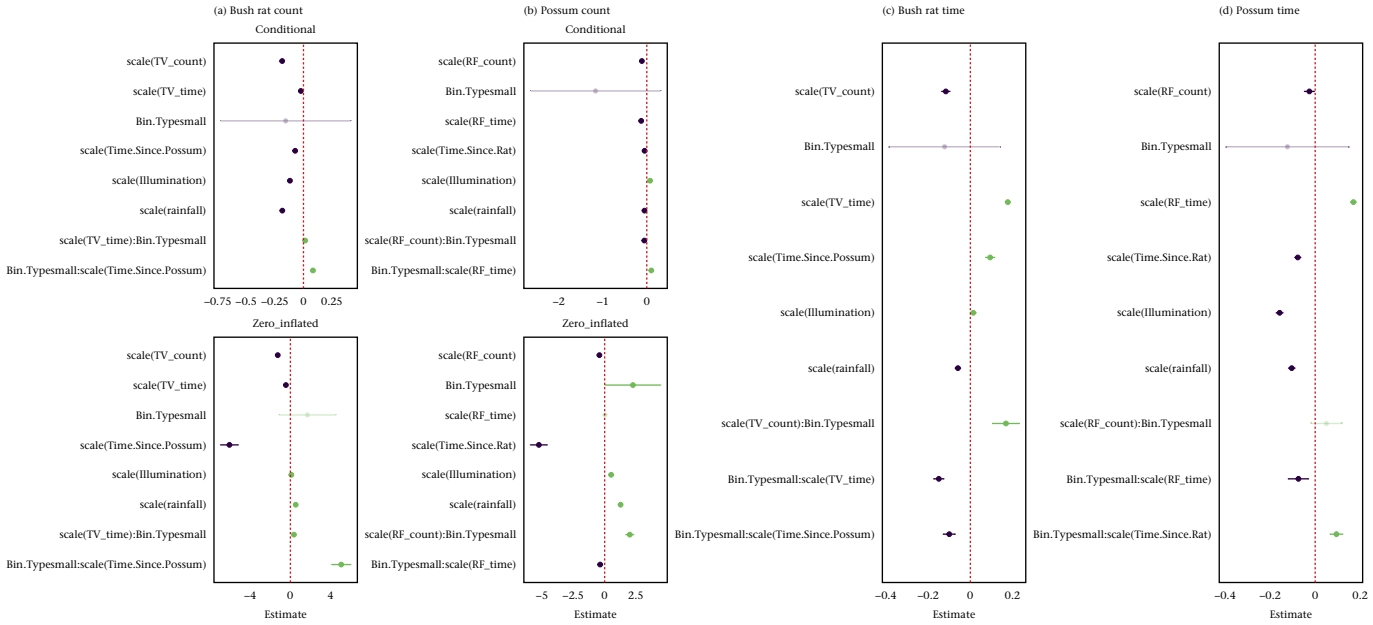

Figure 3. Forest plots of the best fitting subsets of models 1 to 4, showing the effect sizes and confidence intervals. Estimates in purple show negative effects and estimates in yellow show positive effects. Error bars are the 95% confidence intervals, and bars that cross the vertical prediction line demonstrate non-significant effects. (a) The results of the number of bush rat visits to bait sites, including the zero-inflation model (model 1). (b) The results of the number of possum visits to bait sites, including the zero-inflation model (model 3). (c) The results of the duration (s) of bush rat visits (model 2). (d) The results of the duration (s) of possum visits (model 4).

Bin.Type and the possum variable TV_count without the interaction (Fig. S1). Bush rat visits when their main activity was eating bait were shorter when more possums visited regardless of access condition ($m = -0.075$, $P < 0.001$; Fig. 5a). The length of bush rat visits, when they were recorded consuming bait, was positively associated with the overall length of possum visits. This association was more pronounced at full-access sites (Fig. 5b).

Prediction Four: Time Since the Last Visit

Bush rats slightly increased their number of visits at restricted-access bait sites and decreased their number of visits at full-access bait sites, in response to an increase in the time since a possum visited the site (Fig. 6a). Possums decreased their number of visits in response to an increase in the time since a bush rat visited, regardless of access type (Fig. 6b). For bush rats, at full-access sites, the length of bush rat visit time increased with increasing time since a possum visited (Fig. 6c). At restricted-access sites, overall bush rat visit time was low (Fig. 6c). The opposite trend can be seen in the length of possums visits (Fig. 6d).

DISCUSSION

Our experiment aimed to investigate whether the presence of common brushtail possums influenced the foraging decisions and activity of bush rats at supplementary feeding sites. We found evidence that bush rats' foraging activity was influenced by the frequency of visit by possums. In particular, bush rats foraged less frequently and ate bait for shorter periods with increasing numbers of possums (Figs. 4a and 5a).

Foraging decisions play an important role in what and how much food that individuals consume. We aimed to demonstrate two different decision processes the two species could make; exploiting a food source and leaving a foraging patch (Arehart et al., 2023; Baker & Brown, 2014). Many factors influence these decisions including travel time, visibility (e.g. chance of being depredated), food quality and accessibility (e.g. how easily the food is to access and consume), environmental conditions and the presence of other species in the environment (Arehart et al., 2023; Linley et al., 2020). Our results demonstrate three factors that could be influencing foraging decisions: visibility (that is, illumination or moonlight), rainfall and the visit patterns of other species. However, as all our results are correlative, we cannot determine whether any or all of these factors had a causative effect on foraging activity.

Prediction One: Visit Differences in Bush Rats Versus Possums at Restricted Versus Full-Access Sites

The access to bait provided to possums at each of the sites did not influence the visit patterns of either bush rats or possums. Additionally, site characteristics (years since fire, topographic wetness and vegetation type) did not affect bush rat or possum visit. Night-time characteristics, such as rainfall and changes in illumination from moonlight, were associated with active foraging nights.

We suggest that rainfall had a large influence on how long both species spent foraging, with high rainfall influencing the decisions of both species to depart food sources more quickly and visit sites less often. Our study was characterized by high levels of rainfall, with over 700 mm of rain falling in March 2022 (Bureau of Meteorology, 2022). This level of rainfall likely negatively influenced the foraging of all species, with few visits made to the baited sites on nights with the highest rainfall. Some species, especially birds, have been recorded foraging for shorter periods during high rainfall, as factors such as wet feathers can increase the energy required for flight, especially longer-distance travel (De Pascalis et al., 2022). Additionally, rainfall influences the availability of food resources. Williams and Albertson (2006) found that rainfall variability can affect the degradation of grasslands, as well as the variability of grasses, leading to long-term variations in food resource availability. Similarly, in the short-term, Chard et al. (2017)

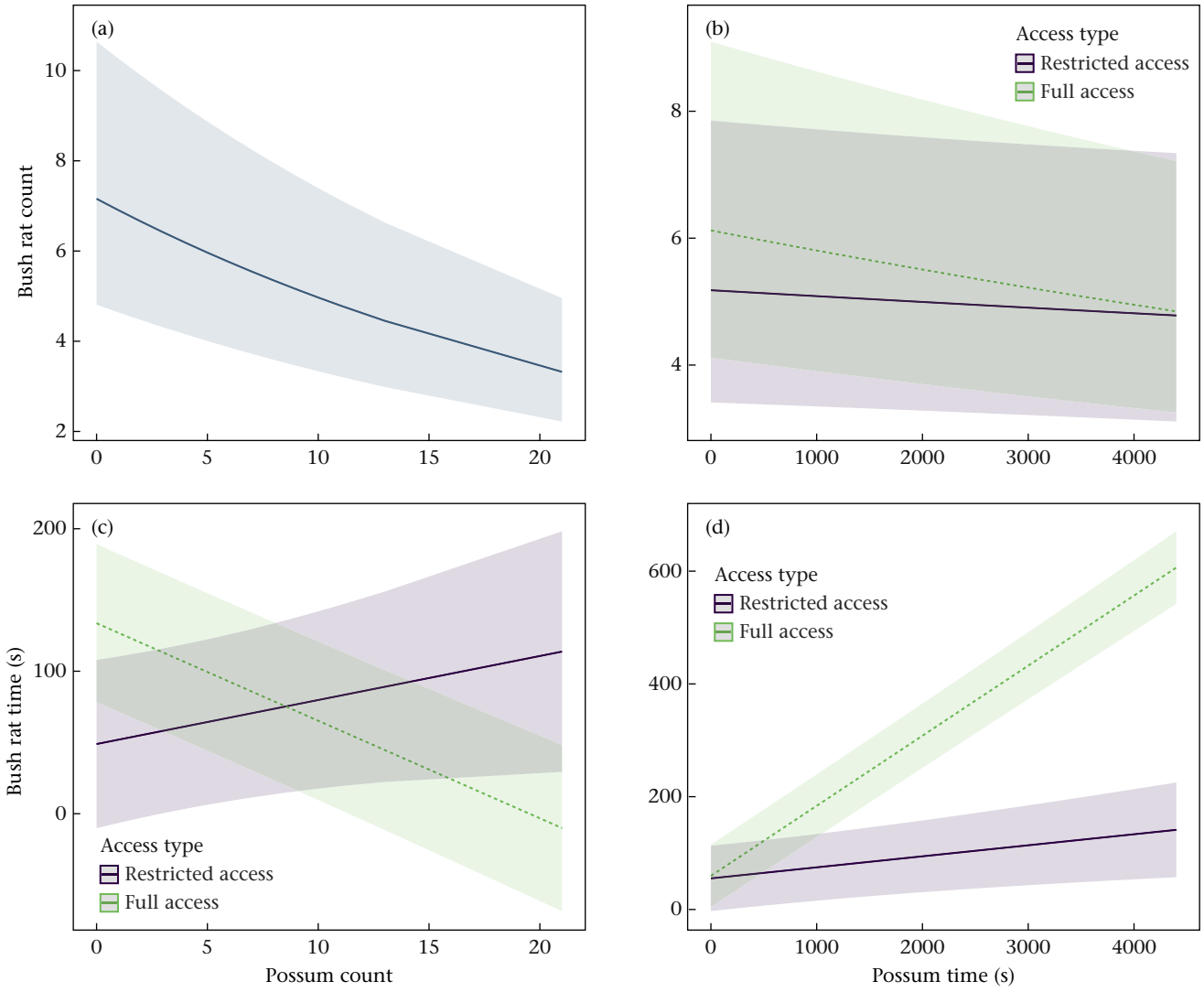

Figure 4. Conditional effects of the generalized linear mixed models. (a) The number of bush rat visits in relation to the number of possum visits at bait sites. (b) The number of bush rat visits in relation to the duration (s) of possum visits at full and restricted bait-access sites. (c) The duration (s) of bush rat visits in relation to the number of possum visits at restricted and full bait-access sites. (d) The duration (s) of bush rat visits in relation to the duration (s) of possum visits at full and restricted bait-access sites. The shaded area represents the SE.

found that rainfall increased the bioavailability of invertebrates while decreasing the availability of anthropogenic food sources. The latter effect was observed in our study, as the quality and structure of our baits were impacted by rainfall, and they became mouldy faster when conditions were humid.

Moon phase and the associated illumination is another factor that can influence foraging activity and, in our study, influenced which nights led to greater foraging activity (Linley et al., 2020; Prugh & Golden, 2014). However, the two study species responded differently to high illumination, with possums overall increasing visit and bush rats decreasing visit to bait stations. Previous research has shown that possums use brighter illumination to assist in foraging and predator detection (Śmielak et al., 2023). Alternatively, many small mammals, like the bush rat, will use lower illumination to avoid detection by predators (Taylor et al., 2023). Therefore, the notable differences in response to moonlight in our study may represent how the two species detect and/or avoid predators, although our data cannot confirm this.

Prediction Two: Bush Rat Responses to Possum Presence

We found that possum presence influenced bush rat visits to bait sites. Bush rats visited sites less often when there were more possum visits. However, the access given to possums had no influence on this visiting behaviour. Access type did influence the length of bush rat visits in response to possum visits, with bush rats spending more time at restricted-access sites when there were more possum visits, and more time at full-access sites when the possums' visits were longer.

The need to forage can lead to increased chances of negative interactions, either by increasing predation risk or increasing encounters with aggressive competitors (Augustine & Springer, 2013; Halliday & Morris, 2013; Mónus & Barta, 2016). Aggression between interacting species can lead to changes in foraging behaviours, including how often a species forages and the sites it preferentially chooses (Beggs et al., 2020). For example, species like the long-legged buzzard, *Buteo rufinus*, in Cyprus organize their use of space in response to the likelihood of encountering a dominant,

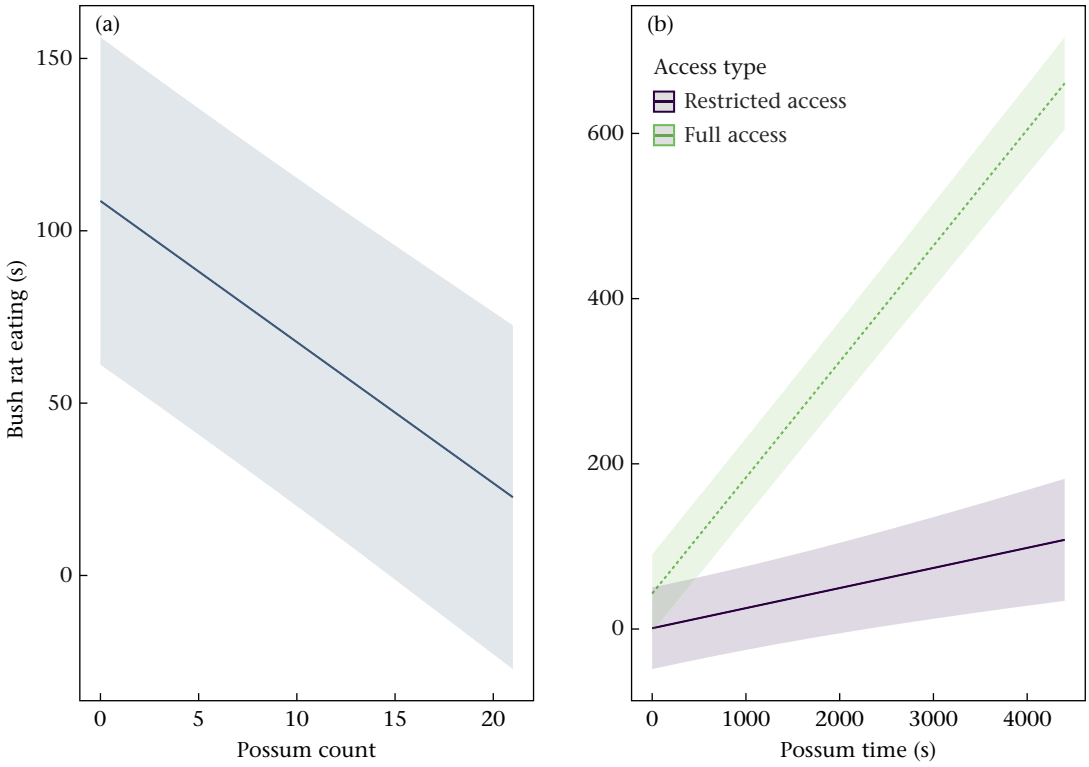

Figure 5. The amount of time (s) bush rats spent at a site where their main activity was eating bait, based on the generalized linear mixed model (model 5). (a) The time in relation to the number of possum visits. (b) The time in relation to the duration (s) of possum visits at full and restricted bait-access sites. The shaded areas correspond to the SE.

larger or more aggressive competitor, such as the Bonelli's eagle, *Aquila fasciata* (Kassinis et al., 2024). Therefore, to reduce the chances of negative outcomes, the ability to detect and avoid aggressive enemies is highly important (Halliday & Morris, 2013; Śmielak et al., 2023). This may lead to a reduction in the number of visits to sites where the aggressive species commonly visit, as we recorded with bush rats. Another way that small mammals do this is by reducing foraging time and effort in habitats that they consider risky, usually showed by higher giving-up densities in more open and uncovered habitats (Denny et al., 2021). Bush rats, specifically, display shorter foraging periods in open habitats, but only when they perceive the presence of an introduced predator (Strauß et al., 2008). Our results indicate that bush rats act as if the full-access sites are riskier habitats, potentially because the restricted-access sites provide an artificial opportunity to hide, whereas the full-access sites do not.

Our results also suggest, unexpectedly, that our study species will spend longer at the same sites. This may suggest a facilitative-like indirect interaction, where either bush rats or possums are using cues from the other to select and spend longer at more suitable sites (Veit & Harrison, 2017). Alternatively, our results may simply be a case of confounding variables which are increasing the suitability of sites, such as the effects of rainfall, with both species responding in similar ways (Denny et al., 2021).

Prediction Three: The Effect of Possums on Bush Rats Eating Bait

We found that bush rat feeding bouts were shorter at sites where possums visited more frequently, suggesting that they chose to depart sooner when the chance of an encounter with a possum was high. Individuals may choose to depart a foraging patch if they perceive that it offers limited benefits or is providing diminishing returns, such as with respect to energy or nutrient availability, or if they perceive that staying in the foraging patch is a risk to their safety (Mella et al., 2018; Shuai et al., 2016). Based on our results, we suggest the latter is more likely. High-quality bait was regularly available; hence, there should have been no reduction in energetic or nutritional returns for bush rats that continued to forage at bait sites. However, if bush rats perceived possums to visit more frequently, perhaps via previous experience or detection of cues to possum presence, such as olfactory cues (Heavener et al., 2014; Prugh & Golden, 2014), short bouts of eating would provide some foraging benefit while reducing the chance of an encounter with possums. Previous research has found that the duration of rodent foraging at a patch can reflect a trade-off between the impacts of interference competition and the need for safety (Shuai et al., 2016).

Prediction Four: Time Since the Last Visit

Bush rats increased their time at full-access bait stations and decreased their time at restricted-access sites with increasing time since a visit by possums (Fig. 6). Bush rats also increased their number of visits at restricted-access sites the longer since a possum visited, whereas they decreased in visit frequency at full-access sites (Fig. 6). Possums, in general, decreased their visits with increasing time since a bush rat had visited. These results may indicate that our two study species use cues from each other in locating and selecting easy-to-access food resources. Locating food resources is an energy-consuming task, where species have many factors to consider, such as the nutritional and energetic benefits of the resource, the amount of energy used to travel and search and the threats posed by other species in the environment (Arehart et al., 2023; Veit & Harrison, 2017). To circumvent such costs, some foragers, such as many sea birds, will follow species with similar diets as a method of locating abundant food sources (Veit & Harrison, 2017). It is possible that possums showed similar

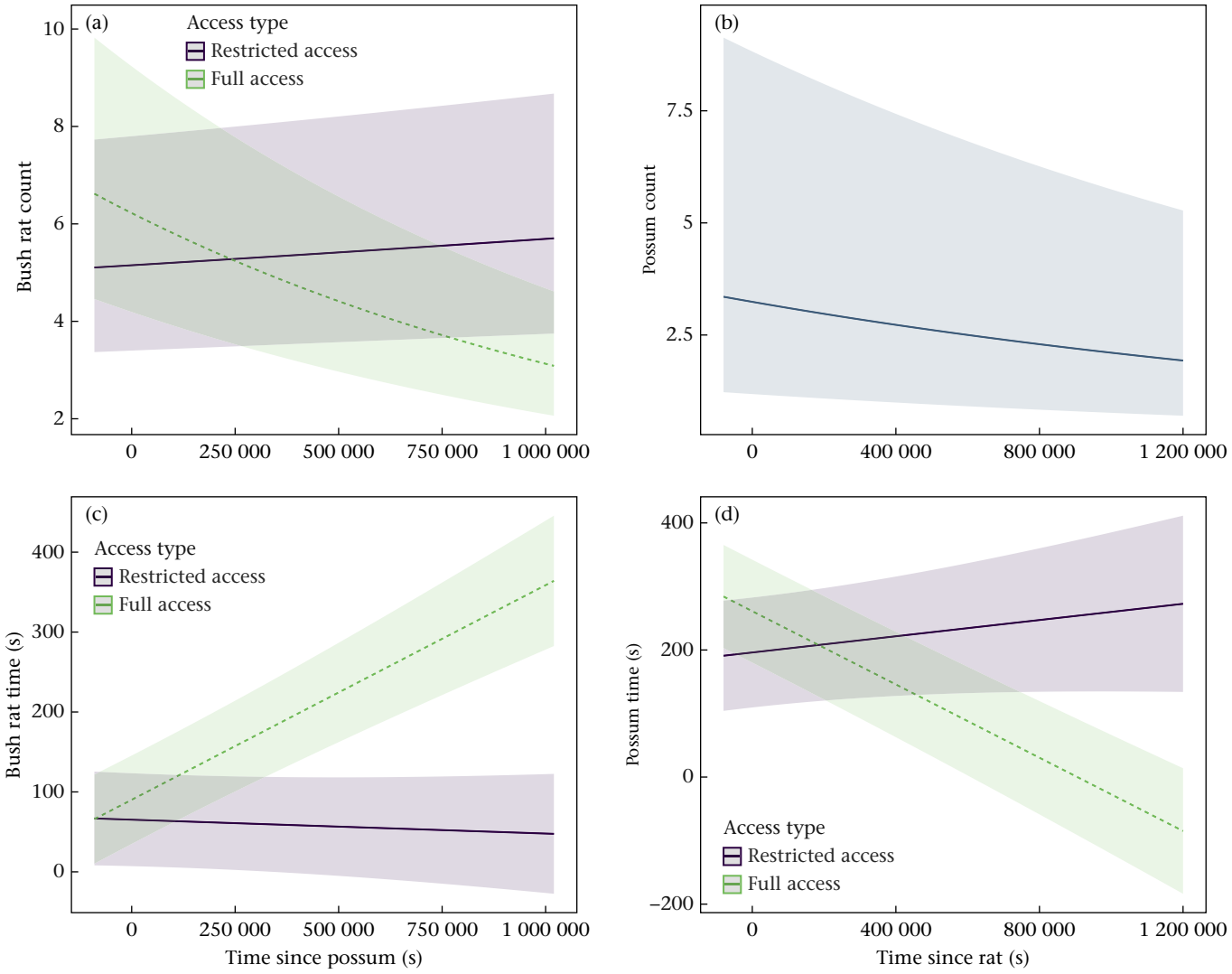

Figure 6. Conditional effects in response to the time (s) since the other species had visited a site, modelled using generalized linear mixed models. (a) The number of bush rat visits in relation to the time since a possum visited (s) at restricted and full bait-access sites. (b) The number of possum visits in relation to time since a bush rat visited (s). (c) The duration (s) of bush rat visits in relation to the time since a possum visited (s) at full and restricted bait-access sites. (d) The duration (s) of possum visits in relation to the time since a bush rat visited (s) at full and restricted bait-access sites. The shaded area corresponds to the SE.

behaviour with respect to exploiting sites foraged by bush rats, and vice versa, but further research is needed to disentangle the cues that both species use to gain information about the other.

Managing Temporal Avoidance

Overall, our study demonstrated temporal avoidance of common brushtail possums in the foraging activity of bush rats. Temporal avoidance allows species to segregate the use of resources (such as food) by time periods (Cordero et al., 2024). In our study, we view this segregation as bush rats temporally avoiding supplementary food during periods when possums are present. Regardless of the drivers behind such avoidance behaviours in the subordinate species, these behaviours have costs. Foraging decisions involving avoidance result in energy-consuming actions and missed opportunity costs that can lead to reduced body condition, resulting in lower long-term survival (Corman et al., 2016; Radovics et al., 2023). Avoidance may also result in species selecting and moving into foraging patches with poorer-quality food (Liu et al., 2020). Temporal avoidance can also result in the subordinate species missing out on good quality food resources, as the dominant may consume all available resources (Burgos et al., 2023; Cordero et al., 2024). Additionally, with the changing populations in BNP leading to greater numbers of possums, the costs of temporal avoidance are likely to be exacerbated (Kanishka et al., 2023; Lindenmayer et al., 2018). Therefore, in our study, we suggest that increased possum numbers following long-term poison baiting of the red fox in BNP are likely to have increased the perception of risk from possums by bush rats (Kanishka et al., 2023). This may have contributed to or exacerbated the potential avoidance behaviours we observed, in turn contributing to the population decline of bush rats across the study area (Kanishka et al., 2023).

In complex ecosystems with many species, the diversity and availability of plant resources are important as food for consumers and for the opportunities they provide for these species to segregate into different niche spaces; these spaces can create refuge habitats for small mammals that represent enemy-free space (Lees et al., 2022; McCain et al., 2018; Mérő et al., 2015). Given the importance of plant resources and vegetation to mammal species (Casula et al., 2017), we recommend focusing conservation on retaining important vegetation classes and structures (e.g. percentage ground cover, tree availability) to increase food resources,

nesting structures and overall habitat suitability for both species, to provide opportunities for niche segregation. Increasing these resources allows for more foraging opportunities while reducing the chance of run-ins between competing species (Casula et al., 2017; Cordero et al., 2024). For example, in managed forests in Sardinia, a large Mediterranean island, the retention of large trees and rock cover has been found to positively influence small mammal abundance while also providing protection from antagonistic species, such as wild boar, *Sus* spp. (Casula et al., 2017).

Conclusion

In conclusion, bush rat foraging decisions may be influenced by the presence of common brushtail possums, especially with respect to how long the rats spend consuming food resources. This temporal avoidance of interactions may result in restricted foraging activity. However, although this study reveals negative and very likely competitive interactions between bush rats and possums, it does not uncover the mechanism(s) driving the interaction. To understand this, we recommend further research on the movement and diet of both species and quantification of the availability of relevant food resources in their shared environment.

Author Contributions

David B. Lindenmayer: Writing – review & editing, Validation, Supervision, Resources, Project administration, Conceptualization. **Nick Dexter:** Writing – review & editing, Validation, Supervision, Conceptualization. **Maldwyn John Evans:** Writing – review & editing, Validation, Supervision, Software, Methodology, Formal analysis, Conceptualization. **Aurelie M. Kanishka:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christopher MacGregor:** Writing – review & editing, Validation, Methodology, Data curation, Conceptualization. **Natasha M. Robinson:** Writing – review & editing, Validation, Supervision, Conceptualization. **Chris R. Dickman:** Writing – review & editing, Validation, Supervision, Conceptualization.

Data Availability

The data that support the findings of this study are openly available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.dncjsxm6k).

Declaration of Interest

The authors declare that there are no conflicts of interest.

Acknowledgments

We would like to acknowledge the Wreck Bay Aboriginal Community who are the traditional owners and co-managers of Booderee National Park (BNP) and thank them for giving us access to the park so our work could be completed. We would like to thank the rangers at BNP for their support during the experimental phases of this work. We would like to thank Tyrone Lavery for his support in the early conception of this study. This work was supported by funds donated by the Lindenmayer Group.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2025.123195.

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