

RESEARCH ARTICLE

The Foraging Ecology of a Threatened Ecosystem Engineer Translocated to Island Safe Havens

Ella Loeffler¹ | Anthony R. Rendall¹  | Nick Porch¹ | Duncan R. Sutherland²  | Amy L. Coetsee³ | Euan G. Ritchie¹

¹School of Life and Environmental Sciences, Faculty of Science, Engineering and the Built Environment, Deakin University, Burwood, Victoria, Australia | ²Conservation Department, Phillip Island Nature Parks, Cowes, Victoria, Australia | ³Zoos Victoria, Wildlife Conservation and Science, Parkville, Victoria, Australia

Correspondence: Anthony R. Rendall (a.rendall@deakin.edu.au)

Received: 12 August 2025 | **Revised:** 13 December 2025 | **Accepted:** 21 December 2025

Keywords: conservation translocation | diet | ecosystem engineer | *Perameles gunnii* | Phillip Island

ABSTRACT

Describing and quantifying the foraging ecology of wildlife is important for fundamental ecological theory and understanding the roles species play within ecosystems. Further, such information can be applied to help guide conservation actions, such as predictions of ecological outcomes resulting from threatened species translocations aimed at reestablishing self-sustaining populations and restoring functions to ecosystems. Our study investigated the diet of two populations of Eastern Barred Bandicoots (*Perameles gunnii*, mainland populations) introduced to fox-free islands (Churchill Island and Phillip Island, southeastern Australia) outside of the species' historical range. Microscopic analysis of faeces revealed that bandicoots exhibit an omnivorous diet, consuming a broad range of invertebrate, plant and fungal material, similar to previous studies of their diet within their natural range. Commonly identified invertebrate taxa included earthworms, beetle adults and larvae, ants, cockroaches, spiders and caterpillars. Notably, crabs were also found in bandicoot diet, indicating the species' ability to adapt to and use coastal (novel) environments. Seasonality was the main factor associated with changes in bandicoot diet at Churchill Island, suggesting that the species is a facultative generalist omnivore that shifts feeding seasonally, likely in relation to variation in food availability. Diet also shifted in response to bandicoot density, likely related to the expansion of the bandicoot population into more diverse habitats across the island. The inherent flexibility of Eastern Barred Bandicoot diet means they are well-suited for additional conservation translocations although prior assessments of recipient ecosystems are needed.

1 | Introduction

Foraging is critical for the growth, reproduction, and survival of wildlife, and can have important ecological effects at population-, community- and ecosystem-levels (Galindo-Leal and Krebs 1998). An animal's diet provides important insight into its ecology and how it interacts within a species community. Identifying and quantifying diet can therefore assist species conservation efforts. This information is vital for threatened species, where the effective management and conservation of

wildlife populations and their habitats requires an understanding of dietary preferences and requirements (Chen et al. 1998; Vogel et al. 2018). For example, sound knowledge of a species' dietary preferences is essential for ensuring there are sufficient food resources at potential release sites. It can also provide insight into the potential effect of an animal's foraging behaviour on the ecosystem to which it is introduced (Coggan and Gibb 2019). Identifying the trophic ecology and diet of a species is essential for implementation of effective management, both at the species and ecosystem level (Dicken et al. 2017).

Ella Loeffler and Anthony R. Rendall contributed equally to this work.

Foraging resources are not static, with seasonal fluctuations well documented (Moeed and Meads 1984; Frith and Frith 1990; Recher et al. 1996; Sinclair et al. 2001; Lo Surdo et al. 2024). For predators, these fluctuations may manifest in a shift in activity (i.e., Mountain Pygmy Possums *Burramys parvus* hibernate during snowfall when resource availability is limited; Kortner and Geiser 1998) or a shift in foraging (i.e., Feral Cats *Felis catus* regularly shift their diet in response to prey availability; Bonnaud et al. 2011; Rendall et al. 2022). In addition, foraging may be influenced by the prevailing density of a species, increasing intraspecific competition and likely driving an increase in sub-optimal foraging at times when populations are large. Swamp Antechinus (*Antechinus minimus*), for example, have been found to have fluctuating litter sizes on offshore islands, thought to be in response to climatic conditions, food resource availability and population density (Sale et al. 2009). Hence, to understand a species' foraging and its impacts, an understanding of foraging shifts in response to climatic conditions and surrounding densities is crucial.

Australia has suffered more mammal extinctions than any other region in the last ~250 years, including many digging mammals regarded as ecosystem engineers (Fleming et al. 2013; Woinarski et al. 2015). In response, returning native, soil-disturbing mammals to ecosystems to reestablish viable populations, reinstate lost ecosystem functions, and aid ecological restoration is a widespread priority for conservation actions (Fleming et al. 2013; Manning et al. 2015; Palmer et al. 2020). In an increasingly modified landscape, assisted colonisations/translocations may also be required, both for species recovery and for potential ecological restoration. Successful conservation translocations require ongoing monitoring (Seddon et al. 2014), both to measure population changes and to assess species' ecological effects/impacts at translocation sites. Characterising a species' diet can provide crucial insight into its ecological role and impact, particularly in novel ecosystems where species conservation can be valued over and above the recipient ecosystem (Hewitt et al. 2011).

With a view to aiding and achieving threatened species recovery and restoration of ecosystem function, the mainland Eastern Barred Bandicoot (*Perameles gunnii*, mainland populations) have been translocated to islands outside of their historical range (Rendall et al. 2018). The species was historically distributed across the basalt plains of south-western Victoria (Seebeck 2001) and far southeastern South Australia (Kemper 1991). Due to introduced predators and habitat loss, the mainland subspecies has suffered a substantial decrease in its range (Seebeck 2001) and was until recently classified as 'Extinct in the Wild' (DSE 2013). In 2015, a small breeding population of 20 captive mainland Eastern Barred Bandicoots was released onto Churchill Island, a 57 ha European Red Fox (*Vulpes vulpes*) and cat free island in Victoria (Rendall et al. 2018). A second population was released on the adjacent Phillip Island in 2017 (Department of Environment, Land, Water and Planning 2021), which is fox-free but has a Feral Cat population. Both these islands are outside of the species' known historical mainland geographic range, but there are historical accounts of Southern Brown Bandicoots (*Isodon obesulus*) on Phillip Island (Kirkwood and Johnston 2006), as well as of an unknown species of bandicoot on Churchill

Island (Grant 1803). Introducing an ecological analogue onto these islands may therefore have a two-fold benefit of returning ecological function to these fragmented, modified and degraded sites (Sutherland et al. 2014) and simultaneously aiding in the conservation of an endangered Australian mammal. The Eastern Barred Bandicoot is an insectivore-omnivore (Mallick et al. 1997) that opportunistically forages for a wide range of subterranean and surface invertebrates, such as beetles, worms, crickets and spiders (Heinsohn 1966; Brown 1989; Dufty 1994; Mallick et al. 1997; Seebeck 2001). They are also known to consume plant and fungal material (Quin 1985; Mallick et al. 1997). A limited number of previous studies on the diet of the Tasmanian populations have found them to be an opportunistic, generalist feeder that forages on invertebrates in proportion to their availability (e.g., Mallick et al. 1997). This study is the first to examine the diet of the mainland Eastern Barred Bandicoot translocated beyond its known historical distribution.

Our study investigated the composition and variation in Eastern Barred Bandicoot diet across two translocation sites immediately post-release and through periods of increasing bandicoot density. We expected Eastern Barred Bandicoots would have a broadly similar diet within their introduced island populations to previous studies of the species. We predicted that dietary variation would vary with season in response to changes in invertebrate availability (Mallick et al. 1997) and soil compaction (Halstead et al. 2019), with above-ground invertebrates anticipated to be more dominant in spring and summer, and subterranean invertebrates more dominant in autumn and winter. We also anticipated that bandicoot density would influence diet composition. We predicted that diet composition would shift in response to increased intraspecific competition and expansion into more diverse habitats across the island and foraging on less optimal food resources. We did not expect to detect differences in foraging preferences between the sexes due to the limited sexual dimorphism in Eastern Barred Bandicoots although we do test for this effect given the potential for different energetic requirements (Dufty 1991).

2 | Methods

2.1 | Study Sites

This study was conducted on Churchill Island (38.4992°S, 145.3379°E), and the Summerland Peninsula on the western tip of Phillip Island (38°30'40.6"S 145°08'56.2"E), in Westernport Bay, southeast Victoria, Australia (Figure 1). The region is a coastal, mesic environment and experiences a temperate climate, with annual mean temperature ranging from 11.7°C to 18.7°C. The average annual rainfall is 619.8 mm (Bureau of Meteorology weather station #086373 at Rhyll, Phillip Island). Throughout the duration of our study (2015–2017), the study region received an average of 742.5 mm a year (Bureau of Meteorology weather station #086373).

Churchill Island is 57 ha and connected to Phillip Island by a 100 m vehicle bridge designed to exclude feral predators and rabbits (Hill et al. 2018). The dominant habitat types on the island

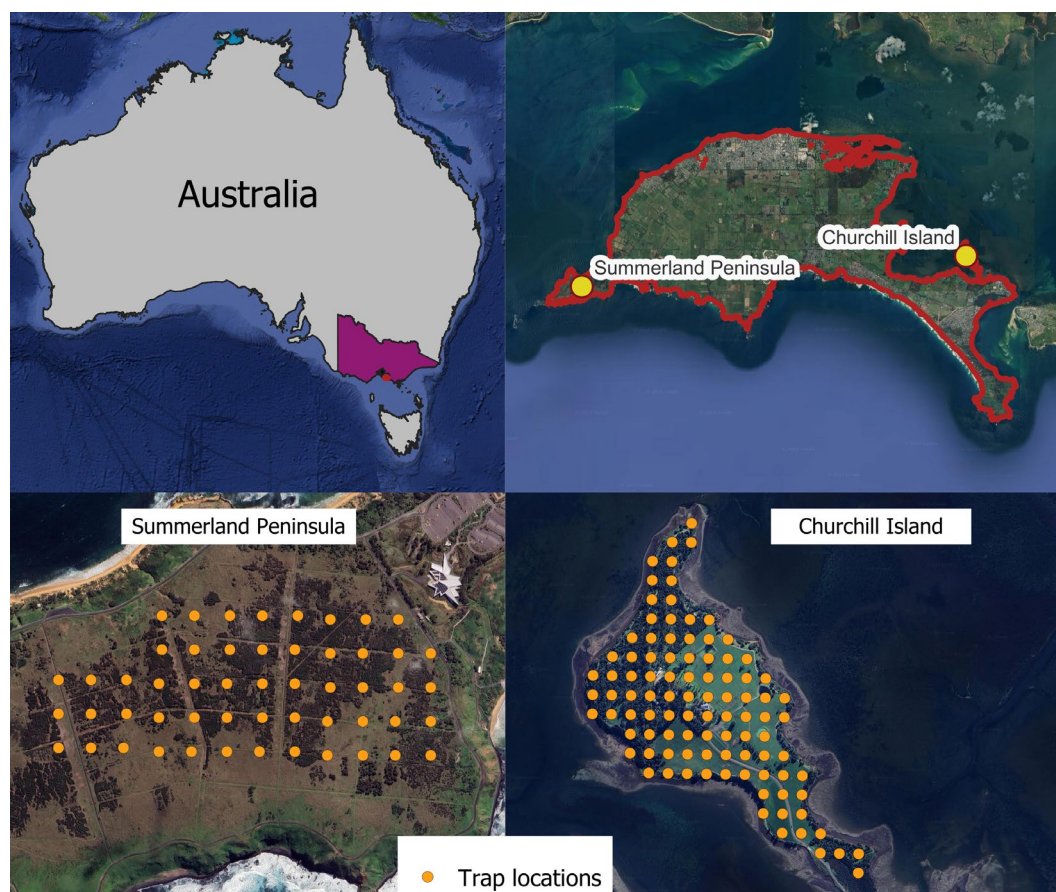


FIGURE 1 | Study sites (top right) in Summerland Peninsula (bottom left) and Churchill Island (bottom right) in Victoria, Australia (top left). Orange dots represent trap locations used during the study.

are closed woodlands and open grassy pasture, with manicured lawns and gardens belonging to a working heritage farm. The Summerland Peninsula is approximately 300 ha with a rocky coastline that rises to 40 m altitude. The study site is an exposed coastal plateau, primarily dominated by tussock grassland and *Melaleuca* woodland (Sutherland et al. 2014). Phillip Island is fox-free but has a feral cat population (Bryant et al. 2022; Rendall et al. 2022). A control program is in place to reduce feral cat abundance on Phillip Island, with a specific focus on Crown Land (Phillip Island Nature Parks 2012). Due to the contrasting histories of both sites, we analyse data separately and compare results between sites.

2.2 | Study Species

The Eastern Barred Bandicoot (herein referred to as ‘bandicoot’) is a small-to-medium-sized digging mammal with a 2–3-year lifespan (Backhouse et al. 1994). Females are highly fecund, producing up to five litters a year with a gestation period of 12.5 days (Backhouse et al. 1994). Weighing ~750 g (Seebeck 2001), the species falls within the ‘critical weight range’ of 35–5500 g (Johnson and Isaac 2009), making it particularly vulnerable to predation by introduced predators such as the Red Fox and Feral Cat. Moreover, large-scale loss of its natural grassland and grassy woodland habitat (> 99% since European settlement) has contributed to the decline of bandicoot populations (Dufty 1994; Backhouse et al. 1994).

Eastern Barred Bandicoots on Churchill Island have shown high rates of population growth since their introduction in 2015. Population estimates now exceed 130 individuals, based on mark-recapture models, and the population has stabilised (D. Sutherland *unpublished data*) and ranges across the whole island on a daily basis (Rendall et al. 2018). Preliminary estimates for Phillip Island are similarly promising (D. Sutherland *unpublished data*), highlighting the potential of successful population establishment even in the presence of Feral Cats (*sensu* Rendall et al. 2021). Predation by Feral Cats and the disease, toxoplasmosis, that is spread into the environment by cats (Adriaanse et al. 2020), still presents a threat to bandicoots (Lynch et al. 2025). However, populations are expected to persist if foxes are absent, and cat populations are controlled (Groenewegen et al. 2017; Rendall et al. 2021; Adriaanse et al. 2024).

2.3 | Trapping and Scat Collection

Bandicoots were live trapped for four consecutive nights, up to four times per year at Churchill Island between August 2015 and March 2018, and at Summerland Peninsula between November 2017 and May 2018 (Figure S1). Trapping periods were initially designed to target the middle month of each Austral season. Wire cage traps were laid out on a grid across the sites and checked at night when animals are active. During live trapping, fresh faecal pellets from trapped

individuals were collected from the base of traps, stored in 70% ethanol for dietary analysis, and labelled with the animal's passive integrated transponder (PIT) tag, trap number, and date of capture. As gut passage time for bandicoots is 10–24 h (Hume 1999), the scats collected were assumed to represent the previous night's foraging.

2.4 | Scat Analysis

Individual scat samples contained between 1 and 12 faecal pellets. To standardise scat volume, a subsample of ~0.5 g was used for analysis from each sample collected. Following the micro-histological techniques outlined by Quin (1985) and Dufty (1994), portions of the scat were gently teased apart in 100% ethanol with fine forceps under a dissecting microscope. The contents were initially examined for the presence of Oligochaeta (earthworm) chaetae, Lepidoptera (moth) scales, and fungal spores. They were then examined for any larger identifiable invertebrate and vertebrate structures. The remaining contents were washed through a 500- μ m sieve over 355- μ m and 63- μ m sieves, using running water to remove dirt and smaller particles. Retained material from the 500- μ m sieve and 350- μ m sieve was further examined for invertebrate structures. The presence of broad plant groups (monocots, dicots) was noted, as well as seeds, roots, and Onion Weed (*Romulea rosea*) bulbs, but plant material was not identified in further detail.

2.5 | Prey Identification

Invertebrate and vertebrate structures and fragments were identified by reference to descriptions, illustrations and published keys (e.g., Bytheway and Dickman 2014), as well as expert taxonomic identification (author NP). Invertebrates were identified to the lowest taxonomic unit possible from whole or fragmented structures, including, but not limited to, legs, mandibles, antennae, forceps, wings, fangs, beetle elytra and larval skins, or head capsules. Only invertebrate data were used for further analysis. While we attempted to identify all items to genus, it was generally only possible to identify to order for most invertebrate items, and family-level for beetles (Coleoptera). This is because beetles were easier to identify, due to the preservation of characteristic structures and their typical condition, and the availability of an expert to assist with identification (author NP). Earthworms, identified through their chaetae, and moths identified through their scales, could not be confidently quantified as these body parts could represent one or multiple individuals. In these cases, the presence or absence was noted within each sample and frequency of occurrence considered. For soft-bodied larvae such as caterpillars and beetle larvae, the sclerotized head capsules, mandibles and legs allowed for some level of quantification, as these were more resistant to digestion.

The minimum number of individuals ingested was estimated for each invertebrate taxa. It was assumed that the remains of a taxon in a scat were from a single individual unless there was evidence for more than one individual. Highly fragmented material that could not be identified was not considered. Count data (estimated number of invertebrates consumed) was recorded, and frequency of occurrence of each dietary item was calculated,

expressed as the percentage of the total number of scat samples containing a particular food item (Davis et al. 2015).

2.6 | Data Analysis

To determine whether sufficient samples had been collected to represent diet at each study site, the cumulative dietary diversity (Brillouin index of diversity) of food categories was plotted against the number of scat samples. The mean cumulative curve and associated 95% confidence intervals were calculated from 1000 curves based upon different random orders of the samples (Dunn 2009). An asymptote in dietary diversity indicates sample size is adequate to describe bandicoot diet at the site of interest (Sutherland 2011).

2.6.1 | Dietary Variation

Only invertebrate groups for which we had recorded a minimum number of individuals of each taxon were used for multivariate analysis. Invertebrate items were grouped to the level of order or higher to reduce the number of dietary items and were considered separately if they occurred in > 10% of scats. The exception was Hymenoptera, which was split at the family-level into ants (Formicidae) and wasps/bees (Hymenoptera other) due to functional differences between these two groups. Multivariate analysis was limited to invertebrates as counts relating to plant and fungi material were difficult.

To understand how bandicoot diet varied with population density we only used data from Churchill Island as this population had reached carry capacity (see Townsend 2020). We generated density estimates for bandicoots for each trapping period using spatially explicit capture-recapture models (Efford and Fewster 2012) in R (R Core Team 2017). These models use recapture data from known individuals to estimate detection probability consisting of an estimate of spatial ranging behaviour of each individual (sigma) and the probability of detection at each trap location (g0). Density was estimated for each session of trapping individually, while additional parameters were included against g0 and sigma including: 'b learning' (where an individual is more or less likely to be trapped again after first capture); 'k learning' (where once an individual is caught at a site, individuals are more likely to be caught again); 'sex' (detection estimates vary for males and females), and 'session' (detection estimates vary for each session). Interactions between b or k learning with sex and session were included. Models were run with a half-normal distribution with the best supported model determined by Akaike's Information Criterion, corrected for small sample sizes (AICc). Full model analysis results are in Townsend (2020). For multivariate analysis density was grouped by low (< 1 bandicoot/ha) reflecting bandicoots initially translocated to Churchill Island, medium (1–2 bandicoots/ha) broadly comparable densities to known and stable bandicoot populations (D. Sutherland *unpublished data*) and high (> 2 bandicoots/ha) density likely reflective of improved environmental conditions. Bandicoot density often fluctuates to a maximum of 2 bandicoots per hectare (A. Coetsee *unpublished data*); hence we consider values > 2 as high density, and < 1 low density. In the case of Churchill Island, low density is also indicative of a recently translocated

population. Rendall et al. (2018) found that individual bandicoots foraged across the whole island, with peak in population density being 150 individuals (Townsend 2020) which coincides with ~3 bandicoots per hectare (Churchill Island is 52 ha).

To determine if there was a difference in community assemblage of invertebrates in scats between seasons, sexes and density levels, we first $\log_{10}(x+1)$ transformed the invertebrate counts to reduce the influence of abundant species. We then calculated a Bray–Curtis similarity matrix between samples (Clarke and Warwick 1994). A permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations was fitted to the similarity matrix using the PERMANOVA+ package in Primer v7 (Clarke and Gorley 2006). Season, sex and density levels were included as fixed factors, with no interactions considered. Individual bandicoots and year of sampling were included as a random factor to account for repeated measures of scats collected from the same individuals through time and to account for possible inter-annual differences.

A significant PERMANOVA can be due to differences in composition between groups, differences in multivariate dispersion among groups, or a combination of the two (Anderson et al. 2008). To assist in determining which of these contributed to differences, we ran the PERMDISP function in the PERMANOVA+ package in Primer v7 (Clarke and Gorley 2006) to test for differences in group dispersions. Pairwise comparisons of group dispersion were used to detect which group pairing contributed to differences in dispersion. For important predictors, we also ran pairwise comparisons between groups for significant factors. Where statistical significance within PERMANOVA was identified, we subsequently ran a canonical analysis of principal coordinates (CAP) to identify which invertebrate species were

most influential in driving differences. Vectors with $>$ or < 0.5 correlation with CAP are displayed.

3 | Results

A total of 332 scat samples from 148 individual bandicoots were collected from Churchill Island, and 65 samples from 39 individuals from Summerland Peninsula, Phillip Island, and allocated to one of four Austral seasons. Both cumulative Brillouin diversity indices reached an asymptote with increasing sample size (Figure S2), indicating that sampling effort was sufficient to adequately describe bandicoot diet at both sites (asymptote was reached at approximately $n=100$ samples at Churchill Island, and $n=50$ samples at Summerland Peninsula).

3.1 | Bandicoot Diet Composition

Bandicoots at Churchill Island exhibited an omnivorous diet consisting of invertebrates, plant and fungal material (Figure 2). A total of 16 major groups of invertebrates were detected including Insecta (Coleoptera, Lepidoptera, Formicidae, Blattodea, Hemiptera, Orthoptera, Hymenoptera, Dermaptera), Annelida, Arachnida (Araneae, Acarina, Opiliones), Crustacea (Isopoda, Brachyura), Diplopoda, and Gastropoda. There was a high incidence of vegetative matter in scats, in particular monocot grasses which were found in almost all scats (Figure 2) and often made up a large proportion of scat volume as visually estimated. Other plant materials included dicot, roots, seeds and onion weed bulbs. Fungi were also consumed at relatively high frequency (47%). The only vertebrate material found was a small number of samples (2%) that contained skink scales or digits.

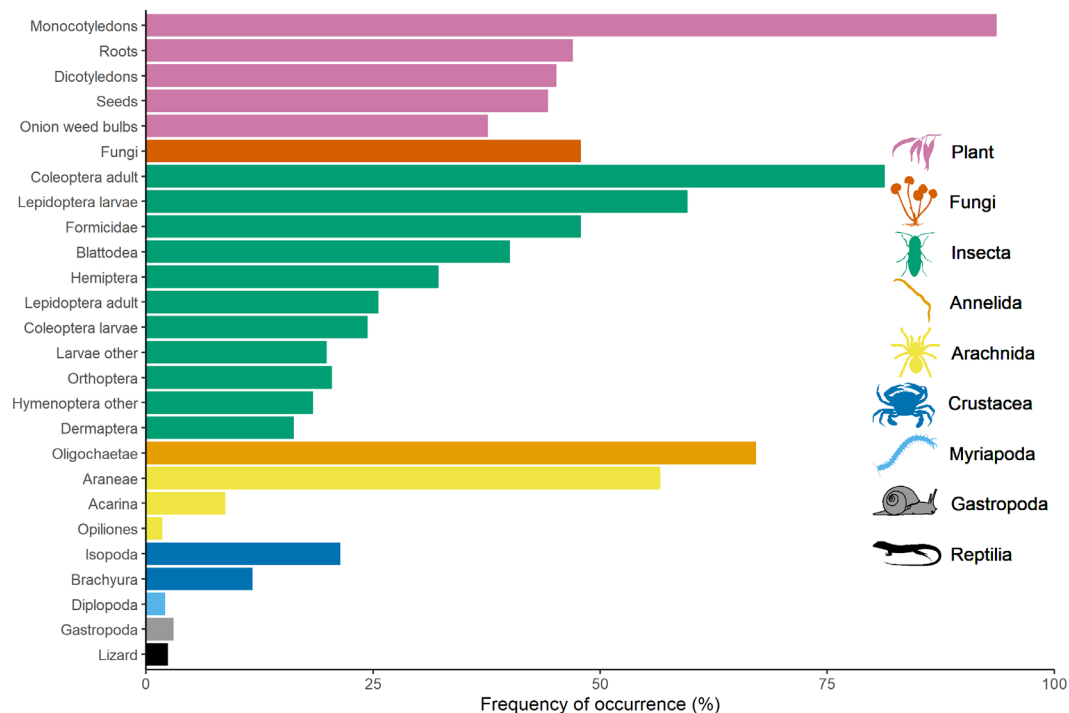


FIGURE 2 | Frequency of occurrence of dietary items present in eastern barred bandicoot (*Perameles gunnii*) scats at Churchill Island, southeastern Australia.

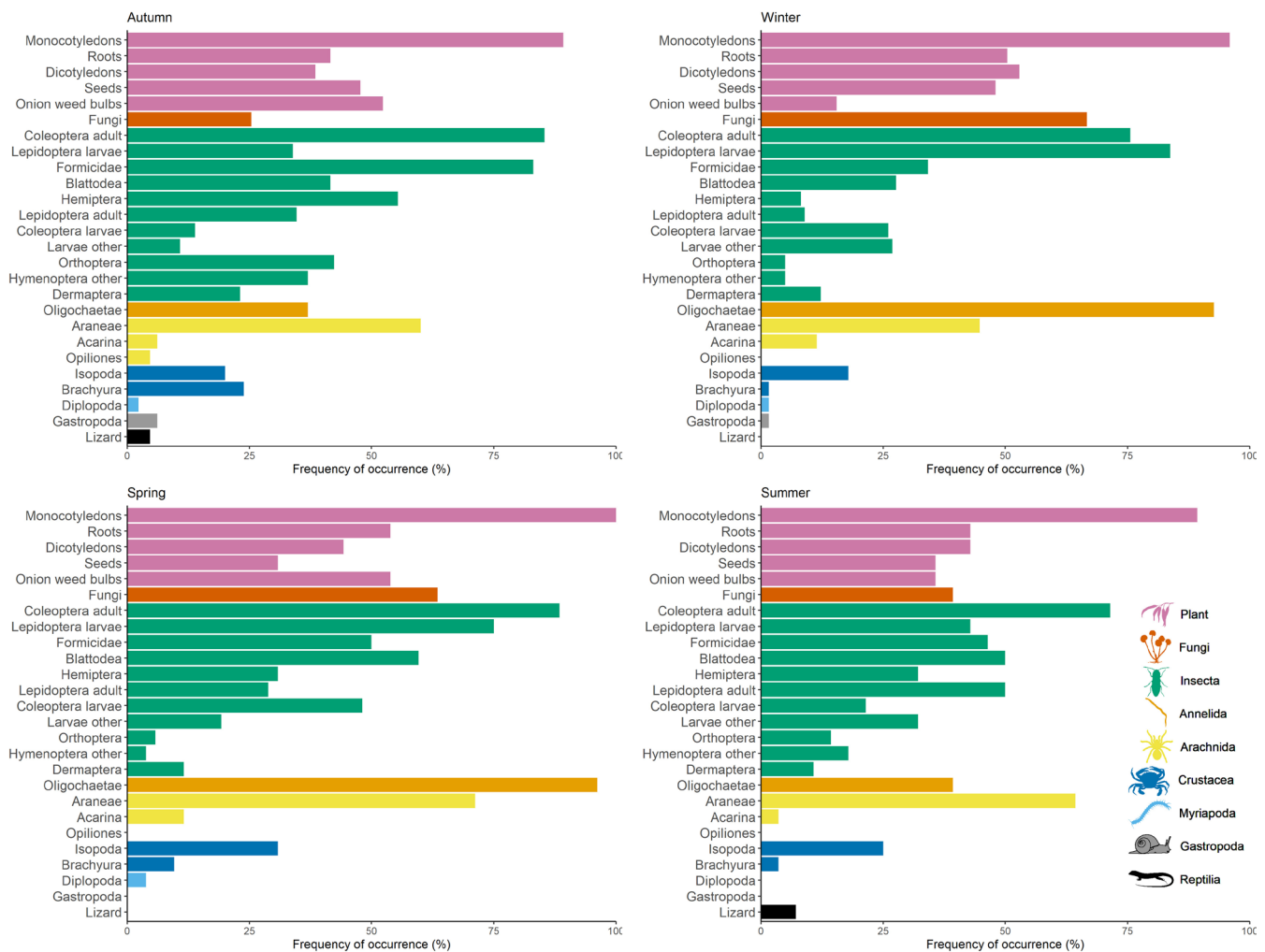


FIGURE 3 | Frequency of occurrence of dietary items present in eastern barred bandicoot (*Perameles gunnii*) scat samples from Churchill Island, southeastern Australia, by season.

The most frequently consumed invertebrate groups were beetles (Coleoptera adults; 88%), earthworms (Oligochaeta; 67%), caterpillars (Lepidoptera larvae i.e., moth and butterfly larvae; 60%), and spiders (Araneae; 59%).

Beetles had the highest contribution to diet in each season, except for winter, when caterpillars were the dominant group in the diet; these were also readily consumed in spring and summer. Ants (Formicidae) were also present in half of the scats examined. Crabs (Brachyura) were found in 12% of scats (Figure 2). Plant material was present year-round. Roots and seeds were ingested at slightly higher frequencies in autumn and winter. Bandicoots ingested fungi at highest frequencies in winter (Figure 3).

Beetles are the most diverse invertebrate taxon and were identified to lower taxonomic levels. In total, there were 26 distinct adult beetle taxa identified to family, genus or species, with 11 other unidentified beetle specimens found in scats. Of the adult beetle families, scarabs (Scarabaeidae) and weevils (Curculionidae) were the most consumed, followed closely by click beetles (Elateridae) and ground beetles (Carabidae, Figure S3). Scarabs were the most common beetle eaten in summer and winter. In summer, bandicoots also ingested click

beetles, weevils, and ground beetles regularly, while weevils were also common in winter (Figure 4). Almost three quarters of spring scats contained click beetles, as well as scarabs at moderate frequency. Consumption of beetle larvae peaked in spring, when they were found in half of scats (Figure 4). These were primarily scarab larvae; beetle larvae were still eaten at lower frequencies during other seasons, but least frequently in autumn (Figure 4).

On the Summerland Peninsula, scats were collected during autumn, spring, and summer, with no sampling in winter months (total $n = 65$). Invertebrates in the diet included 13 groups, comprising Insecta (Coleoptera, Lepidoptera, Formicidae, Blattodea, Hemiptera, Orthoptera, Hymenoptera, Dermoptera), Annelida, Arachnida (Araneae, Acarina), Crustacea (Isopoda), and Diplopoda. Fungal spores were detected in fewer samples on Summerland Peninsula than Churchill Island (13% vs. 48%), while plant material was found in higher frequencies. Skink scales were also detected in a small number (3%) of samples from Summerland Peninsula, while crabs, harvestmen (Opiliones), and snails (Gastropoda) were absent from the diet of this population. Of the 12 invertebrate groups at Summerland Peninsula, spiders were most frequently eaten (64%), followed by beetles (56%),

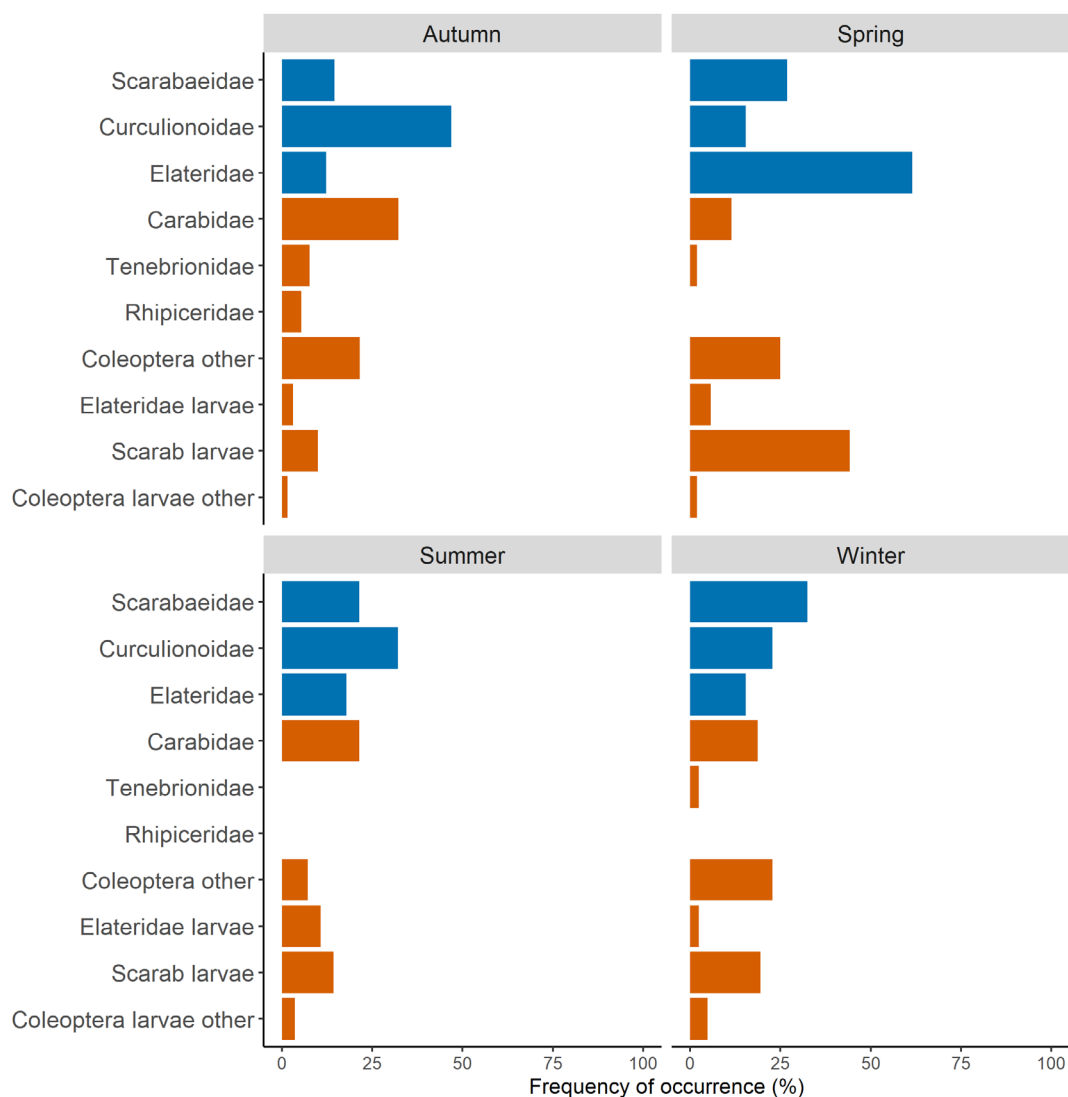


FIGURE 4 | Frequency of occurrence of adult (red) and larval (blue) coleopteran food items in eastern barred bandicoot (*Perameles gunnii*) scat samples, at Churchill Island, southeastern Australia, broken down by family. Autumn (a), Winter (b), Spring (c), Summer (d).

earthworms (56%), cockroaches (55%), and beetle larvae (49%). Millipedes were present in bandicoot diet at a high frequency on the Summerland Peninsula (58%), much greater than on Churchill Island (2%); a majority of these were Portuguese Millipedes (*Ommatoiulus moreletii*), an invasive pest species.

3.2 | Influences on the Dietary Assemblages of Bandicoots

The invertebrate diet of bandicoots on Churchill Island showed significant seasonal variation (pseudo- $F=22.098$, $df=3$, $p<0.001$) and an effect of population density (pseudo- $F=6.450$, $df=2$, $p<0.001$), but no statistical differences between sexes (pseudo- $F=1.739$, $df=1$, $p=0.135$). Dispersion was equal between seasons ($F=2.237$, $df=3$, 328 , $p=0.123$) and density ($F=2.300$, $df=2$, 329 , $p=0.164$). Pairwise comparisons showed differences in invertebrate composition between all seasons ($p<0.001$) except summer and autumn ($p=0.095$). In Autumn, Hymenoptera and Hemiptera dominated bandicoot diet and were less prevalent in winter when

Lepidoptera larvae were most common (Figure 5). Araneae trended towards increasing frequency in both summer and spring (Figure 5). Spring and summer in general had the most similar invertebrate diet assemblages to each other. Spring and summer differed from winter and autumn, which also differed to each other in assemblage. Autumn had the least dietary overlap with all other seasons with respect to diet (Figure 5). When bandicoot density was low, diet was most associated with Coleoptera larvae (Figure 6) while high density populations consumed more Hymenoptera, and medium populations more Lepidoptera larvae (Figure 6).

4 | Discussion

Characterising a species' diet is a key lens through which to better understand possible impacts on ecosystems in the context of conservation translocations. We found that Eastern Barred Bandicoots, introduced to two islands outside of their known historical range, fed on a diverse array of invertebrate taxa, plants and fungi. This broad dietary assemblage is consistent

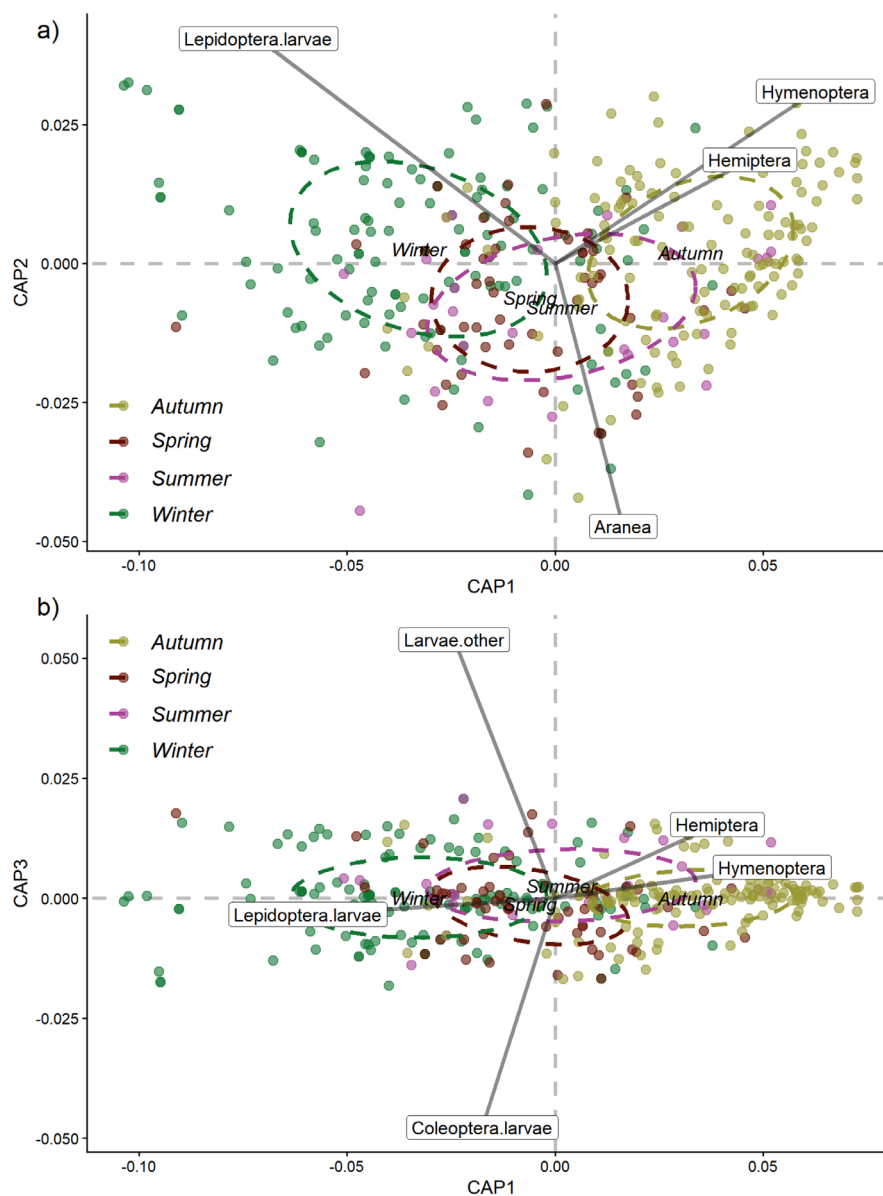


FIGURE 5 | Canonical Analysis of Principle Coordinates based on Bray–Curtis similarity of eastern barred bandicoot (*Perameles gunnii*) dietary composition from Churchill Island, southeastern Australia, showing scatter by season. Each point represents one scat, and the distance between any two points represents their relative dissimilarity (Glen et al. 2011). We represent the first three axes which were deemed important. Species vectors with correlations > 0.5 are displayed with 95% ellipses around grouping variables.

with previous studies, which describe the species as generalist foragers that opportunistically consume a wide range of available food items, including subterranean and surface invertebrates such as beetles, worms, crickets and spiders, as well as plant and fungal material (Quin 1985; Heinsohn 1966; Brown 1989; Dufty 1994; Mallick et al. 1997). Seasonality was the main factor associated with variation in the types of invertebrates eaten, suggesting that bandicoots are facultative, generalist predators. Bandicoots had similar invertebrate diets across islands, although Summerland Peninsula was a recently established population at low density without full seasonal replication making direct comparisons difficult. Our study suggests Eastern Barred Bandicoots are adaptable omnivores meaning that food resources should not be a limiting factor for establishing viable populations in broadly suitable habitat in the absence of red foxes (*sensu* Rendall et al. 2018; Rendall et al. 2021).

4.1 | Variation of Bandicoot Diets

While the general diet of the Eastern Barred Bandicoot (Tasmanian and mainland populations) is known (Heinsohn 1966; Brown 1989; Dufty 1994; Mallick et al. 1997), we are the first to examine the diet of the mainland eastern barred bandicoot translocated beyond its known historical distribution. Bandicoots introduced to Churchill and Phillip Island exhibited an omnivorous feeding pattern, feeding on plants, fungi and a wide range of invertebrates, including beetles, earthworms, caterpillars, spiders, cockroaches and ants. The diets of both populations in the study were similar to those previously reported for both the mainland (Brown 1989; Dufty 1994) and Tasmanian subspecies (Reimer and Hindell 1996), suggesting that this aspect of the bandicoot's ecological role is likely maintained when translocated

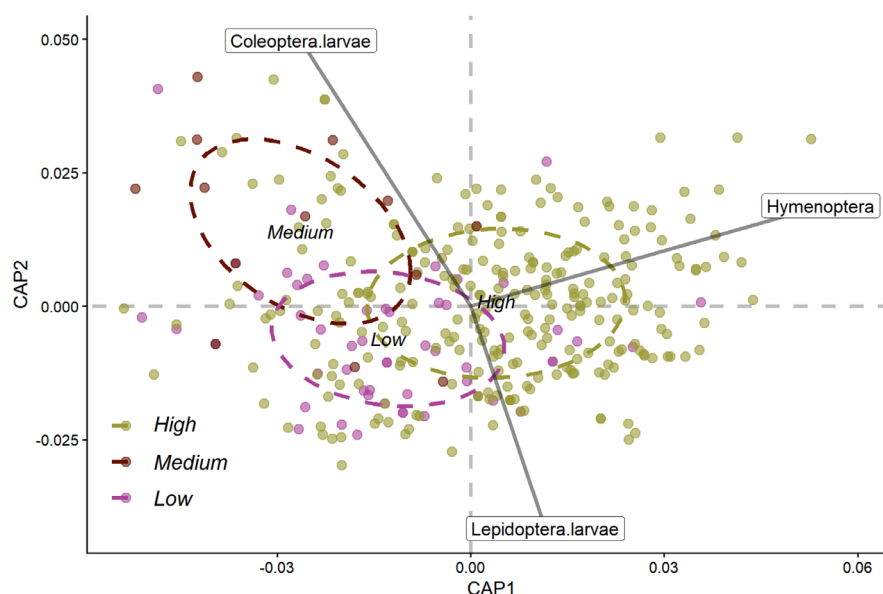


FIGURE 6 | Canonical Analysis of Principle Coordinates based on Bray-Curtis similarity of eastern barred bandicoot (*Perameles gunnii*) dietary composition in relation to bandicoot density. We represent the first two axes which were deemed important. Species vectors with correlations > 0.5 or < -0.5 are displayed with 95% ellipses around grouping variables.

into new areas with appropriate habitat, enabling the species to readily persist in translocation sites, where sufficiently abundant food resources are available.

Our study recorded bandicoots consuming several food types of ecological and management interest, including crabs (*Brachyura*, unknown sp.) and Portuguese Millipedes (*Ommatoiulus moreleti*). The detection of crabs in bandicoot diets suggests that the species has the potential to exploit novel foraging resources—including marine resources—when translocated to new coastal habitats. This may also have been influenced by the relatively small size of Churchill Island, meaning individuals may have searched for novel food sources due to a lack of other resources.

Portuguese Millipedes are a pest species, and despite limited records of other mammals successfully consuming this species due to its toxicity (Baker 1985), were recorded in Eastern Barred Bandicoot scats at high frequency. It is possible that Eastern Barred Bandicoots could serve as an effective management tool to help control populations of pest invertebrate species such as the Portuguese Millipede. However, further research is needed to determine whether their impact is sufficient to contribute meaningfully to pest control efforts.

Some frequently recorded small invertebrate items, such as ants, were likely ingested together with soil while foraging for other food sources, while mites and ticks were likely consumed incidentally during grooming (Gibson 2001). A small number of bandicoot scats contained lizard scales or digits, but it is unknown whether these were actively preyed upon or scavenged, although observations have been made of Long-nosed Bandicoots *Perameles nasuta* consuming Spotted Pardalote *Pardalotus punctatus* (Guppy and Guppy 2017), suggesting vertebrate predation is possible. Plant material previously recorded in Eastern Barred Bandicoot diet includes grasses, dicot, seeds, bulbs of onion weed, fallen orchard fruit

and blackberries (Brown 1989; Dufty 1991). The frequency and abundance of vegetative material found in bandicoot diet in our study suggest that they actively consume some plants as a source of nutrition, as well as incidentally while digging for invertebrates (Mallick et al. 1997). Grass represented the most frequent plant food group in the diet at Churchill Island; as an abundant plant type on the island, the relatively high prevalence in their scats is unsurprising. As Eastern Barred Bandicoots line their daytime nests with grass (Dufty 1991), it is possible that some of the grass was consumed while collecting nesting material. It remains unknown whether bandicoots are seed predators, dispersers or both. Mycophagy was also recorded in our study and is potentially important for the maintenance of ecosystem health through spore dispersal in faeces (Tay et al. 2018).

We observed a trend towards bandicoot diet shifting in response to bandicoot density on Churchill Island. There are a few possible explanations for this: (1) competition for food resources increases with density resulting in increased foraging on sub-optimal food resources; (2) this shift in density coincides with population establishment (Rendall et al. 2018) meaning bandicoot foraging may shift due to discovery of more optimal resources; or (3) bandicoot habitat use and activity (*sensu* Rendall et al. 2018) shift as population density increases resulting in more diverse habitats being occupied and therefore more food resources available. Given the strong signal of seasonal variation in bandicoot diet, we suspect that this trend is more related to the expansion of the bandicoot population into more diverse habitats. These trends are supported for other species where broadscale spatial analyses have been conducted (Doherty et al. 2015; Dell'Arte et al. 2007). However, in the absence of invertebrate availability data it is not possible to tease apart whether increases in density and subsequent shift in bandicoot diet are attributable to declines in invertebrates, a result of exploitative competition, or natural seasonal fluctuations.

4.2 | Seasonal Dietary Variation

To separate seasonal patterns from stochastic variation, dietary data should span many years (Glen and Dickman 2006). Our study had a large sample size, and while long-term ecological studies typically require five or more years, in the context of a short-lived species such as this (2–3 years; Backhouse et al. 1994), 3 years is likely to be sufficient to detect seasonal patterns in population diet. Invertebrate consumption at Churchill Island differed among seasons, driven by differences in both dietary assemblages and their breadth. Eastern Barred Bandicoots appeared to feed on similar invertebrates during spring and summer. However, spring had the lowest dietary breadth of the four seasons; this could either indicate a sampling bias between seasons, that bandicoots are least selective in this season, resulting in greater dietary overlap between individuals, or may simply reflect the availability of a narrower range of invertebrates during this period. Of course, invertebrate abundance, diversity, and availability show strong seasonal trends across ecosystems (Tauber et al. 1986; Gibson 2001). It is likely that such temporal trends in invertebrate assemblage exist at our study sites and may drive patterns in bandicoot diet. For example, moths were frequently found in bandicoot scats in summer, when they are presumably most active, but less so in winter samples. Eastern Barred Bandicoots have also been found to eat some prey items in proportion to their abundance in the environment (Mallick et al. 1997; Thums et al. 2005). Determining if seasonal variation in bandicoot diet at Churchill Island is correlated with patterns of invertebrate availability would require surveys to quantify invertebrate abundance (Glen and Dickman 2006).

Higher availability of above-ground invertebrates in the summer months (Gibson 2001) may also reduce the need to dig for food. Eastern Barred Bandicoot digging rates are lowest in summer when soils are most compact but increase as soil softens in winter, when it is easier to dig (Winnard 2010; Halstead et al. 2019). Subterranean invertebrates move further down the soil profile in warmer, drier conditions (Staley et al. 2007; Reimer and Hindell 1996) but will rise closer to the soil surface again with decreasing soil temperature and increasing soil moisture, becoming more accessible to bandicoots (Anderson and Smith 2000; Staley et al. 2007). High frequencies of worms, fungi, and roots found in winter and spring scats, as well as the small but significant contribution of beetle larvae to diet during these seasons, suggest that subterranean foods may become more important over these cooler months. Heinsohn's (1966) findings support this, noting that insects are common in bandicoot diets during the dry summer months, while earthworms are the most important food item in periods of high rainfall.

Seasonal availability of invertebrates may not be the only factor influencing bandicoot diet. An alternative explanation is that bandicoots actively seek out certain invertebrates. While some food items appeared to be seasonally important, several surface invertebrates substantially contributed to bandicoot diet across all seasons, such as beetles, ants, and spiders. Cook (2001) found that bandicoots ate beetles and millipedes at higher rates than would be expected based on availability and avoided ants, spiders, collembola, and fly larvae. Given that beetles remained a dominant food group throughout the year in the current study, it is possible that bandicoots preferentially selected this food

source. However, there was high dietary diversity in beetle taxa throughout the year and changing seasonal frequencies of different beetle families found in scats. For example, Rhipiceridae was found only in spring when it is likely to be active in this region. Similar patterns in other beetle families and invertebrate taxa in the diet may represent a seasonal pattern in their availability. Importantly, hard-bodied invertebrates such as beetles are more readily found in faeces, and this may overestimate their dominance in the diet (Dickman and Huang 1988).

4.3 | Foraging Beyond Historical Distributions and Restoring Ecological Functions

The relatively small number of sites where native species have been deliberately introduced beyond their known historical distributions (rather than being reintroduced to their former distributions) for conservation purposes means our knowledge of their ecology in such situations is limited (James and Eldridge 2007). Our study offers a unique opportunity to examine two such translocation sites. Our results suggest that bandicoot diet at one site may provide a reasonable indication of their likely foraging ecology elsewhere. By describing the bandicoot's ecological role at Summerland Peninsula, our study also helps inform community members of the potential influence of bandicoots for gardens, farms and agricultural pastures. Such information is vital for appropriate community support and social licence, which are vital for ensuring the long-term success of conservation actions.

Mammal translocations offer the opportunity to restore degraded habitats (Kollmann et al. 2016). Trophic interactions such as top-down predation on invertebrates may have a more direct impact on invertebrate assemblages, and in turn the functions of these species (e.g., pollination, nutrient cycling) at introduction sites (Silvey et al. 2015; Coggan et al. 2016, 2018). Other species of bandicoot historically inhabited both Churchill and Phillip Islands (Grant 1803; Kirkwood and Johnston 2006) but have been lost from these ecosystems since European colonisation. Introducing an analogous species of bandicoot as an ecological replacement has not only helped boost population numbers of an endangered species but has potentially reinstated important ecological processes at the introduction sites through both trophic and engineering pathways (Halstead et al. 2019).

4.4 | Caveats and Study Limitations

Faecal analysis is a reliable, non-invasive method of detecting hard-bodied invertebrate items in animal diet (Dickman and Huang 1988). In contrast, stomach content analysis requires animals to have their stomachs flushed or to be sacrificed (Kronfeld and Dayan 1998). Faecal analysis does present limitations that need consideration in the context of our results. Soft-bodied invertebrates such as larvae and earthworms are often overlooked or underestimated, as they are more easily digestible than adult arthropods (Wroot 1985). The presence of items in faeces reflects their lack of digestibility rather than a true indication of their relative abundance in the diet. Estimation of diet through visual analysis of scats may therefore be biased towards indigestible resources e.g., hard-bodied invertebrates (Kunz and Whitaker

Jr 1983; Dickman and Huang 1988). Using eDNA and genomic approaches to identify the diets of wildlife offers an additional approach to more traditional microscopic faecal analysis, but in turn has limitations (Pompanon et al. 2012).

During our study, most food items could not be identified to species level, primarily due to their high fragmentation following digestion. Taxonomic resolution is likely to affect detection of variability in food webs and communities (Berg and Bengtsson 2007). It is also important to note that neither frequency of occurrence nor minimum number of invertebrates is likely to be exact measures of diet (Dickman and Huang 1988), but are nonetheless useful for providing quantitative estimates of diet when used conservatively.

4.5 | Management Recommendations and Future Research Directions

Our study suggests the generalist and varied nature of Eastern Barred Bandicoot diet makes it well-suited for conservation translocations. Importantly, trophic interactions are complex, and additional research is needed to better understand the possible impacts of bandicoots on local faunal, fungal, and plant communities. Invertebrate surveys are needed at current introduction sites to quantify whether bandicoot diet is correlated with seasonal invertebrate abundance and if they are actively selecting certain invertebrate species. Exclusion plots and pre- and post-monitoring of plant, fungi, and invertebrate assemblages as part of bandicoot translocations are recommended to assess any impacts bandicoots have on invertebrates at a population level. Further, there is little mechanistic understanding of the importance and consequences of fungal and plant material in bandicoot diet, and how this might affect the health and maintenance of vegetation communities and ecosystems.

Amidst rapid global environmental change, many threatened species will likely require conservation translocations to persist (Lunt et al. 2013). While such management interventions can have a range of ecological benefits at relocation sites, they also come with risks of unpredicted consequences. Geographic variation in resources and community composition may impact the roles of ecosystem engineers and other key species (Coggan et al. 2018). Further evaluation of the potential range of impacts of species translocations is therefore urgently required. Our findings highlight the potential of dietary analysis to inform adaptive management when used alongside other ecological indicators.

Author Contributions

Ella Loeffler: conceptualization, data curation, formal analysis, investigation, visualization, writing – original draft, writing – review and editing. **Anthony R. Rendall:** data curation, formal analysis, investigation, supervision, writing – original draft, writing – review and editing. **Nick Porch:** methodology, resources, writing – review and editing. **Duncan R. Sutherland:** conceptualization, investigation, supervision, writing – review and editing. **Amy L. Coetsee:** conceptualization, supervision, writing – review and editing. **Euan G. Ritchie:** conceptualization, resources, supervision, writing – original draft, writing – review and editing.

Acknowledgements

This project was undertaken in accordance with the regulations of Phillip Island Nature Parks Animal Ethics committee under Projects No. 3.2015 and 2.2017 and in accordance with the Department of Environment, Land, Water and Planning (DELWP) Research Permit No. 10007613 and 10008845. The Deakin University Animal Ethics Committee was notified (AEX06-2018) that this study would involve the use of animal ethics on an external project. We thank Deakin University, Phillip Island Nature Parks and Zoos Victoria for providing financial and logistical support for the project.

Ethics Statement

All trapping was performed through approvals from Phillip Island Nature Parks Animal Ethics Committee (3.2015; 2.2017), Deakin University Animal Ethics Committee (AEX06-2018) and Department of Environment Land, Water and Planning Permits (10007613 and 10008845).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made available on reasonable request.

References

- Adriaanse, K., S. M. Firestone, M. Lynch, et al. 2020. "Comparison of the Modified Agglutination Test and Real-Time PCR for Detection of *Toxoplasma gondii* Exposure in Feral Cats From Phillip Island, Australia, and Risk Factors Associated With Infection." *International Journal of Parasitology: Parasites and Wildlife* 12, no. 20: 126–133.
- Adriaanse, K., M. Lynch, D. Sutherland, R. Traub, J. Lowe, and J. Hufschmid. 2024. "*Toxoplasma gondii* Does Not Inhibit the Assisted Colonization of Eastern Barred Bandicoots (*Perameles gunnii*) to Phillip Island, Victoria, Australia." *Journal of Wildlife Diseases* 60, no. 1: 116–125.
- Anderson, J. T., and L. M. Smith. 2000. "Invertebrate Response to Moist-Soil Management of Playa Wetlands." *Ecological Applications* 10: 550–558.
- Anderson, M., R. N. Gorley, and R. K. Clarke. 2008. *Permanova+ for Primer: Guide to Software and Statistical Methods*. PRIMER-E.
- Backhouse, G. N., T. W. Clark, and R. P. Reading. 1994. "Reintroductions for Recovery of the Eastern Barred Bandicoot *Perameles gunnii* in Victoria, Australia." In *Reintroduction Biology of Australian and New Zealand Fauna*, edited by M. Serena, 209–218. Surrey Beatty & Sons.
- Baker, G. H. 1985. "Predators of *Ommatoilus moreletti* (LUCAS) (Diplopoda: Iulidae) in Portugal and Australia." *Journal of the Australian Entomological Society* 24: 247–252.
- Berg, M. P., and J. Bengtsson. 2007. "Temporal and Spatial Variability in Soil Food Web Structure." *Oikos* 116, no. 11: 1789–1804.
- Bonnaud, E., F. M. Medina, E. Vidal, et al. 2011. "The Diet of Feral Cats on Islands: A Review and a Call for More Studies." *Biological Invasions* 13: 561–603.
- Brown, P. R. 1989. *Management Plan for the Conservation of the Eastern Barred Bandicoot, Perameles gunnii, in Victoria*. Arthur Rylah Institute for Environmental Science Technical Report Series No. 63.
- Bryant, S. L., H. Bower, S. Bower, et al. 2022. "Island Partnerships Building Collective Impact." *Pacific Conservation Biology* 28: 303–314. <https://doi.org/10.1071/PC21021>.
- Bytheway, J. P., and C. R. Dickman. 2014. *Identifying the Diets of Insectivorous Vertebrates: A Photographic Reference Guide of Invertebrate*

- Parts. Desert Ecology Research Group, School of Biological Sciences, University of Sydney.
- Chen, X., C. R. Dickman, and M. B. Thompson. 1998. "Diet of the Mulgara, *Dasyurus cristicauda* (Marsupialia: Dasyuridae), in the Simpson Desert, Central Australia." *Wildlife Research* 25, no. 3: 233–242.
- Clarke, K. R., and R. N. Gorley. 2006. *PRIMER v6: User manual/Tutorial*. PRIMER-E Ltd.
- Clarke, K. R., and R. M. Warwick. 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory.
- Coggan, N. V., and H. Gibb. 2019. "Digging Mammal Reintroductions Reduce Termite Biomass and Alter Assemblage Composition Along an Aridity Gradient." *Oecologia* 191: 645–656.
- Coggan, N. V., M. W. Hayward, and H. Gibb. 2016. "Termite Activity and Decomposition Are Influenced by Digging Mammal Reintroductions Along an Aridity Gradient." *Journal of Arid Environments* 133: 85–93.
- Coggan, N. V., M. W. Hayward, and H. Gibb. 2018. "A Global Database and 'State of the Field' Review of Research Into Ecosystem Engineering by Land Animals." *Journal of Animal Ecology* 87: 1096.
- Cook, C. 2001. *Habitat Assessment of the Eastern Barred Bandicoot, *Perameles gunnii*, at Its Reintroduction sites in Victoria*. B.Sc. (Hons) Thesis. University of Melbourne.
- Davis, N. E., D. M. Forsyth, B. Triggs, et al. 2015. "Interspecific and Geographic Variation in the Diets of Sympatric Carnivores: Dingoes/Wild Dogs and Red Foxes in South-Eastern Australia." *PLoS One* 10, no. 3: e0120975.
- Dell'Arte, G. L., T. Laaksonen, K. Norrdahl, and E. Korpimäki. 2007. "Variation in the Diet Composition of a Generalist Predator, the Red Fox, in Relation to Season and Density of Main Prey." *Acta Oecologica* 31, no. 3: 276–281.
- Department of Environment, Land, Water and Planning. 2021. *National Recovery Plan for the Mainland Eastern Barred Bandicoot *Perameles gunnii* (Victorian Subspecies)*. Australian Government.
- Department of Sustainability and Environment [DSE]. 2013. *Advisory List of Threatened Vertebrate Fauna in Victoria*. Victorian State Government.
- Dicken, M. L., N. E. Hussey, H. M. Christiansen, et al. 2017. "Diet and Trophic Ecology of the Tiger Shark (*Galeocerdo cuvier*) From South African Waters." *PLoS One* 12, no. 6: e0177897. <https://doi.org/10.1371/journal.pone.0177897>.
- Dickman, C. R., and C. Huang. 1988. "The Reliability of Fecal Analysis as a Method for Determining the Diet of Insectivorous Mammals." *Journal of Mammalogy* 69, no. 1: 108–113.
- Doherty, T. S., R. A. Davis, E. J. B. van Etten, et al. 2015. "A Continental-Scale Analysis of Feral Cat Diet in Australia." *Journal of Biogeography* 42, no. 5: 964–975.
- Dufty, A. C. 1991. "Some Population Characteristics of *Perameles gunnii* in Victoria." *Wildlife Research* 18, no. 3: 355–365.
- Dufty, A. C. 1994. "Habitat and Spatial Requirements of the Eastern Barred Bandicoot (*Perameles gunnii*) at Hamilton, Victoria." *Wildlife Research* 21, no. 4: 459–471.
- Dunn, M. R. 2009. "Feeding Habits of the Ommastrephid Squid *Nototodarus sloanii* on the Chatham Rise, New Zealand." *New Zealand Journal of Marine and Freshwater Research* 43, no. 5: 1103–1113.
- Efford, M. G., and R. M. Fewster. 2012. "Estimating Population Size by Spatially Explicit Capture-Recapture." *Oikos* 122, no. 6: 918–928.
- Fleming, P. A., H. Anderson, A. S. Prendergast, M. R. Bretz, L. E. Valentine, and G. E. S. Hardy. 2013. "Is the Loss of Australian Digging Mammals Contributing to a Deterioration in Ecosystem Function?" *Mammal Review* 44: 94–108.
- Frith, D., and C. Frith. 1990. "Seasonality of Litter Invertebrate Populations in an Australian Upland Tropical Rain Forest." *Biotropica* 22, no. 2: 181–190.
- Galindo-Leal, C., and C. J. Krebs. 1998. "Effects of Food Abundance on Individuals and Populations of the Rock Mouse (*Peromyscus difficilis*)." *Journal of Mammalogy* 79: 1131–1142.
- Gibson, L. A. 2001. "Seasonal Changes in the Diet, Food Availability and Food Preference of the Greater Bilby (*Macrotis lagotis*) in South-Western Queensland." *Wildlife Research* 28: 121–134.
- Glen, A. S., and C. R. Dickman. 2006. "Diet of the Spotted-Tailed Quoll (*Dasyurus maculatus*) in Eastern Australia: Effects of Season, Sex and Size." *Journal of Zoology* 269, no. 2: 241–248.
- Glen, A. S., M. Pennay, C. R. Dickman, B. A. Wintle, and K. B. Firestone. 2011. "Diets of Sympatric Native and Introduced Carnivores in the Barrington Tops, Eastern Australia." *Austral Ecology* 36, no. 3: 290–296. <https://doi.org/10.1111/j.1442-9993.2010.02149.x>.
- Grant, J. 1803. *Narrative of a Voyage of Discovery, Performed in His Majesty's Vessel the Lady Nelson, of Sixty Tons Burthen With Sliding Keels, in the Years 1800, 1801, and 1802, to New South Wales*. C. Roworth for T. Egerton.
- Groenewegen, R., D. Harley, R. Hill, and G. Coulson. 2017. "Assisted Colonisation Trial of the Eastern Barred Bandicoot (*Perameles gunnii*) to a Fox-Free Island." *Wildlife Research* 44: 484–496.
- Guppy, M., and S. Guppy. 2017. "The Long-Nosed Bandicoot (*Perameles nasuta*) as a Nest Predator." *Australian Mammalogy* 40, no. 1: 106–108.
- Halstead, L. M., R. Sutherland, L. E. Valentine, A. R. Rendall, A. L. Coetsee, and E. G. R. Ritchie. 2019. "Digging Up the Dirt: Quantifying the Effects on Soil of a Translocated Ecosystem Engineer." *Austral Ecology* 45, no. 1: 97–108.
- Heinsohn, G. E. 1966. "Ecology and Reproduction of the Tasmanian Bandicoots (*Perameles gunnii* and *Isodon obesulus*)." *University of California Publications in Zoology* 80: 1–96.
- Hewitt, N., N. Klenk, A. L. Smith, et al. 2011. "Taking Stock of the Assisted Migration Debate." *Biological Conservation* 144: 2560–2572.
- Hill, R., A. Coetsee, and D. Sutherland. 2018. "Recovery of the Mainland Subspecies of Eastern Barred Bandicoot." In *Recovering Australian Threatened Species: A Book of Hope*, 249. CSIRO Publishing.
- Hume, I. D. 1999. *Marsupial Nutrition*. Cambridge University Press.
- James, A. I., and D. J. Eldridge. 2007. "Reintroduction of Fossorial Native Mammals and Potential Impacts on Ecosystem Processes in an Australian Desert Landscape." *Biological Conservation* 138, no. 3–4: 351–359.
- Johnson, C. N., and J. L. Isaac. 2009. "Body Mass and Extinction Risk in Australian Marsupials: The 'Critical Weight Range' Revisited." *Austral Ecology* 34: 35–40.
- Kemper, C. 1991. "The Status of Peramelidae and Thylacomyidae in South Australia." In *Bandicoots and Bilbies*, edited by J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper. Surry Beatty and Sons.
- Kirkwood, R., and M. Johnston. 2006. "Terrestrial Mammals of Phillip and French Islands, Western Port, Victoria." *Victorian Naturalist* 123: 146–156.
- Kollmann, J., S. T. Meyer, R. Bateman, et al. 2016. "Integrating Ecosystem Functions Into Restoration Ecology—Recent Advances and Future Directions." *Restoration Ecology* 24, no. 6: 722–730.
- Kortner, G., and F. Geiser. 1998. "Ecology of Natural Hibernation in the Marsupial Mountain Pygmy-Possum (*Burramys parvus*)." *Oecologia* 113: 170–178.
- Kronfeld, N., and T. Dayan. 1998. "A New Method of Determining Diets of Rodents." *Journal of Mammalogy* 79, no. 4: 1198–1202.

- Kunz, T. H., and J. O. Whitaker Jr. 1983. "An Evaluation of Fecal Analysis for Determining Food Habits of Insectivorous Bats." *Canadian Journal of Zoology* 61, no. 6: 1317–1321.
- Lo Surdo, D., M. A. Weston, A. R. Rendall, and N. Porch. 2024. "Seasonal Changes of Surface-Active Beach Invertebrate Assemblages in Southern Central Victoria, Australia." *Estuaries and Coasts* 47: 1052–1063.
- Lunt, I. D., M. Byrne, J. J. Hellmann, et al. 2013. "Using Assisted Colonisation to Conserve Biodiversity and Restore Ecosystem Function Under Climate Change." *Biological Conservation* 157: 172–177.
- Lynch, M., D. Liyanage, A. Stent, et al. 2025. "Assessing the Impact of *Toxoplasma Gondii* in Endangered Eastern Barred Bandicoots (*Perameles gunnii*) on Phillip and French Islands, Australia." *Journal of Wildlife Diseases* 61: 654–662.
- Mallick, S. A., M. M. Driessen, and G. J. Hocking. 1997. *Biology and Conservation of the Eastern Barred Bandicoot (Perameles gunnii) in Tasmania*. Wildlife Report No. 97/1. Parks and Wildlife Service.
- Manning, A. D., D. J. Eldridge, and C. G. Jones. 2015. "Policy Implications of Ecosystem Engineering for Multiple Ecosystem Benefits." In *Advances in Reintroduction Biology of Australian and New Zealand Fauna*, edited by D. Armstrong, M. Hayward, D. Moro, and P. Seddon. CSIRO Publishing.
- Moeed, A., and M. J. Meads. 1984. "Seasonality of Pitfall Trapped Invertebrates in Three Types of Native Forest, Orongorongo Valley, New Zealand." *New Zealand Journal of Zoology* 12, no. 1: 17–53.
- Palmer, B. J., L. E. Valentine, M. Page, and R. J. Hobbs. 2020. "Translocations of Digging Mammals and Their Potential for Ecosystem Restoration: A Review of Goals and Monitoring Programmes." *Mammal Review* 50, no. 4: 382–398.
- Phillip Island Nature Parks. 2012. *Integrated Pest Mammal Strategy 2013–2018*. Phillip Island Nature Parks.
- Pompanon, F., B. E. Deagle, W. O. C. Symondson, D. S. Brown, S. N. Jarman, and P. Taberlet. 2012. "Who Is Eating What: Diet Assessment Using Next Generation Sequencing." *Molecular Ecology* 21: 1931–1950.
- Quin, D. G. 1985. *Aspects of the Feeding Ecology of the Bandicoots, Perameles gunnii (Gray 1838) and Isoodon obesulus (Shaw and Nodder 1797) (Marsupialia: Peramelidae) in Southern Tasmania*. B.Sc. (Hons) Thesis. University of Tasmania.
- R Core Team. 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Recher, H. F., J. D. Majer, and S. Ganesh. 1996. "Seasonality of Canopy Invertebrate Communities in Eucalypt Forests of Eastern and Western Australia." *Australian Journal of Ecology* 21, no. 1: 64–80.
- Reimer, A. B., and M. A. Hindell. 1996. "Variation in Body Condition and Diet of the Eastern Barred Bandicoot (*Perameles gunnii*) During the Breeding Season." *Australian Mammalogy* 19: 47–52.
- Rendall, A., A. Coetsee, and D. Sutherland. 2018. "Predicting Suitable Release Sites for Assisted Colonisations: A Case Study of Eastern Barred Bandicoots." *Endangered Species Research* 36: 137–148.
- Rendall, A. R., D. R. Sutherland, C. M. Baker, B. Raymond, R. Cooke, and J. G. White. 2021. "Managing Ecosystems in a Sea of Uncertainty: Invasive Species Management and Assisted Colonizations." *Ecological Applications* 31, no. 4: e02306.
- Rendall, A. R., D. R. Sutherland, R. Cooke, and J. G. White. 2022. "Does the Foraging Ecology of Feral Cats Change After the Eradication of Foxes?" *Biological Invasions* 24: 1413–1426.
- Sale, M. G., B. A. Wilson, and J. P. Y. Arnould. 2009. "Comparison of Life-History Characteristics of Island and Mainland Populations of the Swamp Antechinus." *Journal of Zoology* 277, no. 2: 119–125.
- Seddon, P. J., C. J. Griffiths, P. S. Soorae, and D. P. Armstrong. 2014. "Reversing Defaunation: Restoring Species in a Changing World." *Science* 345, no. 6195: 406–412. <https://doi.org/10.1126/science.1251818>.
- Seebeck, J. H. 2001. "*Perameles gunnii*." *American Society of Mammalogists* 654: 1–8.
- Silvey, C. J., M. W. Hayward, and H. Gibb. 2015. "Effects of Reconstruction of a Pre-European Vertebrate Assemblage on Ground-Dwelling Arachnids in Arid Australia." *Oecologia* 178, no. 2: 497–509.
- Sinclair, B. J., J. M. Lord, and C. M. Thompson. 2001. "Microhabitat Selection and Seasonality of Alpine Invertebrates." *Pedobiologia* 45, no. 2: 107–120.
- Staley, J. T., C. J. Hodgson, S. R. Mortimer, et al. 2007. "Effects of Summer Rainfall Manipulations on the Abundance and Vertical Distribution of Herbivorous Soil Macro-Invertebrates." *European Journal of Soil Biology* 43: 189–198.
- Sutherland, D. R. 2011. "Dietary Niche Overlap and Size Partitioning in Sympatric Varanid Lizards." *Herpetologica* 67, no. 2: 146–153.
- Sutherland, D. R., P. Dann, and R. E. Jessop. 2014. "Evaluation of Artificial Nest Sites for Long-Term Conservation of a Burrow-Nesting Seabird." *Journal of Wildlife Management* 78: 1415–1424.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. *Seasonal Adaptations of Insects*. Oxford University Press on Demand.
- Tay, N. E., A. J. Hopkins, K. X. Ruthrof, T. Burgess, G. E. S. Hardy, and P. A. Fleming. 2018. "The Tripartite Relationship Between a Bioturbator, Mycorrhizal Fungi, and a Key Mediterranean Forest Tree." *Austral Ecology* 43, no. 7: 742–751.
- Thums, M., M. Klaassen, and I. D. Hume. 2005. "Seasonal Changes in the Diet of the Long-Nosed Bandicoot (*Perameles nasuta*) Assessed by Analysis of Faecal Scats and of Stable Isotopes in Blood." *Australian Journal of Zoology* 53, no. 2: 87–93.
- Townsend, T. 2020. *Comparing the Population Ecology of Eastern Barred Bandicoot Island Introductions*. Doctoral Dissertation. Deakin University.
- Vogel, J. T., M. J. Somers, and J. A. Venter. 2018. "The Foraging Ecology of Reintroduced African Wild Dog in Small Protected Areas." *Wildlife Biology* 2018: 424.
- Winnard, A. L. 2010. *Reintroduction Biology of the Eastern Barred Bandicoot*. Doctoral Dissertation. University of Melbourne.
- Woinarski, J. C., A. A. Burbidge, and P. L. Harrison. 2015. "Ongoing Unraveling of a Continental Fauna: Decline and Extinction of Australian Mammals Since European Settlement." *Proceedings of the National Academy of Sciences* 20: 201417301.
- Wroot, A. J. 1985. "A Quantitative Method for Estimating the Amount of Earthworm (*Lumbricus terrestris*) in Animal Diets." *Oikos* 44, no. 2: 239. <https://doi.org/10.2307/3544695>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** aec70168-sup-0001-FigureS1-S3.docx.