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RESEARCH

Snacks in the city: the diet of hedgehogs in Auckland urban forest fragments

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Abstract: Urbanisation causes fragmentation of natural habitats, which results in loss of biodiversity, while promoting an environment that can facilitate invasive species. However, forest fragments are an important refuge for native species and therefore understanding and mitigating threats in fragments is critical. While the impacts of some mammalian pest species, such as rats (*Rattus* spp.), are relatively well-known in New Zealand, hedgehogs (*Erinaceus europaeus*) are relatively understudied invasive mammals, and their impacts in urban fragments are unknown. Hedgehogs are abundant and widespread in New Zealand, with a relatively broad diet that can include invertebrates, lizards and bird eggs. We examined the stomach contents of 44 hedgehogs collected from 10 forest fragments in urban Auckland, New Zealand. Hedgehogs were feeding predominantly on invertebrates (Coleoptera, found in 53% of stomachs; earthworms, 43%; slugs, 23%), but also weta (13%), giant centipedes (5%), birds (7%) and lizards (2%) at lower frequencies. Hedgehogs are likely to be affecting community composition primarily through predation of invertebrates, with unknown effects on their populations.

Keywords: *Erinaceus europaeus*, invasive, invertebrates, predation, stomach content analyses, urban fragments

Introduction

Invasive species impact ecosystems in a number of negative ways. These impacts can often be difficult to define (Jeschke et al. 2014) and measure (Blackburn et al. 2014), especially when there is a lack of baseline data prior to the arrival of the invasive species (Parker et al. 1999). However, it is important to understand the nature and severity of impacts caused by an invasive species before deciding on appropriate management actions. The diet of a species can provide information on its role or impact in an ecosystem. These impacts can be direct, such as through predation, or indirect, such as through competition (Blackburn et al. 2014). Competitive impacts occur when species compete for the same resources (e.g. food or nesting spaces), which can result in a loss of fitness to the native species, whereas predation results in direct mortality. These can both influence population dynamics (Parker et al. 1999; Courchamp et al. 2003).

Predation on native species is a common form of pest impact that can result in severe consequences, including extinction (Doherty et al. 2016). The severe impacts of invasive predators can be attributed to the naïvety of native prey species, having evolved in an environment without these predators (Banks & Dickman 2007). Predation can reduce the abundance and/or distribution of prey (Parker et al. 1999). Predation is often difficult to observe directly, but it can be evaluated indirectly using dietary analysis, which often involves examining the contents of the stomach, other parts of the gastrointestinal tract or faeces (e.g. Klare et al. 2011; Sweetapple et al. 2013). Dietary analysis can provide important information on the ecological niche of a predator, the level of invasiveness of a species and its potential severity of impact. Stomach content analysis has been used to describe the diets of a number of vertebrate species, such as rodents, frogs and possums (*Trichosurus vulpecula*) (Sweetapple et al. 2013; Hervías et al. 2014; Courant et al. 2017). In hedgehogs (*Erinaceus europaeus*), stomach content analysis has been used to determine: the composition of the diet in different habitats; the presence of endangered species in the diet; and dietary overlap with native species (Hendra 1999; Jones et al. 2005; Jeffries 2011).

Hedgehogs were introduced to New Zealand in 1870 and are found throughout the country (Thomson 1922; Brockie 1975). Studies of hedgehog diet in New Zealand have shown that they predominantly feed on invertebrates (Berry 1999; Jones et al. 2005; Jeffries 2011). However, in some environments, birds, lizards and eggs are also eaten (Jones et al. 2005; Jones & Norbury 2011). New Zealand invertebrates are particularly susceptible to mammalian predation, as they often have inappropriate or ineffective predator avoidance behaviours (e.g. staying still) (McGuinness 2001, 2007). Predation by rats (*Rattus* spp.) has been shown to adversely affect population sizes of a range of invertebrate species in a number of habitats, with large-bodied invertebrates being at greater risk (St Clair 2011; Ruscoe et al. 2013). As invertebrates are a dominant feature of hedgehog diets, hedgehogs are also

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likely to be having adverse effects on invertebrate populations (e.g. Jones et al. 2005, 2013).

The aim of this study is to understand the potential predatory impact of hedgehogs in urban forest fragments by carrying out stomach content analysis. Hedgehog diet has been studied in a number of habitats in New Zealand including a golf course, pasture, braided riverbed, and forest (Brockie 1959; Campbell 1973; Berry 1999), but not in urban forest fragments. Diet is expected to be different in this setting because of differing availabilities of prey and the potential for urban hedgehogs to exploit human food sources. A Finnish study in urban areas found evidence of human food in 92% of individual guts (Rautio et al. 2016) and supplementary feeding by people has been noted in New Zealand (Thomsen et al. 2000; Owen 2017). We predicted that hedgehogs would be predominately feeding on invertebrates in the urban forest fragments. This diet would be consistent with the findings of the other two dietary analyses of hedgehogs in intact New Zealand forest ecosystems (Berry 1999; Hendra 1999). However, given the forest fragments we investigated are in an urban matrix, and hedgehogs are opportunistic feeders likely to exploit novel food sources (Parkes 1975), we expected that other items such as pet and human food could be detected.

Methods

Hedgehog collection

Hedgehogs were collected by hand (under University of Auckland Animal Ethics Committee Approval No. 001896) from 10 urban forest fragments in Auckland (Table 1) from September 2017 to February 2018. These urban forest fragments contained a range of forest types as classified by the Auckland Council including regenerating vegetation, coastal broadleaved forest and exotic forest (Table 1). These collections were carried out during the first of the two main nocturnal periods of hedgehog activity in the 2 to 3 hours after sunset (Brockie 1974; Campbell 1975). Hedgehogs have a relatively fast gut passage time (Egeter 2014), and can fill and empty their gut multiple times during the night (Campbell 1975; Wroot 1984). Therefore, 2–3 h post sunset was considered the optimal time to collect hedgehogs.

A thermal scope (Pulsar Quantum XD19 Thermal monocular, Pulsar, Mansfield, Texas, USA) and torches (Energizer™ Vision HD Metal Torch 900 lumen, Energizer Holdings, Inc, St. Louis, Missouri, USA) were used to search for hedgehogs in fragments. Hedgehogs were easily approached and picked up and placed into individual cardboard pet carriers using gloves. Euthanasia was carried out on-site using CO_2 gas. Once euthanised, the hedgehogs were stored in a freezer until stomach samples were analysed.

Stomach content analysis

Each stomach was removed, weighed, cut open lengthwise and then everted and washed out. The contents were transferred into a fine-mesh sieve to remove mucus. The empty stomach was then weighed and the weight of the contents equated to the difference between the weight of the stomach before and after the removal of its contents. Food remains found in the stomach contents were then sorted and stored in individual containers containing 75% ethanol and labelled with a unique identifying number. The structures were examined under a microscope and then classified as invertebrates (identified to order), lizards, birds, eggs and vegetation, or to the highest taxonomic resolution possible (e.g. wētā: Anostostomatidae and Rhaphidophoridae). Identification of invertebrate remains was carried out using reference specimens.

We calculated the frequency of occurrence by determining the number of times a particular food type was present in the stomachs and dividing it by the total number of stomachs (Campbell 1973; Berry 1999; Hendra 1999; Jones et al. 2005; Jeffries 2011; Jones & Norbury 2011). We determined the relative volume of each food type by estimating their percentage in each stomach sample. The contents of the stomach were dispersed in a petri dish and the volume of each category as a percentage of the total volume of the stomach was estimated (to the nearest 1%). The 95% confidence intervals were constructed for both the percentage occurrence and the relative volume by bootstrapping with 1000 replications. Where possible, counts were made to determine minimum numbers of specific animals (e.g. wētā, based on six legs per individual).

The frequency of occurrence can over-estimate the importance of foods that are eaten often, but in small quantities (e.g. Yalden 1976; Klare et al. 2011). However, the relative

Table 1. Urban Auckland hedgehog collection sites (forest fragments).

ID	Site	Coordinates (latitude, longitude)	Total area (ha)	Habitat type*	Number of hedgehogs collected
1	Auckland Domain	−36.857504, 174.7732	29.4	EF	8
2	Dingle Dell Reserve	−36.8588, 174.8562	7.68	VS2	3
3	Gitto’s Domain	−36.9258, 174.7053	15.1	EF	1
4	Jaggers Bush Reserve	−36.8589, 174.7198	3.69	Not classified	7
5	Kepa Bush	−36.863, 174.8304	13.4	WF4	9
6	Moire Park	−36.8257, 174.6317	17.1	WF4, VS2, VS3, EF	4
7	Orakei Basin	−36.8654, 174.809	8.21	EF	6
8	Smith's Bush	−36.7917, 174.7524	7.71	MF4, WF7	5
9	Shona Reserve	−36.8819, 174.6209	14.3	WF8	3
10	St John's Bush	−36.871, 174.8416,	3.00	VS5	5

*Habitat type: VS – regenerating ecosystems; VS2 – kānuka scrub/forest; VS3 – mānuka/kānuka scrub; VS5 – broadleaved species scrub/forest; W/MF – forest ecosystem (W = warm temperate and sub-humid, M = mild); WF4 – pōhutukawa, pūriri, broadleaved forest, coastal broadleaved forest; WF7 – pūriri forest; WF8 – kahikatea, pukatea forest; MF4 – kahikatea forest; EF – exotic forest (Singers et al. 2017).

volume within the stomach also has limitations; for example, time of consumption and level of digestion were unknown and would have affected the relative volume. Soft foods that are easily digested may be under-represented relative to hard, relatively indigestible foods (e.g. Klare et al. 2011). Since each method has strengths and limitations, both are presented here.

Statistical analysis

Dietary diversity was estimated using Brillouin's index (Brillouin 1956). A cumulative prey diversity curve was constructed by randomising the order of the stomach samples, then plotting the cumulative diversity against the number of stomachs analysed. When this curve appeared to reach an asymptote, sample size was considered adequate and collection of hedgehogs stopped.

We carried out non-metric multi-dimensional scaling (NMDS) to assess the composition of the stomachs using R version 3.4.0 and the package 'vegan' version 2.4-6 (Oksanen et al. 2018) with the Jaccard index to determine similarity between the samples, based on a presence-absence matrix of the stomach contents. This similarity index that compares samples to determine shared vs distinct taxa in presence-absence species matrices (Real & Vargas 1996). We used NMDS to check for any grouping in the data based on collection location, month of collection, age or sex of the hedgehog. There did not appear to be any differences between groups (see Figure S1 in Supplementary Material) so all data were pooled to be presented as percentage occurrence and the mean relative volumes.

Results

A total of 51 hedgehogs, 75% of which were adults, were collected across the ten sites. The cumulative diversity of the diet samples appeared to reach an asymptote at around 25–30 hedgehogs (Fig. 1).

The stomach contents ranged in weight from 0.04 to 40.67 g (Fig. 2). Two of the hedgehogs had no identifiable food in their stomachs and a further five were excluded from analysis because high levels of digestion prevented identification of the contents. There was no significant difference between the mean content weights for the male (mean = 9.40 ± 11.37 g) and female (mean = 10.14 ± 6.81 g) adults (t = 0.253; p = 0.802), or for male (mean = 4.05 ± 4.96 g) and female (mean = 3.36 ± 3.20 g) juveniles (t = −0.302; p = 0.768).

The 44 stomachs that were analysed contained 25 identifiable taxa (see Table S1 in Supplementary Material). Invertebrates were observed in 100% of the stomachs with a mean relative volume of 51%. Insects comprised the largest group within invertebrates, being found in 82% of the stomachs and making up 28% of the relative volume, on average.

Coleoptera (adults) was the most frequently eaten insect order, occurring in 53% of stomachs, but comprising only 4% of the diet by volume (Figs. 3 & 4). Coleopteran larvae were also present in 29% of stomachs and had a larger relative volume of 12% (Figs. 3 & 4). These larvae were often found in large numbers. For example, stomachs from four individual hedgehogs caught within a few metres of each other on the same night each contained 20–52 larvae.

Wētā (Anostostomatidae and Rhaphidophoridae) were found in a number of stomachs (13%), but they had a small relative volume of 2% (Figs. 3 & 4). There did not appear to be large numbers of wētā in the stomachs, with no more than six legs counted in each stomach.

Vertebrate remains were found in 9% of the stomachs (Table S1). Avian remains (predominantly passerine feathers found mid-December to mid-January) were found in 7% of the stomachs (three stomachs; Fig. 3). Two of these stomachs contained feathers with flesh attached and one of these also had bones associated with it, identified as most likely a juvenile blackbird. The relative volume was 1%. Lizard remains were found in one stomach (relative volume 0.2%), with two feet recorded. These remains were identified as *Lampropholis delicata* (plague skink). Vegetation was found in 91% of stomachs with a relative volume of 13% (Figs. 3 & 4). Grass was the most common type of vegetation (percentage occurrence 61% and relative volume 9%; Table S1).

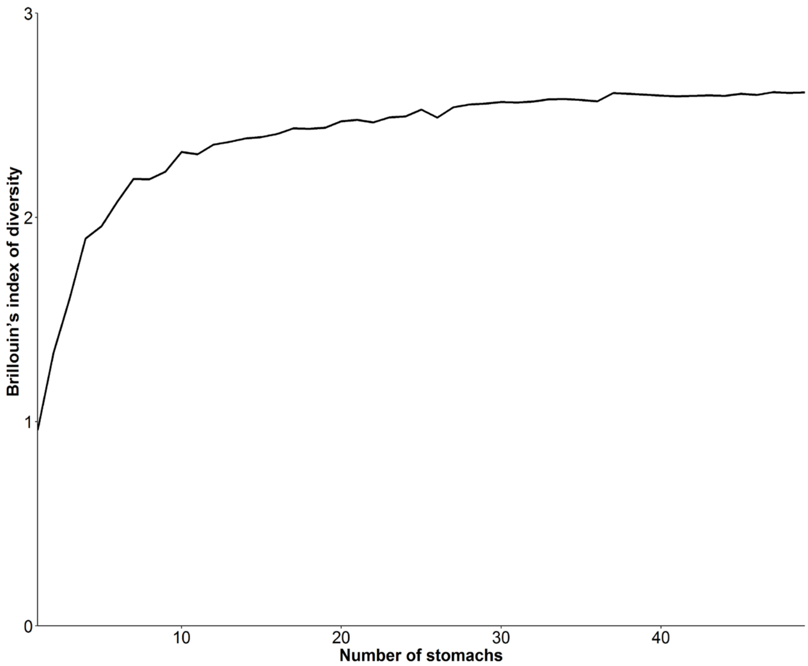

Figure 1. Cumulative diversity of hedgehog diet (estimated using the Brillouin index) with increasing number of stomach samples.

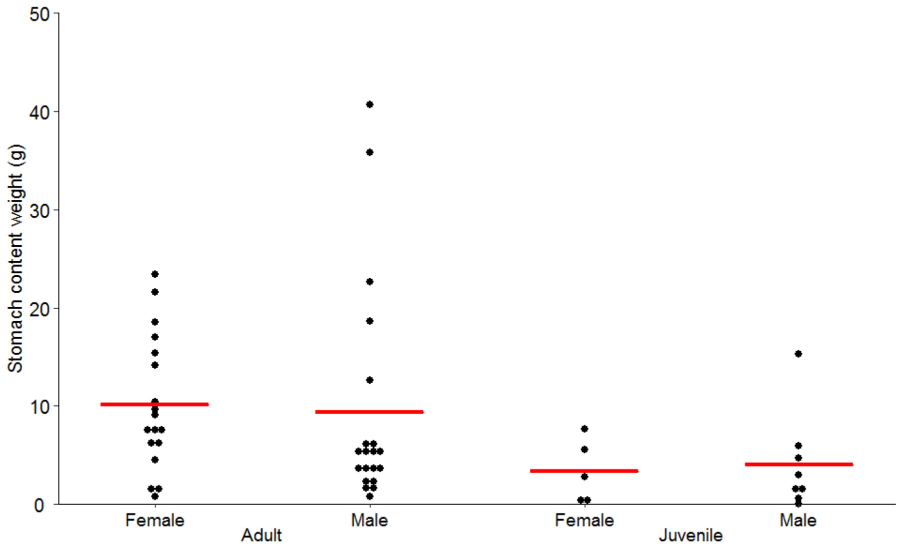

Figure 2. Stomach content weights of the hedgehogs in groups by sex and age.

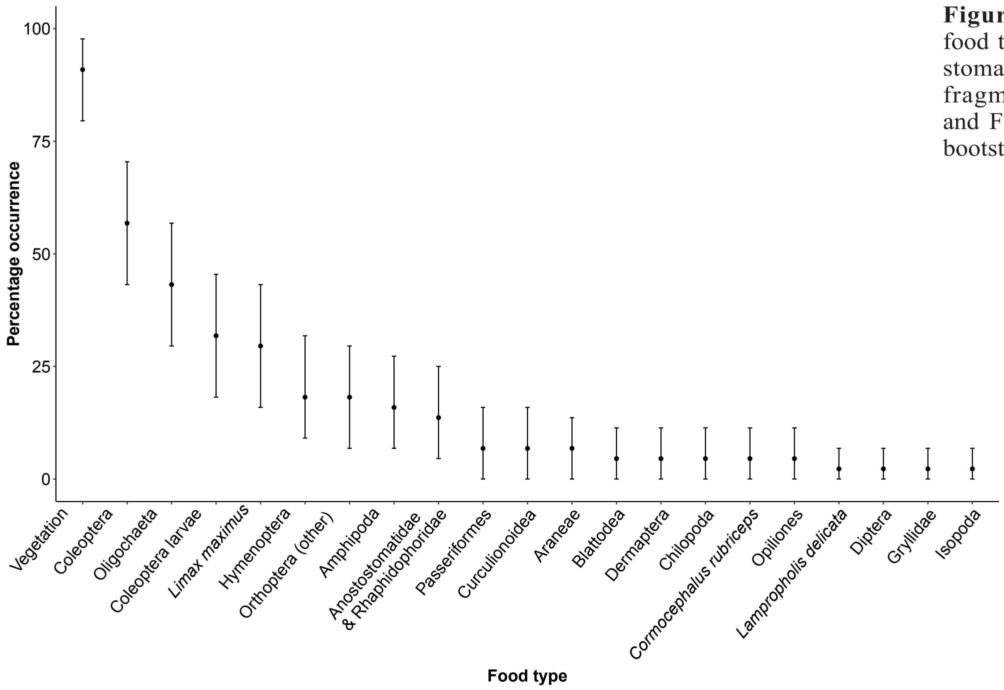

Figure 3. Percentage occurrence of food types identified from the hedgehog stomachs, collected from urban forest fragments between September 2017 and February 2018. Error bars are 95% bootstrapped percentiles.

Discussion

This research is the first empirical study of hedgehog diet in urban forest fragments in New Zealand. The dietary composition of hedgehogs in urban forest fragments was consistent with that in other forested habitats in New Zealand (Berry 1999; Hendra 1999). As hypothesised, invertebrates were the most important part of hedgehog diet in urban forest fragments, with the most commonly found invertebrates being Coleoptera. Oligochaetes and the introduced slug (*Limax maximus*) were also common in the stomachs. Almost all the hedgehogs had vegetation in their guts, but this occurrence is likely due to accidental ingestion while eating prey items. There was also evidence that hedgehogs were feeding on skinks and birds, consistent with studies of hedgehog diet in non-forested environments in New Zealand (e.g. Jones et al. 2005; Jones & Norbury 2011).

Invertebrate predation

Coleopterans were the most common food type; adult coleopterans were found in 59% of the stomachs and coleopteran larvae were found in 32%. These are likely to be high in energy as larvae generally have a high fat content (Xiaoming et al. 2010; Kouřimská & Adámková 2016). Beetles were found to provide a large amount of the energy in hedgehog diets in an United Kingdom study (Wroot 1984). The prevalence of coleopterans in the stomach contents is consistent with other studies in which beetles commonly

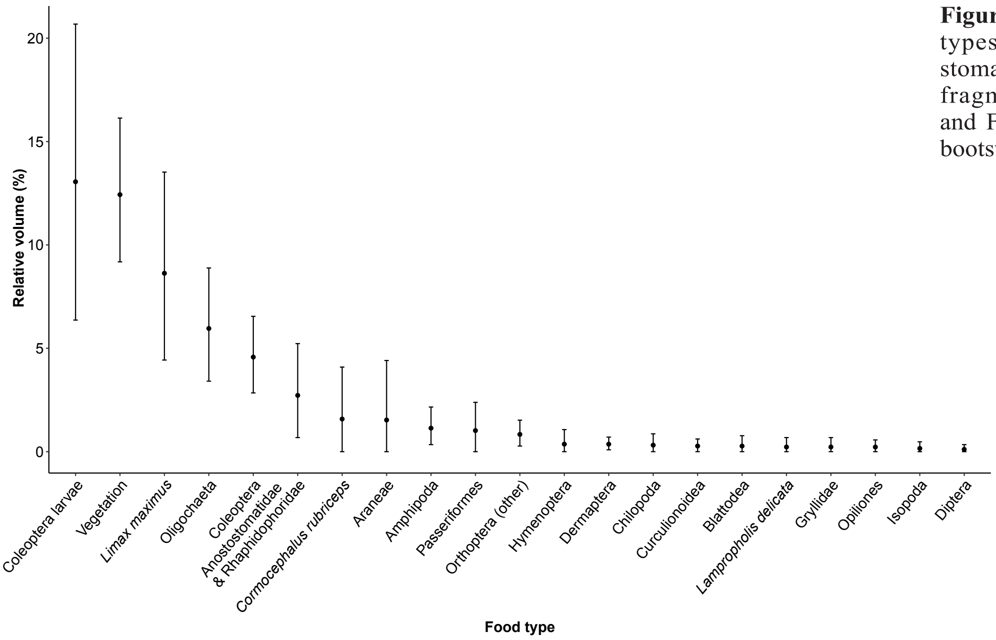

Figure 4. Relative volume (%) of food types identified from the hedgehog stomachs, collected from urban forest fragments between September 2017 and February 2018. Error bars are 95% bootstrapped percentiles.

had a high frequency of occurrence in the guts, stomachs or faeces (e.g. Brockie 1959; Campbell 1973; Jones & Norbury 2011). Although beetles in this study were only identified to order, other studies in New Zealand have found that the most common types of beetle eaten were Carabid and Scarabaeid (Berry 1999; Jones et al. 2005; Jeffries 2011). Urban fragments have high invertebrate diversity; a study carried out in two urban fragments (forest types: VS2, VS3, VS5, CL1, WF4 and EF; Singers et al. 2017) close to our sites in Auckland found 753 endemic beetle species (Kuschel 1990).

Earthworms were also commonly found in the stomachs of the hedgehogs which could be due to prey availability. Studies from a range of environments suggest that where earthworms are abundant, they are frequently eaten by hedgehogs (Micol et al. 1994; Cassini & Foger 1995). Earthworms were a common part of hedgehog diet in other hedgehog dietary studies in New Zealand forest (Berry 1999; Hendra 1999), and in pasture areas (Campbell 1973; Yalden 1976). An urban study in Finland also noted a high percentage occurrence of earthworms (50%). In dryland and sand dune environments in New Zealand there is little to no evidence of earthworms in the diet, presumably because the dry soils do not support earthworms (Jeffries 2011; Jones & Norbury 2011).

The exotic slug *Limax maximus* was commonly found in stomachs and was frequently seen while searching for hedgehogs. Slugs have been found commonly in other hedgehog dietary studies (e.g. Brockie 1959; Wroot 1984; Berry 1999; Hendra 1999; Rautio et al. 2016). *Limax maximus* is an invasive species that is likely to be feeding on plant populations in native forest fragments and can be aggressive towards native slugs (Barker & McGhie 1984). Therefore, hedgehogs will not be negatively affecting forest fragment biodiversity directly via *L. maximus* predation, instead this species potentially could be negatively impacting biodiversity outcomes by supporting hedgehog populations via predator-mediated apparent competition (Norbury 2002).

In the dietary studies carried out in New Zealand, wētā are commonly eaten by hedgehogs (percentage occurrence 22–25%; Berry 1999; Hendra 1999; Jones & Sanders 2005). In this study, 14% of stomachs contained wētā with the differences among studies likely to reflect differences in wētā availability at ground level in the different habitat types.

Two of the stomachs had native giant centipedes (*Cormocephalus rubriceps*) present (and two stomachs had unidentified centipedes). Giant centipedes are often preyed upon before they reach full size, and large individuals tend to be found only in predator-free environments (Minor 2016). Therefore, even with the removal of rats from urban forest fragments by community groups, these centipedes are likely to remain under some predation pressure from hedgehogs. Centipedes and other myriapods were also found in low numbers in other dietary studies of hedgehogs (Yalden 1976; Berry 1999; Hendra 1999; Jeffries 2011).

Urban forest fragments are under pressure from habitat modification and invasive species and this pressure can adversely affect invertebrate diversity (McKinney 2008; Jones & Leather 2012). Invasive mammals, such as rodents, also contribute to invertebrate predation, reducing abundance and diversity (Sinclair et al. 2005; St Clair 2011; Ruscoe et al. 2013). However, there is still a diverse community of endemic invertebrates in urban forest fragments that should not be discounted (Kuschel 1990; DOC & MfE 2000; Lee & Lee 2014). Hedgehog predation will be further contributing to this loss. Many New Zealand invertebrates have not been taxonomically described and are data deficient (Samways 1993; Lester et al. 2014). This lack of information means that predation could be having a severe, unrecognised impact. Invertebrates are also important for a diverse range of ecosystem functions and their loss through hedgehog predation could have flow-on effects for ecosystem processes, such as pollination, decomposition or seed dispersal (Duthie et al. 2006; Sanford et al. 2009; St Clair 2011). However, many native birds also prey on invertebrates, and the potential impacts of bird population recovery versus mammalian predation on invertebrate communities are currently unknown.

Vertebrate predation

Bird remains were found in three of the stomachs. Bird remains have also been found in most hedgehog dietary studies with percentage occurrences up to 21% (in urban Finland) (e.g. Berry 1999; Hendra 1999; Jones et al. 2005; Rautio et al. 2016). The feathers found in this study were identified as most likely belonging to juvenile blackbirds (*Turdus merula*), which is consistent with the stomachs of these hedgehogs being collected when fledglings would be likely to leave the nest and be found on the ground (mid-December–mid-January; Armitage 2017; SPCA Otago 2017). Therefore, while it is feasible that predation had occurred, stomach content analysis cannot distinguish between direct predation and scavenging.

One hedgehog was found with lizard remains in its stomach. In environments where skinks are common, they are commonly found in hedgehog diet studies (van der Sluijs et al. 2009) and there are a number of native, threatened skinks (ornate skink *Cyclodina ornata*) in Auckland's urban forest fragments that might be at risk (Boffa Miskell 2014). However, the skink identified in our study was the plague skink, which has been found in far higher densities in Auckland compared to native species, such as the copper skink (*Cyclodina aenea*) (Peace 2004).

As this study was carried out in an urban environment, we had predicted that human food sources could play a role in hedgehog diet, which was not found to be the case. However, human-derived food sources (such as pet food) could be soft and easily digested making detection in the stomach difficult. Another urban study that carried out dietary analysis found evidence of human food (Rautio et al. 2016). However, that study was conducted in the hedgehog's native range in a cooler climate, where hedgehogs had a far shorter season to reproduce and prepare for hibernation. This environment may have less invertebrate prey available, so hedgehogs are required to seek out alternatives (such as human-derived food) to prepare for hibernation. If hedgehogs were exploiting human-derived food sources, larger populations of hedgehogs could be supported via this supplementary food.

Impact

Although the results of this study show that hedgehogs were eating a variety of animals, it is necessary to consider whether hedgehog predation has an ecologically significant impact on urban forest fragments. Invasive species can have impacts ranging from 'no damage' to 'massive damage' (Blackburn et al. 2014). 'Minor damage' can be considered to be causing a reduction in an individual's fitness, while 'major/massive damage' results in changes to community composition and local extinction of a species (Blackburn et al. 2014). Hedgehogs are unlikely to be causing massive damage in the urban forest fragment environment and the level of impact of hedgehogs in the urban forest fragments we studied could be considered 'minimal' to 'moderate' (as defined by Blackburn et al. 2014), as hedgehogs are likely to be affecting community composition primarily through predation of invertebrates, with unknown effects on their populations. Habitats might be deemed at higher risk if they bordered open sanctuaries where spill-over dispersal would be expected from reintroduced native birds or lizards (Nottingham et al. 2019). Determining the severity of impact would require that studies are carried out on community composition before and after hedgehog removal, which was not possible within the scope of this study.

Interactions among species can be complex and indirect impacts can also occur such as competition. Hedgehog feeding could reduce the availability of invertebrates, thereby reducing the possible population density of insectivorous birds and lizards due to a competitive relationship, as has been suggested between hedgehogs and kiwi (*Apteryx* spp.) (Berry 1999). Hedgehogs could have more severe impacts if they specialise on particular prey types as suggested by some studies (Jones & Norbury 2006; Shanahan et al. 2007; Recio et al. 2013). However, hedgehogs are primarily thought to be generalist predators (e.g. Jones & Sanders 2005; Jones & Norbury 2011), and our study suggests that hedgehogs have a diverse diet in urban forest fragments. As in other studies, hedgehogs are likely to prey switch seasonally, and in different habitats, throughout the year whereby they exploit one type of prey based on availability, before moving on to the next (Yalden 1976; Wroot 1984; Hendra 1999; Haigh 2011). Seasonal differences could not be assessed in this study as hedgehogs were only collected in spring and summer. However, there was evidence that hedgehogs were opportunistically exploiting aggregations of food sources (e.g. coleopteran larvae) as found by other studies (Parkes 1975; Cassini & Krebs 1994).

Conclusion

Predation by hedgehogs in urban forest fragments is predominantly directed towards invertebrate species, such as coleopterans and giant centipedes, with skinks and birds being eaten when available. Hedgehogs are voracious feeders and are collectively capable of consuming a large volume of invertebrates. This predation could be particularly problematic as conservation is not generally directed towards invertebrates (with the exception of a few high-profile species) (DOC 2016). However, invertebrates are critical for ecosystem functioning and their loss can have impacts on a number of trophic pathways. There are potential further impacts to native species through competition with insectivorous birds or lizards. However, further study is required to quantify the extent of the hedgehog's impact through predation. Future work should focus on whether hedgehogs are causing population declines of invertebrate taxa through predation, and how these declines are impacting other aspects of the ecosystem through a loss of functions that these invertebrates would have been carrying out (Blackburn et al. 2014).

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Table S1. The percentage occurrence and relative volumes of food types identified from the hedgehog stomachs, collected from urban forest fragments between September 2017 and February 2018 with the bootstrapped 95% confidence intervals.

Figure S1. Comparison of stomach contents from male and female hedgehogs collected from bush or grass habitats.

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