Relative importance of sugar resources to endemic gecko populations in an isolated island ecosystem

Annette E. Evans[1*], David R. Towns[2,3] and Jacqueline R. Beggs[1]

[1]School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand
[2]Department of Conservation, Private Bag 68908, Newton, Auckland 1145, New Zealand
[3]Institute for Applied Ecology New Zealand, Auckland University of Technology, Auckland 1142, New Zealand
*Author for correspondence (Email: evans.annette9@gmail.com)

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Abstract: In many ecosystems food-web dynamics are driven by spatial and temporal variation in the availability of sugar resources, which form the primary or even exclusive dietary constituents for many species. Scale insects (Hemiptera) produce sugar-rich honeydew, which can be a keystone sugar source in honeydew ecosystems worldwide. In New Zealand, most previous research in honeydew ecosystems has been conducted in areas where herpetofauna are heavily suppressed by introduced predators. Consequently, little is known about potential trophic interactions between endemic lizards and scale insects. Korapuki Island is one of the few remaining locations in New Zealand where endemic scale insects and lizards survive in densities likely to be representative of prehuman conditions. We examined the relative importance of different sugar resources on Korapuki Island to Duvaucel's geckos (*Hoplodactylus duvaucelii*) and common geckos (*Woodworthia maculatus*). We recorded the abundance and morphometrics of geckos attending five sugar-producing plant species (two of which host honeydew-producing scale insects) three times daily along a fixed transect. Large numbers of Duvaucel's and common geckos were recorded nocturnally feeding on honeydew produced by the scale insect *Coelostomidia zealandica* (Coelostomidiidae). Duvaucel's geckos of all sizes and genders fed extensively on honeydew throughout the year, favouring ngaio (*Myoporum laetum*) trees with high scale insect infestations, but were seldom recorded at other sugar resources. In contrast, juvenile common geckos were infrequently recorded on honeydew-producing trees. Common geckos fed on a variety of other sugar resources, with all sizes and sexes abundant on nectar and sap of flax (*Phormium tenax*) and seasonally exploiting nectar of pohutukawa (*Metrosideros excelsa*). The strength of interactions between scale insects and geckos, particularly for the Duvaucel's gecko population on Korapuki Island, indicates the importance of honeydew in addition to more ephemeral sugar resources such as nectar. Accordingly, the re-establishment of honeydew-producing Hemiptera populations should be considered in future conservation and restoration plans.

Keywords: *Coelostomidia zealandica;* common gecko; Duvaucel's gecko; flowers; honeydew; *Hoplodactylus duvaucelii;* island food-webs; nectar; Korapuki Island; *Woodworthia maculatus*

Introduction

Ecological interactions within food-webs constantly adjust over both spatial and temporal scales (Basille et al. 2013). Many organisms tend to preferentially exploit food resources that offer maximum nutritional or energetic returns for the time invested in foraging (Wolf et al. 1975; Pyke et al. 1977; Vollhardt et al. 2010). However, the nutritional attractiveness of a resource must also be offset against the competition pressures and predation risks associated with foraging (Whiting & Greeff 1999). Many organisms rely on ephemeral sugar resources, such as flowers (nectar) and fleshy fruits (Wolf et al. 1975; Rasch & Craig 1988; Timewell & Mac Nally 2004; Fleming & Muchhala 2008; Symes et al. 2008; Abrahamczyk & Kessler 2010; Becker et al. 2010; Vollhardt et al. 2010). To maintain foraging efficiency, these organisms must predict and respond to resource fluctuations through both time and space (Wolf et al. 1975; Pyke et al. 1977; Eifler 1995).

Until recently, the dietary importance of plant-derived resources to lizards had been rarely studied, even though up to 11% of lizard species supplement their diets with plant materials including nectar, sap, fruit and foliage (Whitaker 1987; Eifler 1995; Cooper & Vitt 2002; Rowley et al. 2007). In New Zealand, geckos have been found on a variety of angiosperms, including pōhutukawa (*Metrosideros excelsa*), ngaio (*Myoporum laetum*), and mānuka (*Leptospermum scoparium*) (Whitaker 1987; Eifler 1995). Geckos often return to forage on the same plant (Eifler 1995) and individuals can travel up to 50 m to feed on floral resources (Whitaker 1987). Considering this, we predict that ephemeral sugar resources will strongly influence lizard population behavioural dynamics within ecosystems.

The large suite of invasive species established in New Zealand have significantly suppressed (or have extirpated) mainland lizard populations, restricting many ecologically functioning populations to isolated offshore islands. Consequently, the relationships between endemic gecko populations and plant-derived sugar resources can be difficult to determine and are often only revealed after the eradication of introduced pests (Atkinson & Cameron 1993; Towns 2002a).

On Korapuki Island, off the north-eastern coast of New Zealand, the eradication of kiore (*Rattus exulans*) and rabbits (*Oryctolagus cuniculus*) facilitated the population expansion of an endemic scale insect *Coelostomidia zealandica* (Hempitera: Coccoidea), revealing a previously unknown interaction between the scale insect and the island's two resident gecko species: Duvaucel's gecko (*Hoplodactylus duvaucelii*) and common geckos (*Woodworthia maculatus*) (Towns 2002a; Towns & Atkinson 2004). Scale insects produce honeydew – a carbohydrate-rich waste product that offers similar energetic benefits to floral nectar (Paton 1980; Grant & Beggs 1989). In New Zealand, previous studies have mainly focused on the dietary importance of honeydew for birds, fungi and invertebrates, particularly *Vespula* wasps (Gaze & Clout 1983; Moller & Tilley 1989; Thomas et al. 1990; Harris 1991; Moller et al. 1991; Beggs 2001; Beggs & Wardle 2006; Dhami et al. 2013; Gardner-Gee & Beggs 2013). With some scale insect species producing honeydew year-round (Beggs et al. 2005; Gardner-Gee & Beggs 2013), the dietary importance of honeydew to endemic gecko populations compared with traditional seasonally available sugar sources such as nectar warrants investigation.

We examined the relative importance of different sugar resources to two gecko species on Korapuki Island by evaluating (1) whether there was seasonal variation in the exploitation of different sugar resources by Duvaucel's geckos and common geckos and (2) whether the use of sugar resources varied based on size or gender of individuals within each gecko species. We compared the abundance of geckos on five different sugar-producing plant species during one year. We predicted that since honeydew was available year-round, it would be the most important source of sugar for geckos.

Methods

Korapuki Island (36º39.5′ S, 175º51′ E) is a wildlife sanctuary situated in the Mercury Islands off the north-eastern coast of New Zealand (Fig. 1). Following a history of human disturbance, restoration efforts began by eradicating invasive kiore (1986) and rabbits (1987) (Towns & Atkinson 2004). The positive effects of eradication have rippled through the island's ecosystem: facilitating natural forest regeneration and the expansion of native lizard and invertebrate populations (Towns 2002a). Our study site was situated on the coastal flaxland and regenerating coastal forest in and around the central basin of Korapuki Island, where Duvaucel's geckos, common geckos, and populations of endemic scale insect *Coelostomidia zealandica* growing on karo (*Pittosporum crassifolium*) and ngaio trees co-occur (Towns 2002a,b).

Field sampling

We compared sugar resource use by the two gecko species on Korapuki Island using active searches of five native plant species (Table 1) likely to be attractive to geckos because of nectar, scent or as hosts of honeydew scale insects. The individual native plants surveyed (n = 48), located along a non-linear transect, were searched three times daily: morning (beginning c. 0900 hours), noon, and evening (c. 1800 hours) during five seasonal sampling periods from November 2011 to September 2012 (for number of sampling days see Table 2). The branches, trunks, foliage, flowers, and plant bases of each surveyed plant were systematically examined and the number of geckos present on each plant was recorded.

Of the two species of geckos present on Korapuki Island, common geckos are the smallest, reaching a maximum snout–vent length (SVL) of 89 mm (Cree & Guillette 1995) and attaining sexual maturity at c. 55 mm SVL (Cree 1994). Duvaucel's geckos reach 160 mm SVL (Whitaker 1968), attaining sexual maturity at c. 95 mm SVL (Cree 1994). We captured geckos by hand during each of the five seasonal

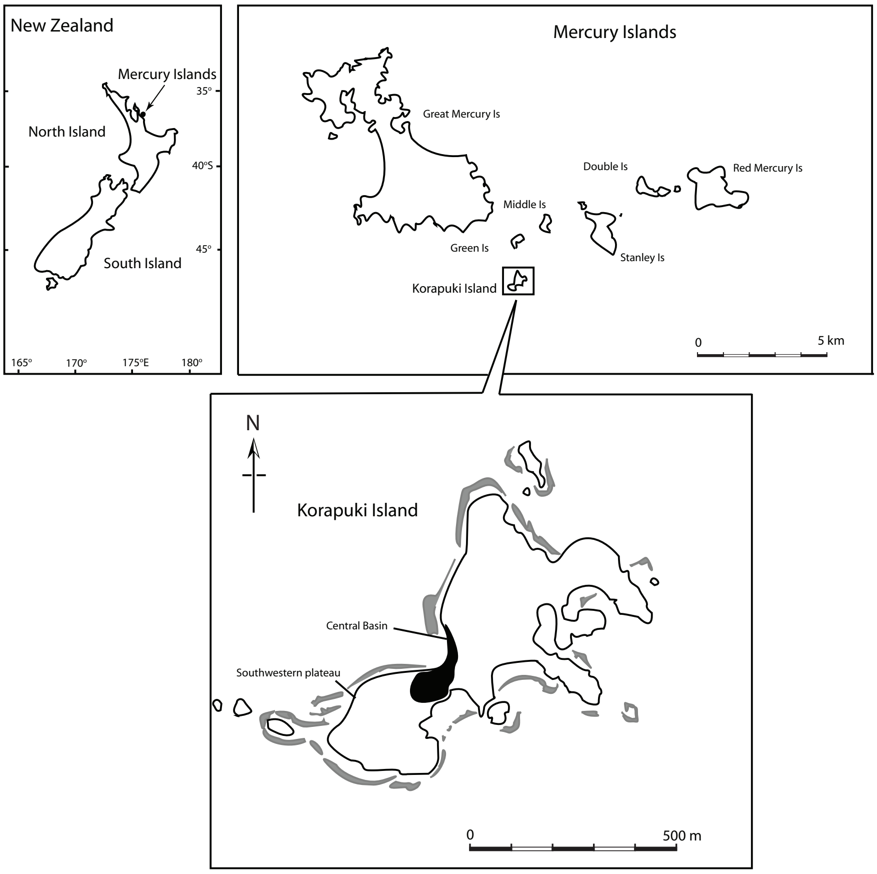

Figure 1. Location of Korapuki Island, Mercury Island Group, north-eastern New Zealand. Area of study highlighted in black; grey areas represent the island's intertidal rocky fringe.

Table 1. Summary of sugar characteristics for the five native plant species surveyed as part of this study on Korapuki Island, north-eastern New Zealand.

Plant species	Scientific name	Life form	Height	Flowering/ fruiting period	Flower/fruit attributes	Scale insect host	References
Flax	*Phormium tenax*	Herb, upright in habit with erect leaves and tall flower heads	2–3 m	Flowers: Oct–Jan Fruits: Nov–Mar	Tubular, hermaphroditic red/yellow flowers arranged in raceme-like stalks 5–6 m tall. Sexual phases are partially separated both temporally (dichogamy) and spatially (herkogamy). Flowers produce large quantities of dilute nectar. Fruits are angled capsules, up to 10 cm long	No	Whitaker (1987); Craig & Stewart (1988); Landcare Research (2005); Tauwhare et al. (2006); Dilks (2004); NZPCN (2012)
Pōhutukawa	*Metrosideros excelsa*	Large, multi-stemmed canopy tree	25 m	Flowers: Nov–Jan Fruits: Jan–May	Red, compound inflorescences with an average of 14.3 hermaphroditic, multi-stamen flowers. Nectar produced diurnally and nocturnally. Small hairy wind-dispersed fruit/seeds	No	Schmidt-Adam et al. (1999, 2009); Landcare Research (2005); Smith (2009); NZPCN (2012)
Māhoe	*Melicytus ramiflorus*	Low-elevation shade-tolerant tree	10 m	Flowers: Nov–Mar Fruits: Dec–July	Fasciculate green-yellow flowers arise on short pedicels from leaf axils, usually in inflorescences of 2–10 flowers. Flowering variable but often occurs in series of short, distinct periods. Small 3–4 mm purple fruits	No	Powlesland et al. (1985); Landcare Research (2005); NZPCN (2012)
Ngaio	*Myoporum laetum*	Light-demanding tree with fleshy, gland-dotted leaves	8–10 m	Flowers: Oct–Jan Fruits: Dec–Jun	Small, white, purple-spotted, flowers in 2–6-flowered axillary cymes. Fruit narrow -ovoid drupe, purple-pink when ripe	Yes	Allan (1961); Towns (2002a); Landcare Research (2005); NZPCN (2012)
Karo	*Pittosporum crassifolium*	Small coastal shrub or tree	9–10 m	Flowers: Aug–Oct Fruits: Sep–Aug	Dark red flowers in terminal 1–10- flowered fascicles, scented at night. Fruit 2–3 cm wide, split into three to display black seeds in yellow pith. Old fruits persist on tree year-round	Yes	Allan (1961); Castro & Robertson (1997); Towns (2002a); Landcare Research (2005); NZPCN (2012)

Table 2. Chi-square tests (family: Poisson) for the total (pooled) number of common geckos (*Woodworthia maculatus*) and total (pooled) number of Duvaucel's geckos (*Hoplodactylus duvaucelii*) attending sampled sugar resources (honeydew, nectar, and fruits) on Korapuki Island, north-eastern New Zealand, during five seasonal periods from November 2011 to September 2012.

Month	No. sampling days	Common geckos			Duvaucel's geckos		
		d.f.	χ^2	*P*	d.f.	χ^2	*P*
November	6	4	3.31	0.424	4	47.23	<0.001
December	9	5	50.03	<0.001	5	32.60	<0.001
January	9	5	42.18	<0.001	5	83.64	<0.001
May	10	5	73.42	<0.001	5	94.14	<0.001
September	12	5	73.83	<0.001	5	32.46	<0.001

sampling periods and recorded the following measurements for each individual: species, time of capture, location of capture, SVL, sex, gravid status, identification number, and any additional characteristic features such as scars or double tails (as additional cross checks for later identification). Pregnancy status was assessed visually and by palpation. All geckos captured were given a unique dorsal identification mark using a silver non-toxic pen (Artline® 993) so individuals could be easily identified if recaptured. Since the marks were visible for up to 4.5 months, we avoided recapturing during the same sampling month, preventing unnecessary double handling. We also made note of the specific location or tree on which individuals were recaptured, and whenever we were able to get close enough to observe, it was clear that geckos were actually feeding on the sugar resources.

To take into account variations in scale insect infestations when estimating honeydew abundance, sampled ngaio trees were divided into two categories: high density scale insect infestation and low density scale insect infestation (Table 3). Infestation levels on karo trees were less variable so natural variance was captured through random sampling. Signs of infestation included anal filaments, mobile scale insect instars, waxy tests or cocoons, and the presence of sooty mould complexes on tree trunks. Flower abundance of flax (*Phormium tenax*) and pōhutukawa was recorded daily, as there was substantial daily variation in floral development. The abundance of flowers and fruit on karo, ngaio and māhoe (*Melicytus ramiflorus*) plants were recorded at the beginning and end of each sampling period.

Statistical analysis

The numbers of common and Duvaucel's geckos seasonally attending the sampled sugar resources were analysed by performing log-linear analysis using chi-square tests (Family = 'Poisson') in R version 2.15.1. Separate models were used to analyse seasonal differences in total gecko numbers, sexes, and age groups using a contingency table where variables including species (common, Duvaucel's), sampling month (November, December, January, May, September), tree species (ngaio (high), ngaio (low), karo, flax, māhoe, pōhutukawa), sex (male, female, juvenile), age (juveniles, adults), pregnancy (gravid, non-gravid) were considered as independent factors. When variances showed evidence of inflation, chi-square tests were corrected using the appropriately calculated test scale factors, and where this technique was inapplicable *F*-tests were conducted using a quasi-Poisson distribution. When comparing the effects of body size on resource attendance, SVL measurements for each gecko species were pooled into adults and juveniles to improve the statistical power of the chi-square tests. Similarly, due to sample size restrictions, the numbers of males, females and juveniles, as well as the numbers of gravid females for each gecko species from each sugar resource, were pooled over the five sampling months and analysed using separate chi-square models. Pōhutukawa trees were added to the study following the first data collection trip in November; consequently the lower degrees of freedom in November statistical tests are due to the omission of pōhutukawa from the analysis.

Recapture data were treated as independent and pooled over the five sampling periods for each gecko species. Recapture incidences were divided into two groups, recaptures on same original tree and recaptures on different trees, and analysed using two-sample *t*-tests. Unlike the other plant species sampled, preliminary analyses showed strong seasonal variations in the number of geckos visiting pōhutukawa trees and we wanted to investigate this trend separately to evaluate whether seasonal trends were explained by the presence of flowers. To examine the relationship between the abundance of pōhutukawa flowers and gecko attendance, the total number of partially open, fully open and senescing pōhutukawa flowers recorded each day were pooled and compared (Pearson's correlation, *r*) to corresponding gecko sightings.

Results

Seasonal exploitation of sugar sources by gecko populations

We captured a total of 1435 geckos – 1154 common geckos and 281 Duvaucel's geckos – over five sampling trips from November 2011 to September 2012. A relatively large portion (16.7%) of individuals was recaptured: 214 (18.5%) common

Table 3. Classification numbering system estimating the abundance of sugar resources available from sampled plant species on Korapuki Island, north-eastern New Zealand.

Sugar resource	Classification number			
	0	0.5	1	2
Honeydew on ngaio and karo	No scale insect infestation	-	Low infestation (*≤ 49% of bark showing signs of infestation*)	High infestation (*≥ 50% of bark showing signs of infestation*)
Ripe fruit	No ripe fruits	-	Fruit present (*<20 ripe fruits*)	Fruit abundant (*≥ 20 ripe fruits*)
Māhoe flowers	No flowers	<20 flower clusters	20–100 flower clusters	>100 flower clusters
Karo/ngaio flowers	No flowers	-	Flowers present (*<20 flowers*)	Flowers abundant (*≥ 20 flowers*)
Flax flowers	No flowers	Female flower (*red style/stamens, orange pollen absent*)	Male flower (*red style/stamens, orange pollen present*)	-
Pōhutukawa flowers	No flowers	Senescing flower (*anthers/stamens lost; only styles remaining*)	Partially open flower (*<80% of red stamens uncurled*)	Fully open flower (*≥ 80% of red stamens uncurled*)

geckos and 26 (9.3%) Duvaucel's geckos, with 44 recaptured geckos still showing their marking 4.5 months after being first marked. Many recaptured individuals did not move far over the course of the study: 81.3% were re-caught on the tree where they were initially caught. Common geckos showed greater plant fidelity than Duvaucel's geckos with 84.6% of recaptured individuals recorded on the same tree, compared with 53.9% of recaptured Duvaucel's geckos (t = 3.79, P < 0.001). For each gecko species, the total number of individuals attending the sampled sugar resources (honeydew, nectar, or fruit) varied between the five seasonal sampling periods, except for common geckos during November (Table 2). Common geckos regularly exploited all sampled sugar resources, but relied heavily on flax in all months except November (Fig. 2a). In contrast, Duvaucel's geckos showed a strong preference for honeydew, with 238 of the 281 Duvaucel's geckos (84.5%) captured from honeydew-infested trees. Moreover, 74.4% of Duvaucel's geckos attending honeydew-infested trees favoured ngaio trees with high scale insect infestations (Fig. 2b; $F_{(2,12)}$ = 20.81, P < 0.001).

There was a positive correlation between the abundance of pōhutukawa flowers and the number of common geckos in attendance (Fig. 3; r^2 = 0.589, P < 0.001). Adult common gecko densities peaked on pōhutukawa during December (d.f. = 3, χ^2 = 123.56, P = 0.025), and foraging geckos were frequently recorded moving directly between inflorescences within the crowns of sampled pōhutukawa. Although the abundance of juvenile common geckos attending pōhutukawa clusters did not significantly vary over the five sampling periods (d.f. = 3, χ^2 = 3.74, P = 0.291), greater numbers of both male and female common geckos were recorded visiting pōhutukawa flowers during December (d.f. = 3, χ^2 = 37.77, P < 0.001 and d.f. = 3, χ^2 = 88.12, P < 0.001 respectively). In contrast, only two Duvaucel's geckos were recorded on pōhutukawa flower clusters during this study.

During November and December, when flax was in flower, common geckos were observed foraging on flowers, often with two or three individuals foraging on the same flax flower stalk. Individuals primarily fed by pressing their heads into the corolla or by licking around the bases of flowers. No aggression between individuals was ever observed, and many continued to feed uninterrupted despite the presence of researchers. Throughout all sampling periods, large numbers of geckos were also observed licking the bases, edges, and surfaces of flax leaves, with many licking at clear droplets of sap – particularly along leaf edges. Invertebrates, including longhorn beetles (Cerambycidae), *Chrysopeplus exploitus* beetles, and moths, were also regularly observed feeding on these clear droplets, which were abundant both day and night.

Differences in adult: juvenile resource use

The number of adult and juvenile common geckos attending sugar resources varied among months (Table 4). Both adult and juvenile common geckos were most abundant on flax, except in November where adult geckos were most abundant on ngaio trees with high scale insect infestations (Appendix, Fig. A1). In common geckos, the use of honeydew was dominated by adults, and juveniles were seldom recorded on honeydew-producing trees (ngaio and karo) (Fig. 4a). There were no significant differences observed in the sugar resource attendance between common gecko genders ($F_{(10,69)}$ = 1.15, P = 0.339), and within male and female populations individuals were consistently most abundant on flax plants ($F_{(5,23)}$ = 7.26, P < 0.001 and $F_{(5,23)}$ = 8.01, P < 0.001 respectively; Fig. 4a).

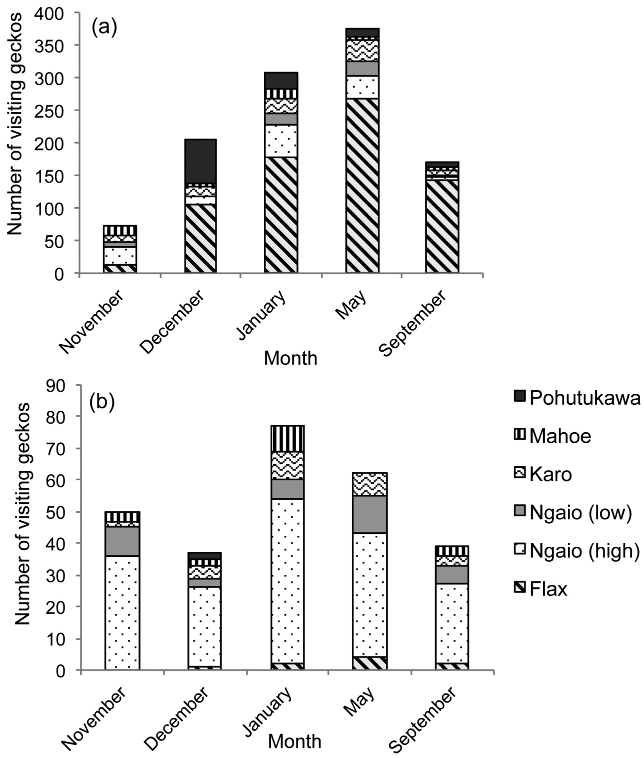

Figure 2. Frequency distribution of the total number of (a) common geckos (*Woodworthia maculatus*) and (b) Duvaucel's geckos (*Hoplodactylus duvaucelii*) visiting the sampled sugar resources on Korapuki Island from November 2011 to September 2012. Sugar resources include flowers and fruits for most plants, plus flax sap exudates, and honeydew produced by ngaio (*Myoporum laetum*) and karo (*Pittosporum crassifolium*) trees. 'Ngaio (high)' denotes ngaio trees with high (heavy) scale insect infestations (≥ 50% of bark showing signs of infestation) while 'Ngaio (low)' denotes ngaio trees with low scale insect infestations (≤ 49% of bark showing signs of infestation).

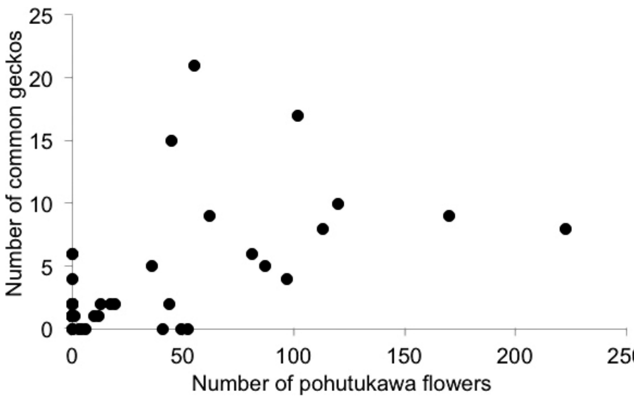

Figure 3. Relationship between the total number of inflorescences in a pōhutukawa cluster and the number of common geckos (*Woodworthia maculatus*) observed in the sampled flower cluster: r^2 = 0.589, P < 0.001.

Gravid common geckos were also most abundant on flax patches ($F_{(5,23)}$ = 3.96, P = 0.010).

Similar numbers of adult and juvenile Duvaucel's geckos attended sugar resources during November, December, and May, with both age groups found primarily on honeydew-producing trees and frequently observed licking at the

Table 4. Chi-square statistics (from Poisson loglinear model) comparing the attendance of juvenile and adult common geckos (*Woodworthia maculatus*) and Duvaucel's geckos (*Hoplodactylus duvaucelii*) to sugar resources on Korapuki Island, north-eastern New Zealand, over five seasonal sampling periods.

	Common geckos			Duvaucel's geckos		
Month	d.f.	χ^2	*P*	d.f.	χ^2	*P*
November	4	3.68	0.006	4	2.82	0.444
December	5	4.49	0.002	5	4.90	0.216
January	5	8.59	<0.001	5	14.67	<0.001
May	5	3.06	<0.001	5	0.49	0.986
September	5	24.68	<0.001	5	7.24	0.013

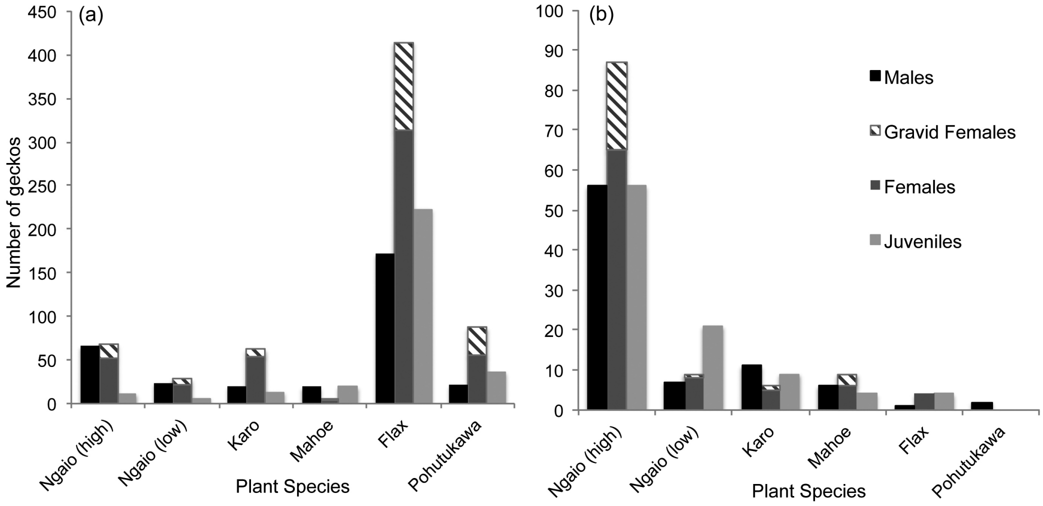

Figure 4. Frequency distribution of male, female, and juvenile (a) common geckos (*Woodworthia maculatus*) and (b) Duvaucel's geckos (*Hoplodactylus duvaucelii*) to the sampled sugar resources on Korapuki Island. Composite bar distinguishes between gravid and non-gravid female geckos. Sugar resources include flowers and fruits for most plants, plus flax sap exudates, and honeydew produced by ngaio (*Myoporum laetum*) and karo (*Pittosporum crassifolium*) trees. 'Ngaio (high)' denotes ngaio trees with high (heavy) scale insect infestations (≥ 50% of bark showing signs of infestation) while 'Ngaio (low)' denotes ngaio trees with low scale insect infestations (≤ 49% of bark showing signs of infestation).

honeydew drops. During January and September, significantly more adult than juvenile Duvaucel's geckos attended the heavily infested ngaio trees (Table 4; Appendix, Fig. A2). While both male and female adult Duvaucel's geckos were most abundant on heavily infested ngaio trees (d.f. = 5, $\chi^2 = 72.79$, $P < 0.001$ and d.f. = 5, $\chi^2 = 101.77$, $P < 0.001$ respectively), juveniles were seldom recorded on ngaio trees with heavy infestations, instead attending ngaio trees with lower density scale insect infestations, especially during November and January. Juvenile Duvaucel's geckos were never recorded attending pōhutukawa clusters (Appendix, Fig. A2) and gravid Duvaucel's geckos were most abundant on ngaio trees with high infestations of scale insects (d.f. = 5, $\chi^2 = 59.55$, $P < 0.001$).

Discussion

We found that sugar resources were frequently used by Duvaucel's gecko and common gecko on Korapuki Island. Common geckos foraged primarily on flax while Duvaucel's geckos were predominantly recorded foraging on honeydew-producing trees. We also found that there were seasonal and life-stage differences in resource use by geckos, with juvenile geckos generally avoiding sugar resources attended by high numbers of adult geckos.

The high numbers of geckos recorded on honeydew-producing trees suggests that endemic scale insects may play an important role in driving and maintaining food-web dynamics on Korapuki Island. Like nectar, honeydew is comprised of a diversity of sugars and typically contains high proportions of sucrose (Grant & Beggs 1989; Dhami et al. 2011); however, unlike flowers and fruit, honeydew is produced year-round (Beggs et al. 2005). Although honeydew is low in protein, the easily accessible, carbohydrate-rich droplets attract large numbers of invertebrates (Moller & Tilley 1989; Gardner-Gee & Beggs 2010, 2013), which may also be predated on by geckos. The added availability of refuge sites on old, densely scale insect infested ngaio trees may add to the attractiveness of these trees to visiting geckos. Although we did not observe geckos interacting aggressively with other geckos, the noticeable absence of juvenile common geckos from heavily infested honeydew trees suggests that small body size may influence resource selection. As we observed large numbers of Duvaucel's geckos on honeydew-producing trees, we suggest the threat of both aggression/predation and competition with other geckos is one likely explanation as to why honeydew attendance by common geckos is largely restricted to adults. Despite inter- and intra-specific lizard predation, the overall predation risk to geckos on Korapuki Island is probably relatively minimal. Major native predators such as morepork (*Ninox novaeseelandiae*) have only recently recolonised the island and diurnal kingfisher (*Halcyon sancta*) populations are likely to pose little threat to nocturnally active geckos (D.R. Towns unpubl. data; Van Winkel & Ji 2012). The large numbers of female geckos from both species attending flax and honeydew resources during our study show that resource selection could be influenced by the high energetic costs associated with reproduction (Bonnet et al. 1998; Kubička & Kratochvíl 2009). Duvaucel's gecko gestation periods conservatively range between 7 and 12 months (Barwick 1982; Cree 1994) while northern populations of common geckos follow an annual reproductive cycle centred on a 3- to 5-month pregnancy over the summer (Cree 1994). Flax bushes and Korapuki's old, crevice-riddled ngaio trees may also be important for shelter for gravid common geckos, which are less agile during pregnancy (Cooper et al. 1990). Rock et al. (2002) found that gravid common geckos often maintain higher body temperatures than non-gravid females and males. Hence flax bushes and ngaio crevices may protect gravid females against harsh environmental conditions, enabling them to retain optimal body temperatures.

The exploitation of flax plants by gecko species that we recorded has been previously observed in New Zealand (Whitaker 1987; Eifler 1995; Hoare et al. 2007). Studies of flax sugars typically focus on the abundance of the tubular protandrous flowers on flowering stalks, which produce large quantities of dilute nectar that are seasonally exploited by birds, insects, and lizards (Eifler 1995; Dilks 2004; Thorogood et al. 2007). However, flax can also produce large quantities of sap (McIlroy 1951; Tauwhare et al. 2006) – an additional, viscous sugar source that is available year-round. The abundance of invertebrates (including moths, and beetles such as *Chrysopeplus exploitus*) we observed consuming the clear droplets of sap along leaf edges suggests that flax sap may also be important in the diet of many other native species. Some of these sap consumers may also be prey for geckos. Flax exudates are largely comprised of xylan, a complex polysaccharide predominantly made of the monosaccharide D-xylose (McIlroy 1951; Sims & Newman 2006; Tauwhare et al. 2006). Although only a few studies have examined the importance of sap in the diets of New Zealand fauna (Beggs 1988; O'Donnell & Dilks 1989; Moorhouse 1997), there is widespread evidence elsewhere that sap can provide an important food resource, particularly when other food resources are scarce (Southwick & Southwick 1980; Blendinger 1999; Schlatter & Vergara 2005; Rowley et al. 2007; Macchi et al. 2011). Flax patches may also have attracted large numbers of geckos because of invertebrate prey inhabiting flax leaf refuges and the shelter flax provides for geckos against predators and harsh environmental conditions.

The increase in visitation rates by adult common geckos to pōhutukawa clusters during December reflects the peak flowering period of pōhutukawa, which produce large quantities of nectar both day and night (Smith 2009). A single pōhutukawa flower produces an average 46 µl (± 5.9) of nectar over a 24-h period, supplying a mean daily energetic value of 160 J (Schmidt-Adam et al. 1999). The high visitation rates of common geckos to the sampled pōhutukawa clusters and positive correlation between common gecko numbers and inflorescence abundance is consistent with earlier observations from Korapuki Island made by Eifler in 1995. Thus it is likely that geckos monitor and exploit favoured sugar resources as they become seasonally available. While Duvaucel's geckos were rarely observed on pōhutukawa clusters, this may be due to sampling bias, as it was only possible to observe the lower branches of trees. If Duvaucel's geckos preferentially forage on higher pōhutukawa inflorescences, we would not have seen them.

Conclusion

Duvaucel's and common geckos on Korapuki Island differ in their use of sugar resources. Duvaucel's geckos congregate on ngaio trees with high density scale insect infestations and exploit the honeydew exuded. In contrast, common geckos are most frequently found on flax, foraging on floral nectar and flax leaf exudates; the latter have been largely overlooked as a food resource for geckos. Our findings suggest that ecological restoration projects on New Zealand's offshore islands should consider seasonal availability of sugar-rich resources. In the future, projects could consider increasing flax plantings and/or restoring honeydew-producing scale insects on islands from which they have been lost. However, as honeydew can also support high numbers of introduced *Vespula* wasps (Thomas et al. 1990; Gardner-Gee & Beggs 2013), we advise caution and recommend that inclusion of honeydew in restoration strategies is reviewed and implemented on a case-by-case basis.

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Appendix

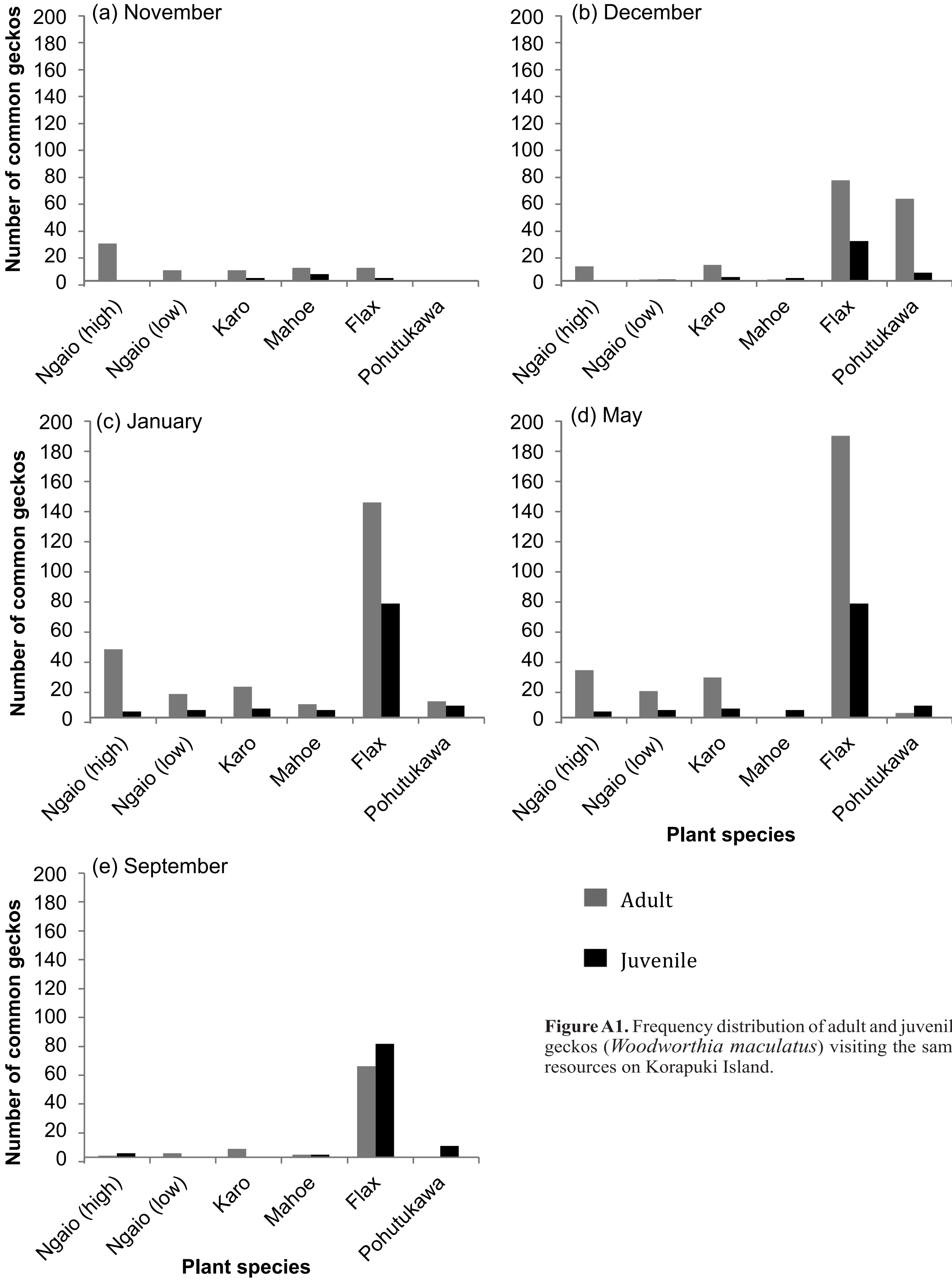

Figure A1. Frequency distribution of adult and juvenile common geckos (*Woodworthia maculatus*) visiting the sampled sugar resources on Korapuki Island.

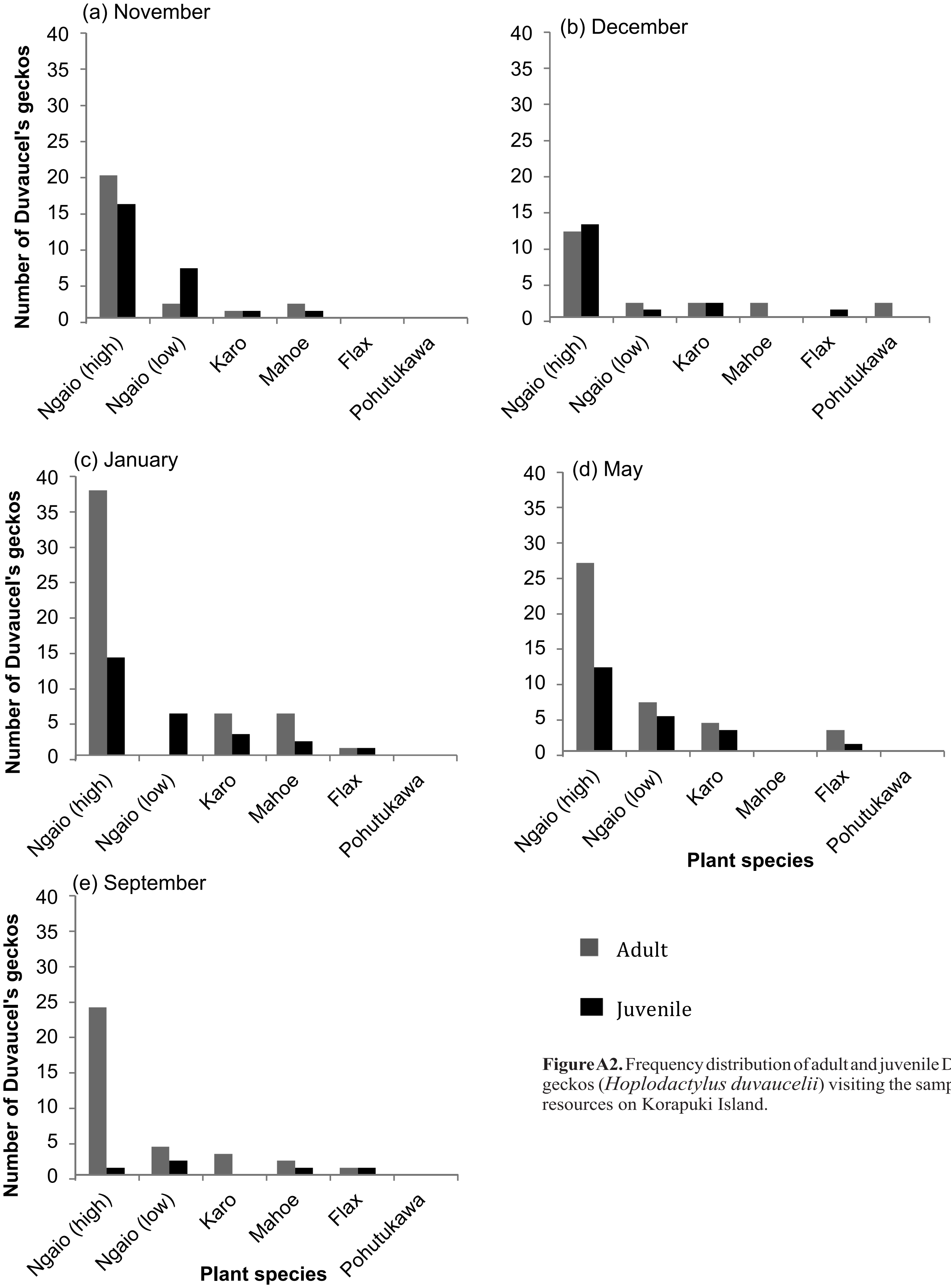

Figure A2. Frequency distribution of adult and juvenile Duvaucel's geckos (*Hoplodactylus duvaucelii*) visiting the sampled sugar resources on Korapuki Island.