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Season and sugar concentration affect bird behaviour at urban sugar-water feeders

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ABSTRACT

Sugar-water bird feeding in residential backyards is increasingly popular, but its effects on wildlife are poorly understood. One concern is whether it results in maladaptive behaviour, such as reliance on artificial food or increased aggression due to increased density of visiting individuals. We studied sugar-water feeder-associated bird behaviour in two cities with different climates. We investigate whether season, city, or sugar concentration influenced bird foraging activity and aggressiveness. We then test whether feeder presence affected backyard bird composition. Birds were most aggressive and used sugar-water feeders most actively in winter, especially the omnivorous native tauhou (*Zosterops lateralis*). We also found city and seasonal differences in sugar-water feeder usage and aggression. Further, in Auckland, the city with the warmer climate, New Zealand's largest nectarivorous species, tūī (*Prosthemadera novaeseelandiae*), was more likely to be aggressive at feeders with higher sugar concentrations but foraged longer at feeders with lower sugar concentrations. Neither feeder presence nor sugar concentration influenced garden bird species richness or abundance. We discuss the effects of sugar-water feeding on bird behaviour at the global and local scale and suggest future study directions.

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Introduction

Supplementary bird feeding is a perennially popular pastime in residential gardens and backyards (Jones 2018). Access to supplementary food sources can benefit urban avian wildlife by supporting populations that are limited by the availability of natural food, leading to increased winter survival and enhanced breeding success (Brittingham and Temple 1992; Schoech *et al*. 2008; Symes *et al*. 2008; Robb *et al*. 2008a). However, there are potentially harmful effects associated with behaviour alterations (Borowske *et al*. 2012; Galbraith *et al*. 2017), such as increased aggression and loss of fear of humans (Armstrong 1992b; Steyaert *et al*. 2014).

Changes in behavioural patterns can impact the entire urban ecosystem (Sekercioglu 2006). Unlike in rural habitats, supplementary feeding in cities can lead to birds concentrating in areas too small to support the increased population density (Plummer *et al*. 2015; Tryjanowski *et al*. 2015a, 2015b; Greig *et al*. 2017). Nectarivorous and frugivorous birds preferentially exploiting feeders rather than natural food sources can compromise plant pollination or seed dispersal (Bascompte *et al*. 2003; Whelan *et al*. 2008; du Plessis *et al*. 2021).

Sugar-water feeders are often used to attract nectarivorous birds (Armstrong 1992a; Galbraith *et al*. 2014; Erastova *et al*. 2021). This practice is widespread globally with feeder visitors including hummingbirds (Trochilidae) in North and South America (Harris-Haller and Harris 1991; Chalcoff *et al*. 2008; Graves 2013; Greig *et al*. 2017), sunbirds (Nectariniidae) in South Africa (Coetzee *et al*. 2018, 2021), and honeyeaters (Meliphagidae) and parrots (Psittaciformes) in Oceania (Armstrong 1992b; Down 1997). Sometimes sugar-water feeders attract other generalist urban birds (Erastova *et al*. 2021). Despite its popularity, sugar-water feeding is still greatly understudied, and its effect on wild birds, specifically their behaviour, is poorly understood (Galbraith *et al*. 2014; Erastova *et al*. 2021).

The main body of research conducted worldwide on nectarivorous birds at sugar-water feeders focuses on either digestion physiology and energy balance (Armstrong 1992b; Down 1997; Napier *et al*. 2013) or

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foraging behaviour. Studies on foraging behaviour mainly focus on sugar type and concentration preferences (Roberts 1995; Lotz and Schondube 2006; Chalcoff *et al.* 2008; Fleming *et al.* 2008; Franke *et al.* 2008) or time spent feeding (Bandivadekar *et al.* 2018). Both types of studies have been conducted in captivity or parks rather than in urban backyards.

Less data are available on seasonality, latitudinal effects, or variance in behaviour in connection to sugar type and concentration. Experiments with hummingbird feeders in the USA showed that migratory hummingbirds increased sugar-water intake in spring compared to winter (Harris-Haller and Harris 1991). In contrast, New Zealand householders reported non-migratory urban birds visiting sugar-water feeders mostly in winter (Erastova *et al.* 2021). Another study comparing wider bird feeding practices between Northern and Southern Hemispheres showed a geographical difference in how birds use feeders (Reynolds *et al.* 2017). Thus, there is likely variability in the behaviour of birds interacting with sugar-water feeders in different climates.

Foraging-associated aggressive behaviour of nectarivorous birds has been studied primarily around natural nectar sources in urban and rural areas (Wolf 1978; Rasch and Craig 1988; Armstrong 1992a; Waite 2013). A few studies have demonstrated the dominance of resident birds over non-residents or migrants, dominance of males over females, and adults over juveniles in Mexican hummingbirds and New Zealand honeyeaters (Bergquist 1989; Roper 2012; Nuñez-Rosas and Arizmendi 2019). Finally, studies on hummingbirds in Brasilia and nectarivorous species in South Africa showed that sugar-water feeders affected avian communities by increasing species diversity of some populations (Sonne *et al.* 2016; Coetzee *et al.* 2018).

Here we determine how backyard sugar-water feeding affects foraging and aggressive behaviour of New Zealand nectarivorous birds. We investigated: (a) climatic and seasonal differences in sugar-water consumption and associated aggressiveness by comparing bird behaviour in two cities with different climates (Auckland and Dunedin) in two different seasons (summer and winter); (b) the effect of sugar concentration on sugar-water consumption and aggressiveness by comparing gardens with different feeding regimes; and (c) the effect of sugar-water feeder presence on garden bird composition, by comparing bird counts before and six weeks after the installation of experimental feeders.

Methods

Study species and observed behaviours

We collected behavioural data on three nectarivorous species that are the most common visitors to sugar-water feeders in urban New Zealand (Erastova *et al.* 2021): tūī (Tui, *Prosthemadera novaeseelandiae*), korimako (New Zealand Bellbird, *Anthornis melanura*), and tauhou (Silvereye; *Zosterops lateralis*). Additionally, we collected behavioural data on the House Sparrow (*Passer domesticus*), a generalist introduced species that we previously observed drinking from sugar-water feeders (Erastova *et al.* 2021).

We recorded foraging and aggression occurring at or near sugar-water feeders (Supplemental material 1). Each record reflected a single behavioural action conducted by a single observed individual bird. We included the following behaviours in the analysis: (1) 'Feeder visitation' resulting in sugar-water consumption (which species visited and their numbers). (2) 'Time spent foraging' or the duration of sugar-water consumption. We quantified foraging duration by recording start and stop time using multiple electronic stopwatches (one for each visiting bird). (3) 'Direct fight', physical altercation between individuals. (4) 'Dislodge', the displacement of another visiting individual. For behaviours 3–4, we recorded the species that won or lost the encounter. (5) 'Indirect aggression', which included threat displays and territorial song.

Study sites

We studied bird behaviour in two types of urban backyards: (1) gardens with already existing non-standardised sugar-water feeders with various sugar concentrations (termed 'pre-existing feeders'), and (2) gardens with newly established standardised feeding stations with controlled sugar concentrations (termed 'experimental feeders'). We recruited participants by word-of-mouth and social media, targeting organisations involved in scientific research and conservation. We visited all properties offered for the study (n_{total} = 33) before recruitment to assess suitability. Criteria for including the garden in the study included: the ability to conduct behavioural observations; sufficient vegetation at least 1.5 m high on at least one boundary; a minimum lawn/open backyard area of 20 m^2 with an unobstructed view; and situated at least 100 m away from any multi-lane roads and highways. All study properties were more than 500 m apart to reduce the probability of repeat counts of the same birds.

Pre-existing feeders

To understand bird behaviour patterns at sugar feeders that have been in place for some time, we visited gardens with pre-existing feeders in suburban Dunedin (n = 8) and suburban Auckland (n = 8), New Zealand (Supplemental material 2), between November 2018 and September 2019. We chose the two cities as climatic extremes of urban centres, but they also differ in the presence of korimako (absent in Auckland). Auckland (36°50′54"S, 174°45′48"E) is the largest city on the North Island, with a human population density of 2,400/km^2 in 2020 (New Zealand Census data, www.stats.govt.nz). Auckland has an oceanic warm temperate climate with a mean annual temperature of 15.5°C; Tmax = 22.9°C in February and Tmin = 9.5°C in July; and mean annual precipitation of 1,114 mm (https://en.climate-data.org). Dunedin (45°52′27″S, 170°30′13″E) is the second-largest city (>100,000 people) on the South Island and is the furthest south, with a human population density of 420/km^2 in 2020 (New Zealand Census data, www.stats.govt.nz). Dunedin has an oceanic mild temperate climate with a mean annual temperature of 9.7°C; Tmax = 17.7°C in January and Tmin = 2.5°C in July; and mean annual precipitation of 806 mm (https://en.climate-data.org).

Experimental feeders

To understand the effect of sugar concentration on bird activity, we recruited gardens with no previous sugar-water feeding history in Auckland (n = 17) between August and November (austral spring) 2019 and June and September 2020 (austral winter). We chose winter and early spring months to increase the likelihood that our target species would visit feeders, as our previous research shows sugar-water feeders are visited more often in colder months (Erastova *et al.* 2021, 2022). We recruited these gardens using the same method described for the pre-existing gardens. In 2019, we used 14 gardens, however, two householders subsequently opted out, and we recruited another three properties, resulting in a total of 15 for winter 2020 (Supplemental material 3). Additional criterias for inclusion were that there should not be a pre-existing feeder and that householders would reliably follow the study's experimental guidelines (sugar concentration and cleaning regime).

Experimental feeding regime

An earlier study (Erastova *et al.* 2021) showed that most New Zealand households use ½ or 1 cup of sugar per 1 litre of water for bird feeding. This amount can roughly be translated into 10% and 20% sugar solution, respectively, which corresponds to the range of nectar concentrations in native New Zealand plant flowers visited by nectarivorous birds (Gaze and Clout 1983; Ladley *et al.* 1997). Experimental gardens were randomly assigned into two treatment groups: feeding with 10% or 20% concentration glucose sugar-water (n = 7 and n = 7 in 2019; n = 7 and n = 8 in 2020, respectively). All volunteers started feeding birds simultaneously with their allocated treatment using Tui Nectar Feeder™ (the most widespread type, based on Erastova *et al.* 2021), following instructions provided. We asked all householders to clean their feeders by washing them with hot water and soap twice a week (based on Erastova *et al.* 2021). At the end of the experiment, all householders stopped feeding on the same day.

Behavioural observations

Pre-existing feeders

To identify seasonal and climatic behavioural patterns, we conducted a series of direct behavioural observations in Auckland and Dunedin gardens in the austral summer 2018/19 and winter 2019. We visited each study site twice: for 1 hour in summer and 1 hour in winter on fine days without heavy rain or strong winds, between 0700 h and 1100 h local time when birds forage most actively (n = 8 hours per each season in each city, n_{total} = 32).

Experimental feeders

The experiment in Auckland gardens began in August 2019 and finished in late November 2019, with no success in attracting birds to feeders, hence we repeated the experiment from June to mid-September 2020. In 2020, we conducted a series of direct behavioural observations to compare behavioural patterns in gardens with different sugar concentrations. There were 6 hours of observations per garden but only where birds visited feeders (n_{total} = 72 hours). For each hour of observation, we recorded ambient temperature using MetService app (https://www.metservice.com/).

Bird counts

We conducted bird counts in Auckland experimental gardens in the winter of 2020. We used a standard 5-minute bird count technique (Dawson and Bull 1975) based on a similar study of bread and seed feeders in Auckland (Galbraith *et al.* 2016), and recorded the maximum numbers of each species seen at a time. All counts took place in the morning hours when birds are most active (between 0700 h and 1100 h local time). We conducted counts over three consecutive clear days to visit all properties within this timeframe. We avoided rainy or windy mornings. We completed one round of initial counts at each property before installing the feeders, followed by fortnightly counts once the experimental feeding started (n_{total} = 105).

Camera data

Motion-activated camera data complemented the direct observations to determine how rapidly the feeders attracted various species and how often birds were visiting. We installed cameras 1–2.5 m away from feeding stations at the height of 1.5–2 m with an unobstructed view of the feeder. In 2019, we used the Browning Dark Ops Pro XD Trail Camera, and in 2020 we used Bushnell 16MP Trophy Cam HD Essential E3 cameras. Cameras recorded in photo mode from 20th August till 15 November 2019 and in hybrid photo/video mode continuously from 1st June till 15 September 2020. We analysed all the photos (120,500) and videos (13,700) manually and recorded the detected species, bird number and behaviour.

Statistical analysis

Pre-existing gardens

To test for city differences in behaviour (feeder visitation, time spent foraging at feeders (s), and aggressiveness) in pre-existing gardens for all study species combined, we built a series of generalised linear mixed models (GLMMs). Each model included the following fixed effects: city (Auckland/Dunedin), season (winter/summer), pre-existing sugar concentration as reported by the householders (a continuum ranging from 3.6% to 25%), interactions between city and concentrations, and between city and season. To test whether or not birds use the sugar-water feeder and whether or not we observed any aggressive behaviour, we used a logistic model (yes/no), while a negative binomial error distribution provided the best fit and residuals for the amount of time spent foraging.

To test for species-specific differences in feeder-associated behaviour, we built another set of GLMMs, with the same response variables. However, the model included species, season, sugar concentration, species × concentration, and species × season interactions as fixed effects. Each model included garden ID as a random effect.

Experimental gardens

Tauhou visited only three of the newly established experimental feeders, House Sparrow did not use them and korimako are absent from Auckland, where the experimental gardens were established. Thus, we only had sufficient data for tūī analyses. To test the effects of sugar concentration on tūī behaviour (sugar-water consumption, time spent foraging (s) and aggressiveness), we built a set of GLMMs. Each model included temperature, season (winter, spring), experimental sugar concentration (10%, 20%), and interaction between season and concentration as predictors. For the probability of feeder use and aggressiveness display, we used a logistic model, while a negative binomial error distribution provided the best fit for the time spent foraging. Models included garden ID as a random factor. We used simple linear regression analysis to test whether low *vs.* high sugar concentration affected tūī presence before and after feeder installation in the experimental gardens.

To assess whether there was a difference in numbers of native nectarivorous birds before and after feeder installation or in gardens with various sugar concentrations, we calculated average bird numbers (as a percentage of all counts) for each week of observations.

We performed all statistical analyses in R 3.6.2. We built GLMMs using *lme4* package (Bates *et al.* 2014). We used *stargazer* package (Hlavac 2018) for the summary result tables, and visualised results using *ggplot2* (Wickham 2017).

Results

Bird species at feeders

Tūī were recorded at feeders in the largest number of gardens (87% of all studied gardens), followed by korimako (75% of Dunedin gardens). Tauhou was the most frequent feeder visitor in pre-existing gardens (75% of all the gardens, 93% of all sugar-water foraging records). In experimental gardens, tauhou visited only one-third of the feeders (24% of all records). The House Sparrow used feeders at a third of the pre-existing study sites (31% of the gardens), but we never observed it using experimental feeders. We occasionally observed other non-nectarivorous introduced species perching on experimental feeding stations but never consuming sugar-water: Eurasian Blackbird (*Turdus merula*), Song Thrush (*T. philomelos*), and Common Myna (*Acridotheres tristis*).

City and seasonal effects on feeding

City comparison

Although, birds visited feeders in pre-existing gardens more often in winter compared to summer in both

Table 1. Results from the generalised linear mixed model (GLMM) testing the effects of location (Auckland, Dunedin), season (summer, winter), and sugar concentrations (a continuum of values) on bird behaviour in pre-existing gardens. Significant values shown in bold at: P < 0.10; * P < 0.05; ** P < 0.01. Parameter estimates (β) and their lower (LCL) and upper confidence limits (UCL) are shown at the reference levels stated in brackets, along with chi-square test statistics from likelihood ratio tests.

		Feeder visitation				Time at feeder (s)				Aggression		
		logistic				*negative binomial*				*logistic*		
	β	LCL	UCL	X^2	β	LCL	UCL	X^2	β	LCL	UCL	X^2
Intercept	−0.267	−2.22	1.71	0.08	2.537	0.21	4.76	0.07	4.778	1.79	7.64	0.28
City (Dunedin)	0.160	−1.82	2.11	0.14	**−0.217**	**−2.16**	**1.77**	**0.13**	**−1.825**	**−4.01**	**0.49**	**0.44**
Season (summer)	**−1.432**	**−3.59**	**0.89**	**0.13**	**−0.928**	**−2.95**	**1.22**	**0.13**	**−0.823**	**−2.81**	**1.24**	**0.21**
Concentration	**0.034**	**−1.93**	**1.99**	**0.01**	**0.023**	**−1.94**	**1.98**	**0.01**	**−0.102**	**−2.06**	**1.86**	**0.02**
City (Dunedin) x season (summer)	**0.394**	**−1.59**	**2.34**	**0.18**	**0.935**	**−1.11**	**2.92**	**0.17**	−0.504	−2.46	1.49	0.34
City (Dunedin) x Concentration	**−0.014**	**−1.97**	**1.95**	**0.01**	**−0.022**	**−1.98**	**1.94**	**0.01**	**0.177**	**−1.79**	**2.13**	**0.03**
Observations		6,444				3,323				6,444		
Log Likelihood		−4,339.610				−12,211.270				−938.605		
Theta						0.803						
						0.018**						
Akaike Inf. Crit.		8,691.221				24,434.530				1,889.209		

cities, some regional behavioural differences were evident in the comparison of the two cities with different climates (Table 1). Birds in Auckland used higher sugar concentration feeders more often than low concentration ones across all seasons (Supplemental material 4). In contrast, in Dunedin, they used high sugar concentration feeders more often in summer and low sugar concentration feeders more often in winter. In both cities, aggressiveness was more likely to be observed in winter compared to summer (raw means: winter = 89.87, summer = 16.62). However, in Auckland, the occurrence of aggression was lower across the seasons compared to Dunedin (raw means: Auckland = 19.89, Dunedin = 23.37). At feeders with high sugar concentration, aggression increased in Dunedin but decreased in Auckland. The time spent at feeders was consistently higher in Auckland than in Dunedin (observed mean Auckland = 16.92, Dunedin = 10.32). In Dunedin, the time spent at feeders was stable across the seasons, while in Auckland, this time varied, reaching its maximum in winter (Supplemental material 4). The time spent at feeders increased with the increase in sugar concentration in Auckland, while in Dunedin, the trend was the opposite (Table 1).

Frequency of feeder visits

In pre-existing Auckland gardens, tauhou and tūī visited feeders more often in winter (Table 2), with tauhou being the most frequent visitor. Higher sugar concentration increased the probability of tauhou feeder visitation but decreased the probability of tūī visitation (Table 2). There was no seasonal effect on how often the House Sparrow visited feeders; however, they used feeders with higher sugar concentrations more often (Supplemental material 5). In Dunedin, only season had a significant effect on feeder visitation, with tauhou consuming sugar-water at feeders more often in winter than summer (Table 2).

Aggression

In pre-existing Auckland gardens, aggressiveness at feeders varied in relation to sugar-water concentration and season. While tūī showed no difference in aggression levels across seasons, tauhou were significantly more aggressive in winter compared to summer (Table 2). The likelihood of tauhou aggressiveness was lower at higher concentration feeders, while for tūī the likelihood of aggression increased proportionally to sugar concentration (Supplemental material 5). In Dunedin, the likelihood of aggression was higher for tauhou in winter and tūī, and korimako at high sugar concentrations feeders (Table 2).

Tūī won more aggressive contests (75%) than any other species (54% for korimako; 46% for tauhou. Species varied in how often they demonstrated different types of aggression: tauhou most often displayed 'dislodge' (54% of all observed aggressive interactions in Auckland and 57% in Dunedin), while tūī most often displayed 'indirect aggression' (84% in Auckland; 61% in Dunedin).

Time spent at feeders

In Auckland, tauhou spent more time at feeders in winter compared to tūī (Table 2; Supplemental material 5), and increased their foraging time if sugar concentration was higher, although the effect was small (effect size, ES = 0.2). In Dunedin, tauhou spent less time foraging at feeders than any other species (insignificant, ES = −1.79), while tūī spent less time at higher sugar concentrations feeders than tauhou (insignificant, ES = 0.006).

Table 2. Results the GLMM testing the effects of the season (summer, winter), species (tauhou, tūī), and sugar concentrations (a continuum of values) on feeder-associated behaviour in Auckland and Dunedin pre-existing gardens. Garden ID is a random factor. Significant values shown in bold at: P < 0.10; * P < 0.05; ** P < 0.01. Parameter estimates (β) and their lower (LCL) and upper confidence limits (UCL) are shown at the reference levels stated in brackets, along with chi-square test statistics from likelihood ratio tests.

		Feeder visitation		Time at feeder (s)		Aggression	
		logistic		*negative binomial*		*logistic*	
		Auckland	Dunedin	Auckland	Dunedin	Auckland	Dunedin
Intercept	β	**−1.795**	−0.768	**3.273**	**4.015**	**−2.571**	−1.149
	LCL	**−3.89**	−2.74	**1.07**	**1.71**	**−4.64**	−3.15
	UCL	**0.39**	1.25	**5.41**	**6.26**	**−0.45**	0.92
	X^2	**0.35**	1.06	**0.72**	**1.06**	**0.44**	1.03
Tauhou	β	**1.232**	1.315	−1.692	−1.789	**2.898**	0.054
	LCL	**−1.34**	−1.31	−3.78	−3.90	**−0.94**	−1.92
	UCL	**3.56**	3.70	0.50	0.42	**6.87**	2.00
	X^2	**0.36**	1.06	0.73	1.06	**0.45**	1.04
Tūī	β	**1.564**	−1.36	1.311	−0.017	0.571	1.008
	LCL	**−1.24**	−3.78	−0.70	−1.98	−1.60	−1.41
	UCL	**4.16**	1.29	3.29	1.94	2.55	3.18
	X^2	**0.45**	1.25	0.78	1.24	0.54	1.18
Season (summer)	β	−0.201	**−0.976**	0.151	−0.390	−0.025	0.808
	LCL	−2.14	**−3.04**	−1.83	−2.34	−1.98	−1.36
	UCL	1.79	**1.26**	2.09	1.64	1.93	2.82
	X^2	0.28	**0.43**	0.33	0.30	0.33	0.46
Concentration	β	0.045	0.061	−0.108	−0.078	0.053	0.007
	LCL	−1.92	−1.90	−2.06	−2.03	−1.91	−1.95
	UCL	2.00	2.02	1.86	1.89	2.01	1.97
	X^2	0.02	0.05	0.05	0.05	0.03	0.05
Tauhou x season (summer)	β	**−1.012**	0.651	−0.907	0.111	**−1.954**	**−1.962**
	LCL	**−3.05**	−1.42	−2.92	−1.85	**−4.33**	**−4.34**
	UCL	**1.16**	2.63	1.23	2.06	**0.59**	**0.59**
	X^2	**0.33**	0.47	0.37	0.33	**0.54**	**0.51**
Tūī x season (summer)	β	**−2.142**	1.533	−1.126	0.561	1.078	−1.117
	LCL	**−4.60**	−0.83	−3.19	−1.49	−1.12	−3.18
	UCL	**0.49**	3.73	1.09	2.53	3.12	1.09
	X^2	**0.78**	0.63	0.80	0.44	0.43	0.63
Tauhou x concentration	β	**0.032**	−0.078	**0.197**	0.084	**−0.161**	0.022
	LCL	**−1.93**	−2.04	**−1.77**	−1.88	**−2.12**	−1.94
	UCL	**1.99**	1.89	**2.15**	2.04	**1.81**	1.98
	X^2	**0.02**	0.05	**0.05**	0.05	**0.026**	0.05
Tūī x concentration	β	**−0.107**	0.028	0.016	0.006	0.013	−0.003
	LCL	**−2.06**	−1.93	−1.94	−1.95	−1.98	−1.95
	UCL	**1.86**	1.99	1.98	1.96	1.97	1.97
	X^2	**0.03**	0.07	0.05	0.06	0.03	0.06
Observations		4,223	2,049	2,190	1,129	4,223	2,049
Log Likelihood		−2,631.43	−1,389.15	−8,246.69	−3,800.16	−2,245.90	−1,294.66
Theta				0.740	1.200		
				0.021**	0.051**		
Akaike Inf. Crit.		5,280.879	2,796.306	16,511.380	7,618.321	4,509.812	2,607.320

Effect of sugar concentration on tūī

In experimental gardens, tūī visited low sugar concentration feeders more often in spring and high concentration feeders (20%) more often in winter (Table 3, Supplemental material 6). Tūī spent longer foraging at feeders at lower ambient temperatures in winter than in spring, but in both seasons they spent more time at low sugar concentration feeders (Table 3). Again, tūī were more likely to exhibit aggressiveness in winter compared to spring, at lower ambient temperatures, and more so in high sugar concentration (20%) gardens (Table 3). Finally, tūī had 1.3 times more wins than losses in hetero- and conspecific contests in the gardens with the low sugar concentration, and 1.6 times more wins in gardens with the high concentration

Species richness and abundance

There was considerable variation in how long it took birds to discover the experimental feeders, ranging from 1 to 14 weeks (Supplemental material 7). Tauhou used experimental feeders in three gardens; they were the first species to discover feeders in two of these gardens. Tūī used feeders in 12 out of 15 gardens. There were

Table 3. Results from GLMM testing the effects of the season (winter, spring) and sugar concentration (10%, 20%) on tūī behaviours (sugar-water consumption, time spent at feeder, and aggression) in experimental Auckland gardens. Garden ID is a random factor. Significant values are bold at: P < 0.10; *P < 0.05; **P < 0.01. Parameter estimates (β) and their lower (LCL) and upper confidence limits (UCL) are shown for each model at the reference levels stated in brackets, along with chi-square test statistics from likelihood ratio tests.

		Feeder visitation				Time spent on feeder (s)				Aggression		
		logistic				*negative binomial*				*logistic*		
	β	LCL	UCL	X^2	β	LCL	UCL	X^2	β	LCL	UCL	X^2
Intercept	−2.920	−5.32	−0.38	0.74	3.420	0.80	5.92	0.27	−0.534	−2.49	1.46	0.65
Temperature	**0.150**	**−1.82**	**2.10**	**0.05**	**−0.044**	**−2.00**	**1.92**	**0.02**	**−0.220**	**−2.17**	**1.76**	**0.05**
Season (winter)	−0.339	−2.29	1.68	0.32	**0.818**	**−1.36**	**2.83**	**0.12**	**2.082**	**−0.73**	**4.71**	**0.41**
Concentration (20%)	−1.147	−3.27	1.17	0.74	**−0.980**	**−3.04**	**1.26**	**0.23**	**1.316**	**−1.07**	**3.51**	**0.47**
Season (winter) x concentration	**1.938**	**−0.48**	**4.21**	**0.68**	0.498	−1.52	2.46	0.26	−1.082	−3.11	1.06	0.54
Observations		668				172				598		
Log Likelihood		−372.502				−685.666				−238.188		
Theta						2.708						
						0.322**						
Akaike Inf. Crit.		757.004				1,381.333				488.375		
Bayesian Inf. Crit.		784.030								514.737		
Garden variance		0.65				<0.001				0		

fluctuations in the average numbers of these native nectarivorous birds with no clear patterns between experimental treatments (10% vs. 20% sugar concentration), nor before and after installing the feeder (Supplemental material 8). Sugar concentration explained minimal variation in the relative abundance of tūī at the feeders before and after feeder installation ($R^2 < 0.1$; Figure 1).

Discussion

Species diversity at sugar-water feeders

Our research shows that in urban New Zealand, sugar-water feeders primarily attract native nectarivorous birds: korimako, tauhou and tūī, confirming householder observations published earlier (Erastova *et al.*

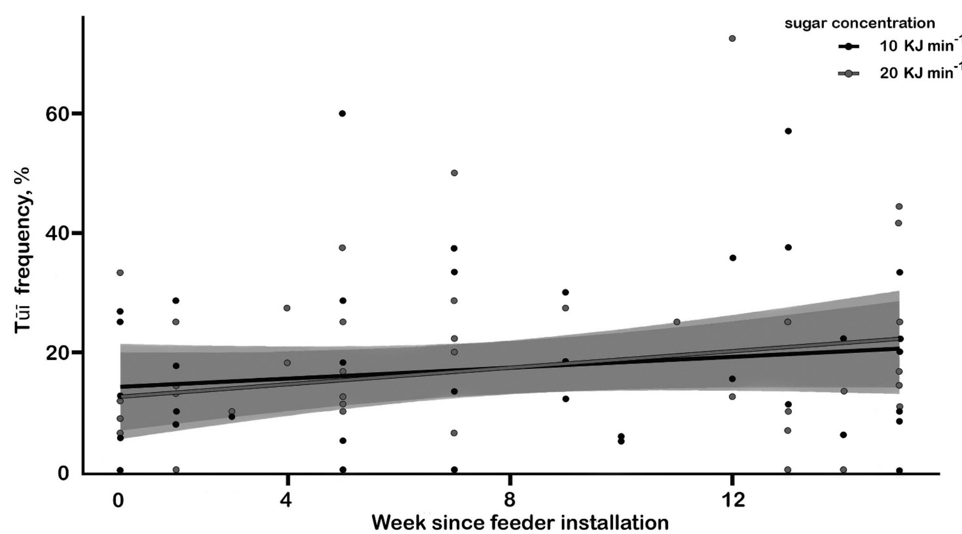

Figure 1. Simple linear regression for tūī presence frequency (as a percent of all birds recorded during 5-min bird counts) at sugar-water feeders with different sugar concentrations in experimental Auckland gardens in winter 2020. Error lines represent 95% confidence intervals; $R^2 < 0.1$; $P > 0.1$.

2021). Therefore, sugar-water feeding may be a good alternative to bread and seed feeding, which attracts only introduced generalist species and has a negative effect on riroriro (Grey Warbler, *Gerygone igata)*, a native insectivorous species (Galbraith *et al.* 2014, 2015).

We also observed generalist House Sparrows using feeders in the pre-existing feeder gardens in both cities. However, we never observed House Sparrows taking sugar-water from our experimental feeder type, a model explicitly designed for nectarivorous species, only allowing birds with long and slender bills to reach for food through narrow holes in the feeder cover. Erastova *et al.* (2021) showed that this type, and functionally similar, feeders are significantly more effective at attracting nectarivorous birds than generalist feeder types with uncovered access to sugar-water, such as open dishes.

Although the House Sparrow is primarily granivorous (Brzek *et al*. 2009), in New Zealand, this species has been observed foraging on flower nectar and even sugar packets (Ladley *et al*. 1997; Davy 2019). Other studies report House Sparrows consuming plant nectar (Leveau 2008; Cecere *et al*. 2011). The use of sugar-water feeders by House Sparrows could potentially impact native bird behaviour, but we did not observe any direct competition between House Sparrow and other species. Pathogen transmission might be another issue, as House Sparrows can carry avian poxvirus, *Salmonella* spp., and *Yersinia* spp., and could expose naïve native species to novel pathogens (Galbraith *et al.* 2017; Rouffaer *et al*. 2017; Erastova *et al*. 2022).

Seasonal trends

Our results show that nectarivorous species use sugar-water feeders and display aggression more in winter. It may reflect a lower availability of natural foods in urban areas during winter and consequent increased competition for supplementary food. However, species varied in how they visited feeders throughout the year. Tauhou showed extreme differences in sugar-water feeder visitation across the seasons, with visitation strongly associated with winter, similar to a trend reported in a previous New Zealand bread and seed feeding study (Galbraith *et al.* 2017). It could be due to tauhou's nomadic nature; this species tends to form migrating winter flocks and travel long distances searching for food (Kikkawa *et al.* 1986). Although known to travel far outside of the breeding season (Stewart and Craig 1985; Bergquist 1987; Fitzgerald 2019), tūī and korimako are highly territorial, and adults tend to remain near where they breed year-round and defend the food sources available there (Bergquist 1985, 1989). It may explain why there was less seasonal variation in the behaviour of honeyeaters.

Although previous research on nectar feeding in South Africa found no seasonal effect on the density of sunbirds (du Plessis *et al.* 2021), other studies have identified seasonal variation in sugar-water feeder use. Hummingbird feeder visitation increases in spring before the breeding season, but any effect of supplementary feeding on breeding has not been explored (Harris-Haller and Harris 1991). Long-term observations of Australian honeyeaters have demonstrated that sugar-water feeders are extensively visited in all seasons except when *Banksia ericifolia* is flowering, and although aggression at feeders is generally low, some species tend to defend this food source throughout the year (Armstrong 1992b).

Climatic trends

Our results show that nectarivorous species visited feeders more often and for longer time periods in Auckland's warmer and more humid climate. An American study identified that hummingbirds were more active at sugar-water feeders in humid tropical climates than in dry areas (Wethington *et al.* 2005). In our study, higher feeder usage in Auckland may also be related to differences in habitat and natural food availability. Auckland, which has a larger and denser human population, may provide fewer natural food options compared to Dunedin (van Heezik *et al.* 2008; Heggie-Gracie *et al.* 2020).

There were also regional differences in aggression, with tūī, in particular, being more aggressive in Dunedin. This difference could be explained by the presence of another relatively large nectarivorous species in Dunedin, korimako, which creates competition for tūī. We observed tūī actively chasing and attacking korimako, and to a lesser extent tauhou, around feeders. Korimako, in turn, actively chased tauhou away from feeders. This observed hierarchy is comparable to that found in relation to natural flower nectar (Craig 1985; Craig and Douglas 1986; Armstrong 1992a).

Effects of sugar-water concentration

Tūī spent more time taking sugar-water at feeders with a lower (10%) sugar concentration. Castro and Robertson (1997) showed that nectarivorous New Zealand species have different energetic requirements according to their body size: only 0.10 kJ min^{-1} for korimako, but 0.25 kJ min^{-1} for tūī. These authors concluded that a species with lower requirements (korimako) could benefit from selectively feeding on predominantly highly energetic sources (high sugar concentration nectar). At the same time, a species with higher requirements (tūī) cannot cover its energetic needs by selective feeding, and needs to forage also on low energetic sources (low sugar concentration nectar). If this is the case, prolonged tūī visitation to low sugar concentration feeders may represent non-selective feeding, as suggested by Castro and Robertson (1997). In addition, at all our experimental feeders, tūī had longer foraging bouts, and they were more aggressive at lower ambient temperatures, supporting our suggestion that birds must consume more calories for maintenance in colder times.

A factor that could have affected our results on observed differences in tūī behaviour was the presence of fruiting trees in three out of six experimental gardens with feeder with high sugar concentration. Towards the end of the experiment we observed tūī feeding extensively on flower nectar and fruit in these gardens, even when feeders were available and previously used. While some studies showed that certain species heavily rely on winter supplemental feeding (Reynolds *et al.* 2017), others show the lack of such dependency (Brittingham and Temple 1992; O'Leary and Jones 2006; Aichele *et al.* 2020; Lajoie at al. 2021). Our observations suggest a preference for high-value natural food over low-value sugar-water in tūī. However, further experimental research on food preferences in nectarivorous species would be required to test this (Tryjanowski *et al.* 2018).

Tūī tend to aggressively defend high-value natural food resources, specifically blossoming plants, and chase less dominant hetero- and conspecifics away (Bergquist 1985; Craig 1985). Our findings support this, with tūī showing greater aggression in experimental gardens with the higher sugar concentration (20%) feeders. However, in gardens with high sugar concentration feeders, we observed more individuals of other species not associated with sugar-water feeding being attacked by tūī (e.g. Eastern Rosella, *Platycercus eximius*). This higher occurrence of other species could occur by a mere chance.

There were other species-specific differences in sugar-water concentration preferences in Auckland and Dunedin. Several additional factors may drive these differences, such as climatic variations in ambient temperature. For instance, Dunedin experiences shorter summers and occasional snowfalls in winter (Census data, www.stats.govt.nz, accessed 28.08.2021). This may explain differences in birds' basic energetic needs in winter and increased energetic needs related to breeding in spring, hence the preference for lower or higher sugar concentration. Another factor could be the inconsistency in sugar types (white/glucose, brown/sucrose) the householders used in pre-existing gardens. Studies show that many nectarivorous and frugivorous birds have preferences for different sugar types at various concentrations in both flower nectar and feeders (Downs and Perrin 1996; Down 1997; Schondube and Del Rio 2003; Brown *et al.* 2008, 2010; Fleming *et al.* 2008; Franke *et al.* 2008; Napier *et al.* 2013). There is no information on sugar-type preferences in New Zealand nectarivores, and we suggest further research is required.

Species richness and abundance

Neither sugar-water feeder presence nor sugar concentration affected backyard species richness in this study. Of course, species composition and the presence of other feeders in the surrounding neighbourhood could have influenced the feeder discovery rate in our experimental gardens. Unfortunately, it was not possible to estimate the abundance of other feeders due to private property access issues. However, there was no correlation between high or low numbers in our bird counts and faster or slower feeder discovery rate. Unlike other countries with more diverse nectarivorous bird assemblages, where sugar-water feeders can impact species diversity in urban areas (du Plessis *et al.* 2021; Ramirez-Burbano *et al.* 2021), New Zealand has a relatively depauperate urban nectarivorous community, and therefore, changes in species numbers are unlikely. Another possible source of bias is the species detectability in winter gardens with feeders (Tryjanowski *et al.* 2015a,b). However, the focus species in this study are recognised as equally detectable in urban New Zealand (van Heezik and Seddon 2018; Heggie-Gracie *et al.* 2020).

Key factors reducing bird species richness and abundance in urban New Zealand are habitat loss leading to reduced natural food availability (Sullivan *et al.* 2009; van Heezik and Seddon 2018) and introduced mammalian pests acting as nest predators (Moorhouse *et al.* 2003; van Heezik *et al.* 2008; Innes *et al.* 2010). We conclude that in New Zealand, although urban sugar-water feeders attract native nectarivorous birds, they serve as a supplementary food source and do not increase the richness of urban nectarivorous communities.

Future directions

Given that sugar-water feeding attracts native species, an increased understanding of the impacts this practice might have on birds enables us to identify the associated risks (Robb *et al.* 2008b; Reynolds *et al.* 2017; Jones 2018; Donald *et al.* 2022). Future studies should explore other potential effects of sugar-water feeding on native birds, such as feeder-associated pathogens, supplementary food dependency, and whether using feeders decreases plant visitation by bird pollinators and seed dispersers.

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Data availability statement

Original datasets from this study are available at: https://figshare.com/articles/dataset/direct_behavioural_bird_observations_existing_sugar_water_feeders_Auckland_Dinedin_2018-2019/15153552; https://figshare.com/articles/dataset/direct_behavioural_bird_observations_experimental_sugar_water_feeders_Auckland2020/15133860; https://figshare.com/articles/dataset/Untitled_Itemgarden_bird_counts_experimental_suagr_water_feeders_Auckland_2019-2020/15133950; https://figshare.com/articles/dataset/experimental_sugar_water_feeders_camera_data_photo_Auckland_2019-2020/15133911; https://figshare.com/articles/dataset/experimental_sugar_water_feeders_camera_data_video_Auckland_2020/15133932.

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No potential conflict of interest was reported by the author(s).

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Geolocation information

This study was conducted in Auckland (36°50′54"S, 174°45′48"E) and Dunedin (45°52′27″S, 170°30′13″E), New Zealand.

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