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Artificial nectar feeders reduce sunbird abundance and plant visitation in Cape Fynbos adjacent to suburban areas

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ABSTRACT

Globally, people feed wild animals to interact with nature. Attracting nectarivorous birds to gardens using artificial nectar feeders is increasingly popular, yet little is known about its influence on birds and the plants they pollinate. We investigated effects of nectar feeders on African birds and their plant mutualists, by conducting feeding experiments in gardens and natural vegetation along the suburban edge of the Cape Peninsula, South Africa. We compared relative abundance and local distribution patterns of nectar-specialist, nectar-opportunist and non-nectarivore bird species between feeder and control treatments. We then tested whether nectar feeders in gardens affected visitation rates to two sunbird-pollinated *Erica* species in neighbouring vegetation compared to control sites. Nectar feeders increased the density of nectarivores (but not non-nectarivores) in gardens but decreased their density in neighbouring vegetation, even in winter when floral abundance was high. These changes in sunbird distribution patterns had no detectable influence on visitation rates to *E. abietina*, but decreased visitation to *E. plukenetii* flowers by on average 16% at least up to 300 m of gardens with feeders. Thus, although supplementary nectar feeding may have conservation value for nectarivorous birds by reducing their urban sensitivity, it can inadvertently interfere with bird-plant pollination networks by competing with native flowers for birds' attention.

1. Introduction

Exposure to nature can promote human wellbeing and overall health (Cox and Gaston, 2016; Taylor et al., 2018). For example, bird song may improve mental health (Ferraro et al., 2020). However, as humanity becomes increasingly urban and people concentrate in cities with impoverished biodiversity, there is progressive disengagement with the natural world (Seymour et al., 2020a). Disconnected individuals can be deprived of the wellbeing benefits associated with biodiversity. To mitigate this, there is a growing interest in creating wildlife-friendly urban areas (Maruyama et al., 2019; Meehan et al., 2020; Mnisi et al., 2021). In addition to establishing diverse native plant assemblages (Evans et al., 2009; Mnisi et al., 2021), people also use supplementary resources such as feeders and water baths to attract animals to gardens (Evans et al., 2009; Fuller et al., 2008). As a result, wild animal feeding has become one of the most common forms of wildlife interactions in many countries (Cox and Gaston, 2018).

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Wild bird feeding is a multi-billion-dollar industry, so widespread that it is effectively a global experiment (Jones and Reynolds, 2008), yet its implications for conservation are poorly understood (Galbraith et al., 2014). Whilst supplementary feeding can bring positive benefits in certain scenarios (Orros et al., 2015), there are also numerous potential negative consequences. At certain times, food provision allows persistence of species in an urban habitat mosaic (Thabethe and Downs, 2018) and can increase their reproductive success (Coetzee et al., 2020a, 2020b; Shutt et al., 2021). However, primary concerns include increases in avian disease transmission and predation risk around feeders (Reed and Bonter, 2018; Robb et al., 2008; Jones, 2011), and changes in the composition of bird communities, by favouring exotic species (Galbraith et al., 2015; Galbraith et al., 2017) or favouring species that make use of feeders (Shutt et al., 2021).

Artificial nectar feeders are used by many bird enthusiasts (Coetzee et al., 2018) and researchers (Inouye et al., 1991) in countries in which nectarivorous birds occur, but how these relatively novel urban food sources influence bird distributions within the landscape, and their ecological impacts, remain largely unknown. They can facilitate nectarivore presence in urban areas, allowing gardens to act as stepping stones between natural habitat fragments (Coetzee et al., 2018; Pauw and Louw, 2012). However, most flowering plants require animal pollinators (Ollerton et al., 2011), and nectar feeders could disrupt bird-plant pollination mutualisms if they attract birds away from the plants they pollinate, leading to reduced seed set in nearby populations. To date, the ecological impact of artificial nectar feeding has only been studied in the Americas, where nectar feeders are associated with significant increases in hummingbird and bat abundance (Arizmendi et al., 2007; Avalos et al., 2012; Brockmeyer and Schaefer, 2012; Greig et al., 2017; Maguiña and

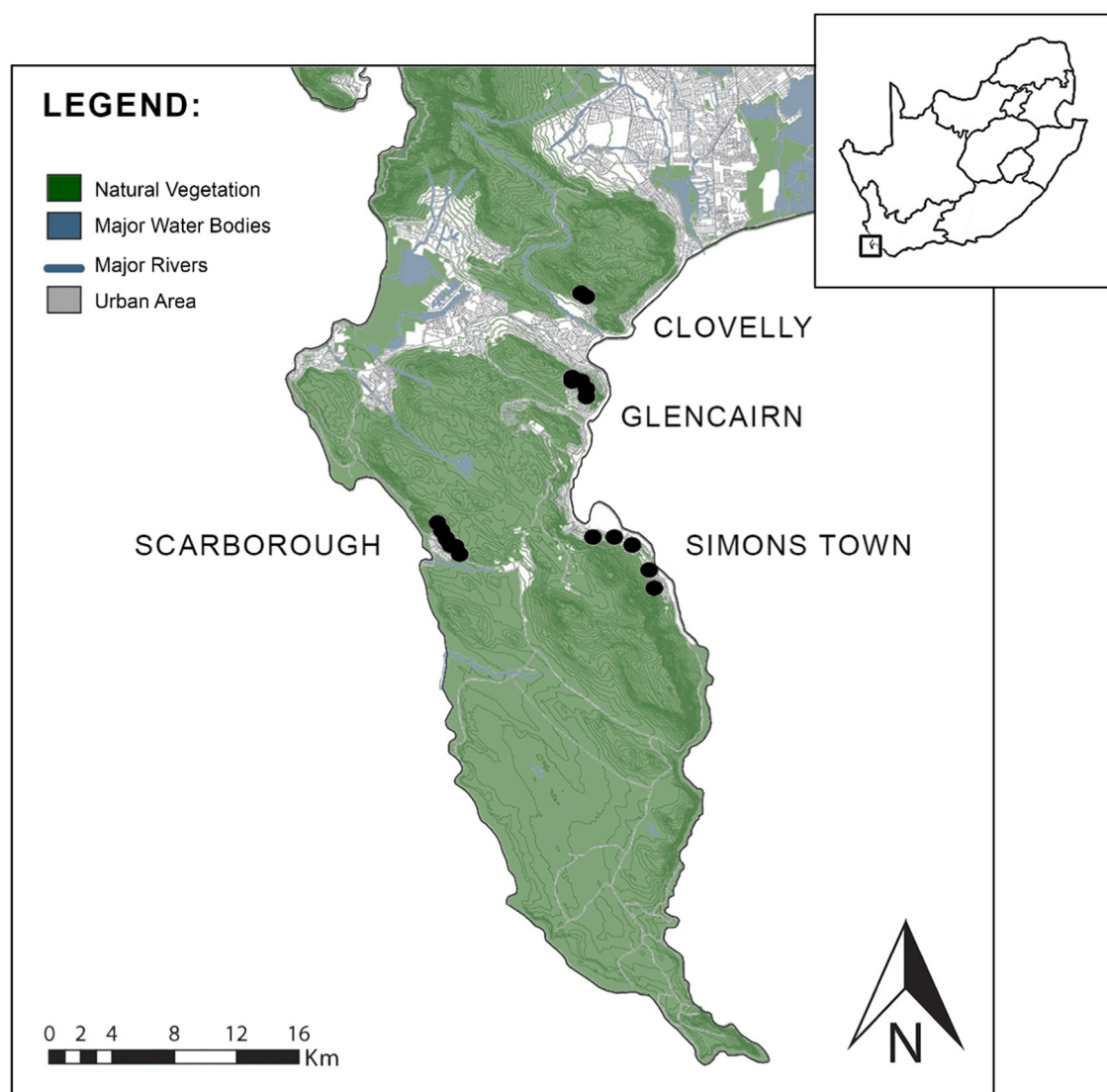


Fig. 1. Location of the 18 gardens (black dots) on the suburban edge included in this study in the Cape Peninsula (enlarged map) of South Africa (top right inset). Grey and white areas represent urbanized areas and green areas represent natural (non-transformed) areas of the Cape Peninsula. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Muchhala, 2017; McCaffrey and Wethington, 2008; Sonne et al., 2016). However, how this affects bird flower visitation in feeder vicinity remains debated.

In the Cape Floristic Region (CFR), a biodiversity hotspot on the southwestern tip of South Africa (Myers et al., 2000), bird pollination is key to many plant species primarily pollinated by just four nectar-specialist bird species (Rebelo, 1987). Although these birds are abundant in natural fynbos vegetation, the suburban environment of Cape Town, which extends onto the Cape Peninsula (Fig. 1) presents an almost impermeable barrier to the endemic orange-breasted sunbird *Anthobaphes violacea* and Cape sugarbird *Promerops cafer*, and reduces movement of the long-billed malachite sunbird *Nectarinia famosa* (Pauw and Louw, 2012). Only the short-billed southern double-collared sunbird *Cinnyris chalybeus* occurs throughout the urbanized landscape, but it is unable to successfully pollinate many of the longer-tubed flowers in this region (Geerts, 2016; Geerts and Pauw, 2009).

Nectar feeders also attract generalist species that include nectar in their diets (hereafter referred to as “nectar opportunists”). These species also generally contribute to pollination of flowers with floral structures more available to generalist bird pollinators (Arenas et al., 2013; Botes et al., 2008; Brown et al., 2009; Rebelo, 1987). Feeders may also indirectly affect birds that do not include nectar in their diets, for example through competition for nesting sites or food sources shared with nectar-opportunists (Galbraith et al., 2015; Orros et al., 2015). Therefore, to fully understand the effects of nectar feeders on bird and plant communities, all feeding groups should be assessed.

We carried out a feeding experiment using a matched pairs design along the urban edge of the Cape Peninsula to investigate whether artificial nectar feeders change bird distributions at local scales, and in so doing, affect bird visitation to local bird-pollinated plants. We conducted bird surveys in gardens and neighbouring vegetation to compare local bird abundance and relative distribution patterns of three avian feeding guilds (specialist nectarivores, nectar opportunists and non-nectarivores) between feeder and control treatments. These experiments were conducted in the wet winter when many plant species are flowering, and the dry summer, to test whether nectar feeders vary in attractiveness to birds with change in floral resource availability. Finally, we tested whether sunbird visitation rates to two co-occurring specialised sunbird-pollinated species, *Erica plukenetii* subsp. *plukenetii* L. and *Erica abietina* subsp. *atrorosea*, differ between feeder and control treatments, and with distance from gardens.

2. Methods

2.1. Study site

The Cape Peninsula, south of the city centre of Cape Town, South Africa (Fig. 1) falls within the Cape Floristic Region, a biodiversity



Fig. 2. A cluster of four plastic artificial nectar feeders was placed in the gardens. Each pair of feeders was mounted on a stick attached perpendicularly to an iron rod recessed into the ground. Birds perch on the sticks as they await their turn to feed. The transparent bottles were filled with a colourless 1:4 sugar to water solution and then attached to a red platform. The solution is channelled towards three feeding holes, large enough for larger-beaked nectar-opportunistic species to access the solution. A perch is located at each feeding hole to allow birds to rest as they feed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 3. Nectarivorous species feeding at artificial nectar feeders in gardens on the suburban edge of the Cape Peninsula. Nectar-specialist species: A) female Cape sugarbird *Promerops cafer*, B) male malachite sunbird *Nectarinia famosa*, C) male orange-breasted sunbird *Anthobaphes violacea*, and D) male southern double-collared sunbird *Cinnyris chalybeus*. Nectar-opportunistic species: E) southern masked weaver *Ploceus velatus*, F) Cape bulbul *Pycnonotus capensis*, G) male Cape weaver *Ploceus capensis*, and H) Cape white-eye *Zosterops virens*. Nectar feeders were filled with a colourless 1:4 sugar to water solution (Images by Monique du Plessis).

hotspot with thousands of endemic plant species (Holmes et al., 2012; Linder, 2005). Experiments took place in 18 gardens (17 for flower visitation experiments) across four suburbs (Scarborough, Simon's Town, Glencairn and Clovelly; Fig. 1), at least four kilometres apart, and where nectar feeders are often used (Coetzee et al., 2018). We selected gardens along the urban-natural vegetation edge, which includes a 10 m wide firebreak between garden and vegetation, and at least 250 m apart to increase chances of independence of visiting birds. Gardens bordering vegetation with healthy, mature *Erica* shrubs within 200 m were selected. Garden sizes varied between 52 and 650 m². Where nectar feeders were in use, these were removed at least one month prior to experiments. Floral abundance in gardens and vegetation was estimated as the total number of all healthy, mature flowers of any bird-pollinated species, not just the two focal *Erica* species in this study, or inflorescences (e.g., bird-pollinated *Protea* species).

2.2. Nectar feeders

To determine the effect of nectar feeders on bird distribution and *Erica* visitation, we conducted a seven-day experiment in which nectar feeders were present or absent, in a matched pairs design. Feeder treatments consisted of four feeders, mimicking bird-feeding habits of many garden owners, because it increases chances of detection by birds and reduces competition between birds for a single feeder. Feeders were filled with a 20% (weight/weight) sucrose solution, commonly used in feeders (Coetzee et al., 2020a), comparable to concentrations found in South African bird-pollinated plants (20–25% w/w) (Nicolson and Fleming, 2003). Feeders were placed in clusters close to a shrub or tree to provide perches (Fig. 2). Feeders were refilled regularly to ensure a continuous supply of sugar water throughout the experiment and cleaned thoroughly between trials to minimize pathogen transmission.

2.3. Birds

2.3.1. Bird species

Four specialist nectarivores are commonly found in our study area: *P. cafer* (Fig. 3- A), *N. famosa* (Fig. 3- B), *A. violacea* (Fig. 3- C), and *C. chalybeus* (Fig. 3- D). Amethyst sunbird *Chalcomitra amethystine* is scarce in our study area and was not recorded during this study. All bird species observed during surveys were categorized a priori as nectar-specialist, nectar-opportunist or non-nectarivorous



Fig. 4. Pollinator visitation rate was monitored for two *Erica* (Ericaceae) species common along the suburban edge of the Cape Peninsula, namely A) *Erica abietina* subsp. *atrorosea* and B) *Erica plukenetii* subsp. *plukenetii*. C) An unvisited *E. plukenetii* flower with an intact anther ring. D) A ruptured anther ring after a visit from an orange-breasted sunbird (Images by Monique du Plessis).

(Table A1) (Hockey et al., 2005).

2.3.2. Bird surveys

To assess effects of nectar feeders on small-scale bird distributions, birds were surveyed along a transect perpendicular to the garden/natural vegetation boundary: within the garden itself, and in three plots in neighbouring natural vegetation at approximately 50 m, 100 m, and 150 m from gardens. Surveys took place during the wet winter (from May to June, repeated in July 2019) and dry summer (November, repeated in December 2019) to determine whether the attraction of nectar feeders differed with season. When flower nectar is abundant in natural vegetation, nectar feeders may be less attractive (Inouye et al., 1991; McCaffrey and Wethington, 2008), and vice versa. Treatments were allocated to gardens randomly so that, initially, 10 of the 18 gardens received feeders, and eight did not. The following month, gardens received the opposite treatment.

An observer stationed at a single point that provided the widest view of the survey area counted all birds seen or heard over 20 min in 40 m x 40 m natural vegetation plots, and in gardens of different sizes. Garden sizes were measured and statistically controlled for in analyses. Bird abundance was recorded as the maximum number of individuals seen simultaneously within the restrictions of the garden or plot boundaries, to ensure that individual birds were not counted twice.

Bird surveys started on the fourth day after feeder placement, to allow birds to acclimatize to feeder presence. Surveys were repeated on the seventh day to reduce influence of circumstantial effects on bird activity, e.g., unfavourable weather conditions. We avoided surveying on very wet, hot ($> 30^{\circ}\text{C}$) or windy days (wind $> 11 \text{ m.s}^{-1}$), as measured using a hand-held Kestrel 3000 weather meter (Nielsen-Kellerman Co., Boothwyn, Pennsylvania). Unfavourable weather only occurred on one of our sampling days, and we therefore completed sampling on the next available day with appropriate weather. Bird surveys were conducted during peak bird activity hours in the mornings (one to four hours after sunrise) and afternoons (from four hours before sunset) (Collins and Briffa, 1983).

2.4. Flowers

2.4.1. Flowering species

Erica species (Ericaceae) are primary food sources for nectarivorous birds. Approximately 15% of the 680 *Erica* species are considered bird-pollinated (Rebelo et al., 1985) and the relatively short-billed *A. violacea* is their main pollinator.

We assessed flower visitation to the two most common bird-pollinated *Erica* species (*Erica plukenetii* subsp. *plukenetii* and *Erica abietina* subsp. *atrorosea*) co-flowering on the suburban edge during peak flowering (winter: May and June) (Fig. 4A and B). Both species produce inflorescences with long, tubular corollas, typical of bird pollination (Rebelo et al., 1985). *E. abietina* subsp. *atrorosea* is endemic to the Cape Peninsula and flowers from midsummer to early spring (December to August). *E. plukenetii*, which flowers predominantly in winter in our study area (March to September), is common in montane fynbos in the western CFR (Goldblatt and Manning, 2000).

2.4.2. Visitation rate

Erica visitation rate experiments were only conducted during winter because flowers were scarce in summer. Flowers on these species tend to last for multiple days, but at one of the 18 sites, all *Erica* flowers died during the seven days of the experiment and that site was therefore excluded from analysis. Feeders were present in 10 gardens at these sites, the remaining 7 gardens had no feeders. At each site, we assessed *Erica* visitation rate in natural vegetation bordering gardens, noting distances of these patches from gardens, up to 300 m from the firebreak. One to six *Erica* plants (depending on their abundance) were selected in each of two to six patches ($10 \times 10 \text{ m}$). We used flower anther status as a proxy for visitation rates (Geerts and Pauw, 2011). Before a visit, *Erica* anthers are fused into a ring (Fig. 4C), but birds' probing beaks rupture the anther rings, releasing pollen (Fig. 4D) (Rebelo et al., 1985; Schumann et al., 1992). Proportion of total flowers visited per plant was quantified one day before nectar feeders were placed in gardens and again seven days after feeders had been placed in gardens.

2.5. Statistical analyses

2.5.1. Bird abundance analysis

We analysed the three feeding guilds, and also the specialist nectarivore species separately. We constructed Generalized linear mixed models (GLMM) for each dataset. We set bird abundance as the response variable, and treatment, distance, and season as predictor variables. Wind speed, floral abundance, time of day, presence of previous feeder and pets were set as control variables and garden identity as a random factor (see Table A2 for details). We tested whether presence of feeders changed bird abundances of specialist nectarivore species and birds in each feeding guild. This effect may, however, differ with distance from urban edge and/or season, which enables a possibility of up to a three-way interaction between treatment, distance, and season. We used a model selection approach to assess the relative importance of these three variables by comparing separate models encompassing all possible interactions between these three variables, including a three-way interaction and various two-way interactions, along with the remaining control variables. We corrected for differences in size of area surveyed by including logarithm of plot/garden size as an offset. The presence of feeders in neighbouring gardens within a 150 m radius from our study gardens had no significant effect on bird abundance and was therefore excluded from further analysis.

The lme4 package (Bates et al., 2014) was used to fit Poisson models and the glmmTMB package (Brooks et al., 2017) for negative binomial models, both using a log link function. An observation-level random effect was included in Poisson models to correct for

overdispersion (Browne et al., 2005). Candidate models were ranked using Bayesian Information Criterion (BIC) and BIC weights (w_i) with the MuMIn package to penalize the number of parameters more strongly, given large sample sizes. Thereafter, effect sizes were calculated as the difference between means ($\Delta\mu$) with 95% confidence intervals (provided in square brackets with $\Delta\mu$) using the emmeans package (Lenth, 2020). Confidence intervals that did not include zero were considered statistically meaningful.

We tested for overdispersion and zero inflation (DHARMA package, Hartig 2019), and used an information-theoretic approach using differences in corrected Akaike Information Criterion (AICc) (Burnham et al., 2011) to identify the most appropriate error structures.

2.5.2. Visitation rate analysis

The two *Erica* species were analysed separately, and linear mixed-effects models were fitted for each species separately. The main goal in this study was to test whether different treatments (feeder vs. control) resulted in different visitation rates to *Erica* flowers and whether this effect differed with distance from the feeders. We considered visitation as proportion of flowers visited per plant at the beginning of the experiment subtracted from the proportion of flowers visited at the end of experiment. Negative values were occasionally produced when flowers died, or new flowers bloomed during the seven days. Floral abundance in each patch and the presence of previous feeders in gardens did not significantly predict *Erica* visitation rate in the full model and so were excluded from the final model. Site was modelled as a random intercept effect to account for multiple sampling of plants per site. Patch ID was not included as a random factor in the final models because the proportion of variance explained by this variable was zero. A weights term was included in models as the square root of the number of flowers on each plant, to give more weight to plants with more flowers as these provided a more robust estimate of visitation rate.

To compare treatment groups and determine the magnitude of the effect on visitation rate, effect sizes were calculated the same way as described above.

2.5.3. Model assessment

All data exploration and analyses were conducted in R 3.6.1 (R Core Team, 2019). To assess model fit, we plotted histograms of normalized residuals and plotted them against fitted values. Variance Inflation Factors (VIFs) showed that none of the predictor variables had strong relationships (VIFs < 3). Variance explained by fixed and fixed and random effects were calculated by deriving marginal (R^2_m) and conditional pseudo- R^2 values (R^2_c), respectively, using the r.squaredGLMM function in the MuMIn package (Barton, 2019; Nakagawa and Schielzeth, 2013). In all models, garden identity was included as a random intercept to account for multiple sampling per site. All continuous response variables were standardized to comparable scales.

3. Results

3.1. Bird surveys

Nectarivorous birds, including all four nectar-specialist species, visited artificial nectar feeders within at least four days across all study sites. In a total of 564 bird surveys, we recorded 499 nectar-specialist birds in gardens (383 with feeders, 116 without feeders) and 1 110 in natural vegetation plots (528 adjacent to feeder treatments, 582 adjacent to controls).

3.1.1. Nectar-specialists

Feeders affected relative abundance and local distribution of nectar-specialists: the best model included interactions of treatment-distance and season-distance (see Table A3 for full model set & Table A5 for detailed statistics: $w_i = 99\%$, $R^2_m = 0.48$, $R^2_c = 0.88$). Nectar feeders attracted higher densities of nectar-specialists towards gardens (Fig. 5: mean bird density (μ) = 1.02 bird/log(m²); gardens without feeders (μ = 0.31)) and had more birds than the neighbouring 50 m vegetation plots (difference in mean densities ($\Delta\mu$) = - 0.12). Feeders were also associated with reduced density of nectar-specialists in natural vegetation: sums of average bird densities in the three vegetation plots ($\Sigma\mu$) were lower for feeder ($\Sigma\mu$ = 1.01) than controls ($\Sigma\mu$ = 1.15). For controls, nectar-specialist densities were greater in 50 m vegetation plots and declined into gardens ($\Delta\mu$ = - 0.12). Season had no effect on density of nectar-specialists, despite higher floral abundance in natural vegetation during winter (sum of mean number of flowers/inflorescences in vegetation plots: winter = 4 206; summer = 867).

3.1.2. Species-specific responses

When the four nectar-specialist species were considered individually, feeders affected each species differently: a model including a treatment-distance interaction and separate species-distance interaction best explained abundance of nectar-specialists (Tables A4 and A6: $w_i = 98\%$, $R^2_m = 0.35$, $R^2_c = 0.72$). Densities of all four species were greater in gardens with feeders than gardens without (Fig. 6). The treatment-distance interaction shows that with feeders, bird densities were greater in gardens than in neighbouring vegetation, whereas the inverse was true for gardens without feeders, except for *C. chalybeus*, which occurred at greater densities in gardens than natural vegetation regardless of feeder presence.

The significant species-distance interaction demonstrates that the four species followed different distribution patterns along the suburban edge, for both feeders and controls. When feeders were absent, *P. cafer* was the most abundant species in gardens (Fig. 6: mean bird density (μ) = 0.13 bird/log(m²)), followed by *C. chalybeus* (Fig. 6: μ = 0.10), and least abundant were *A. violacea* and *N. famosa* (Fig. 6: μ = 0.04 for both species). When feeders were present, however, *C. chalybeus* was the most abundant species in gardens (μ = 0.31), followed by *P. cafer* (μ = 0.25) and *N. famosa* (μ = 0.25), and lastly *A. violacea* (μ = 0.22).

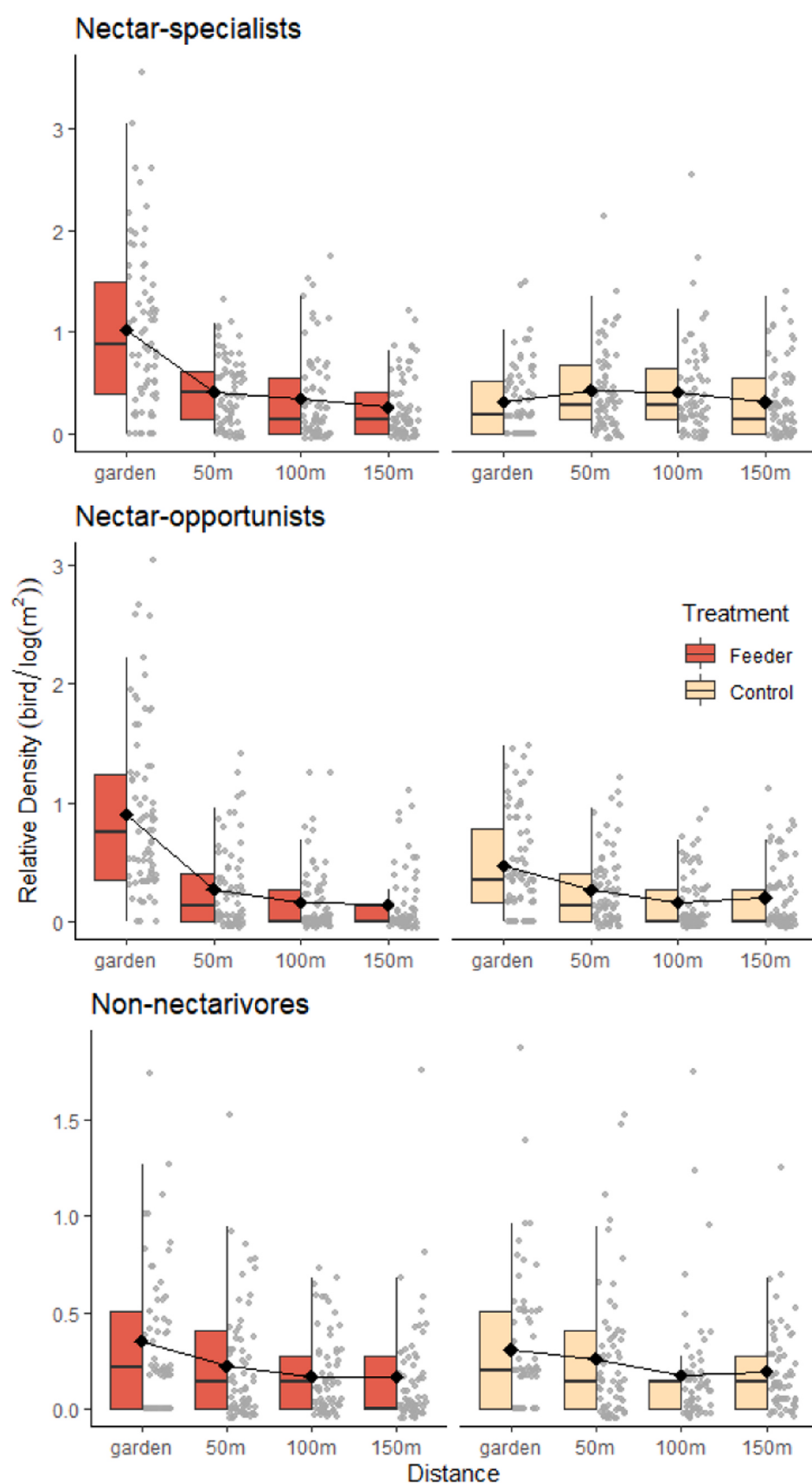


Fig. 5. Relative densities (bird/log(m²)) of three avian feeding guilds in gardens and three survey plots in neighbouring natural vegetation along the urban edge of the Cape Peninsula, for both feeder and control treatments, during winter and summer 2019. Within each jittered scatterplot, a grey dot represents total bird density observed during a survey. Box plots show variations in relative bird density, black diamonds indicate mean bird density (μ), and vertical lines indicate error bars around the mean. Grey dots positioned outside the error bars are considered outliers. Note the y-axis scale varies with feeding guild.

When feeders were present, *C. chalybeus* densities followed the steepest increase from 50 m natural vegetation plots into gardens (Fig. 6: $\Delta\mu = 0.23$). Their densities were also greater in gardens compared to natural vegetation plots, even when feeders were absent. In contrast, there were few *A. violacea* birds in gardens when feeders were absent, and their densities declined dramatically from 50 m vegetation plots into gardens ($\Delta\mu = -0.12$). Despite this, nectar feeders attracted higher densities of *A. violacea* to gardens ($\mu = 0.22$) compared to controls ($\mu = 0.04$), and to any survey plot in neighbouring natural vegetation. Similarly, few *N. famosa* birds visited gardens without feeders, although they were also rare in natural vegetation plots, at least up to 150 m from the suburban edge. Feeders not only increased *N. famosa* densities in gardens, but also increased their densities in the 50 m natural vegetation plots, whereas overall densities of other species decreased in natural vegetation plots. Changes in *P. cafer* densities and distribution patterns with feeders were less marked compared to the other species, but still significant.

3.1.3. Nectar-opportunists

Nectar feeders affected relative abundance and local distribution of nectar-opportunistic species: the best model included the treatment-distance interaction (Tables A3 and A5: $w_i = 77\%$, $R^2_m = 0.67$, $R^2_c = 0.71$). Nectar-opportunists were more common in gardens than natural vegetation regardless of feeder presence (Fig. 5), although feeders had greater densities (mean bird density (μ) = 0.90 bird/log(m²)) than gardens without feeders ($\mu = 0.46$), and feeders slightly decreased densities in natural vegetation plots (sum of average bird densities in vegetation plots: feeders: ($\Sigma\mu = 0.57$); controls: ($\Sigma\mu = 0.62$)). These effects did not differ with season.

3.1.4. Non-nectarivores

Feeders did not influence local abundance or distribution of non-nectarivorous bird species, since an effect of feeders was not included in the best model for bird abundance (Fig. 5, Tables A3 and A5: $w_i = 83\%$, $R^2_m = 0.41$, $R^2_c = 0.77$).

3.2. Visitation rate

Feeders in gardens affected visitation to *E. plukenetii*. On average, birds visited 16% fewer flowers at feeder versus control sites during the experiment ($\Delta\mu = -0.16$ [− 0.31; − 0.01], $R^2_m = 0.01$, $R^2_c = 0.01$; Fig. 7 and Table A7). The distance-treatment interaction was not significant, suggesting the effect of feeders on *E. plukenetii* visitation extended up to at least 300 m. In contrast, feeders had no significant effect on visitation for *E. abietina* ($\Delta\mu = 0.21$ [− 0.35; 0.77], $R^2_m = 0.04$, $R^2_c = 0.11$). The relatively small sample size for *E. abietina* ($n = 69$ plants), which was sampled towards the end of its flowering period, may have prevented detection of an effect, compared to peak-flowering *E. plukenetii* ($n = 153$ plants).

4. Discussion

We undertook the first experimental test of possible ecological effects of nectar feeders on an African bird-pollination system. We found altered local distributions of nectarivorous birds (but not non-nectarivores) along the suburban edge of the Cape Peninsula, South Africa, regardless of season. This reduced bird visitation rates to *Erica plukenetii*, although not to *E. abietina*.

4.1. Bird abundance and distribution

Consistent with studies on hummingbirds and bats, nectar feeders affected relative abundance (Brockmeyer and Schaefer, 2012; McCaffrey and Wethington, 2008; Sonne et al., 2016) and small-scale distributions (Avalos et al., 2012) of nectar-specialists. Unlike previous studies, however, we found no seasonal differences. Nectar-specialists were expected to rely less heavily on artificial feeders during the wet winter, when floral abundance is greater than during the dry summer. Instead, nectar feeders seem to decouple the relationship between nectarivorous bird density and abundance of their floral resources, by attracting more birds to gardens compared to flowers in natural vegetation, even when flowers were abundant.

Given that nectarivorous bird abundance and diversity are strongly correlated to nectar volume at small spatial scales (Geerts et al., 2020), it is not surprising that birds are attracted in high numbers to feeders. Feeders offer large and predictable quantities of food, compared to the dispersed and variable source offered by flowers (Coetzee et al., 2020a). Artificial sugar water used in feeders is generally similar in concentration and nutritional value to flower nectar. Although artificial feeders lack minerals, amino acids, and microbes that natural flower nectar contains, these are usually in small quantities and probably merely supplement nutrition obtained by feeding on insects (Leseigneur et al., 2007). Thus, birds can efficiently gain their required carbohydrates at feeders, although competition around nectar sources may reduce this advantage.

Aggregation of high densities of birds around feeders may have negative consequences for birds by increasing avian disease transmission (Lawson et al., 2018) and predation risk (Robb et al., 2008). Given that pets occur at far higher densities than natural predators (Seymour et al., 2020b), gardens with feeders may act as sinks if predation by pets is high. Conversely, we could speculate

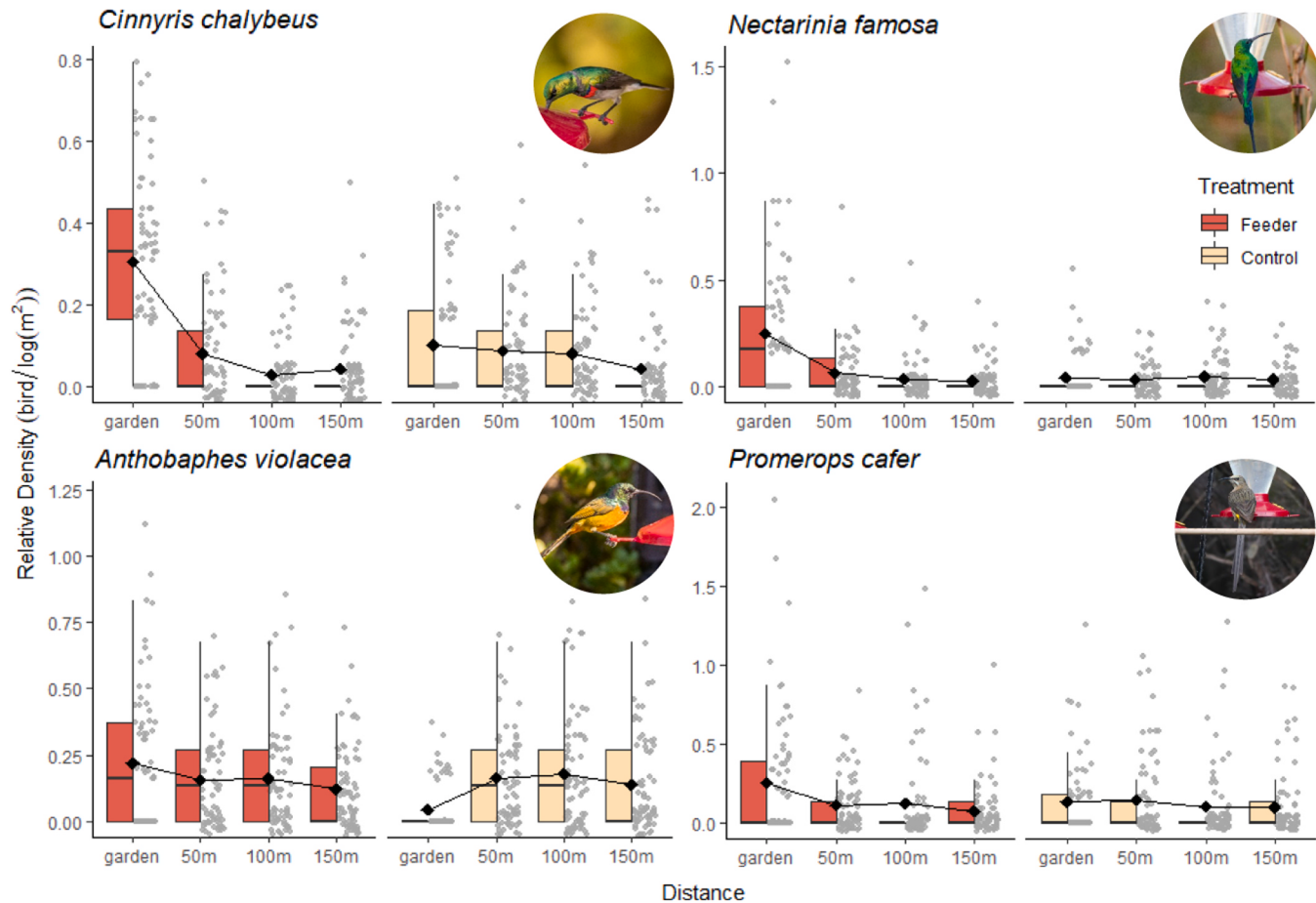


Fig. 6. Relative densities (bird/ $\log(m^2)$) of four nectar-specialist species in gardens and three survey plots in neighbouring natural vegetation along the urban edge of the Cape Peninsula, for both feeder and control treatments, during winter and summer 2019. Within each jittered scatter plot, a grey dot represents total bird density observed during a survey. Box plots show variations in relative bird density, black diamonds indicate mean bird density (μ) at each survey plot, and vertical lines indicate error bars around the mean. Grey dots positioned outside the error bars are considered outliers. Note the y-axis scale varies with species.

that feeders could support birds after fire: sunbirds and sugarbirds flee post-fire environments, relocating to unaffected habitat (Geerts et al., 2012), but fragmented landscapes can limit their movement. Neighbouring suburban gardens potentially provide shelter and food for nectarivores immediately after fire.

4.1.1. Nectar-specialists

Nectar feeders affected abundance and distribution patterns of all four nectar-specialist species. *C. chalybeus* was abundant in suburban gardens regardless of feeder presence, confirming their more generalist habits (Pauw and Louw, 2012). Nevertheless, nectar feeders attracted them in even greater numbers to gardens, decreasing their densities in natural vegetation.

In contrast, *N. famosa* rarely occurred in gardens and natural areas up to 150 m from the suburban edge when feeders were absent. Long-tubed flowers, that usually contain more nectar and are preferred by *N. famosa* (Geerts and Pauw, 2009), were rare in these areas and more abundant higher in the mountains. Feeders increased *N. famosa* densities not only in gardens, but also natural areas close to the suburban edge. Thus, feeders may draw this species in from greater distances, facilitating their presence in and near gardens, but at the cost of luring them away from natural areas farther away. Future studies could clarify the distance over which feeders may influence bird behaviour, given that feeders can attract hummingbirds over distances of 3 km (Avalos et al., 2012).

A. violacea was only in gardens with feeders, confirming that although sensitive to suburban environments (Pauw and Louw, 2012), feeders can overcome their aversion to gardens. Feeders decreased their densities in neighbouring natural vegetation, though less drastically than that of *C. chalybeus*. Longer-term exposure to feeders could possibly reveal a more conspicuous pattern.

P. cafer is also considered sensitive to urban areas (Pauw and Louw, 2012), but were the most abundant nectar specialists in gardens when feeders were absent. This may be because many gardens in this study contained bird-pollinated Proteaceae shrubs to which *P. cafer* is tightly linked (Geerts et al., 2020). Nevertheless, feeders further increased sugarbird densities in gardens, though not as markedly as for the other species. This is possibly attributable to their highly territorial behaviour (Calf et al., 2003) which could limit the number of individuals around a highly valued resource.

4.1.2. Nectar-opportunists

Although opportunistic nectarivores preferred gardens over natural habitat irrespective of nectar feeder presence, feeders increased their abundance in gardens, and slightly decreased their densities in natural vegetation in both winter and summer. Thus, nectar feeders could also affect pollination services of plant species pollinated by opportunistic nectarivores (such as *Aloe* spp., (Brown et al., 2010)).

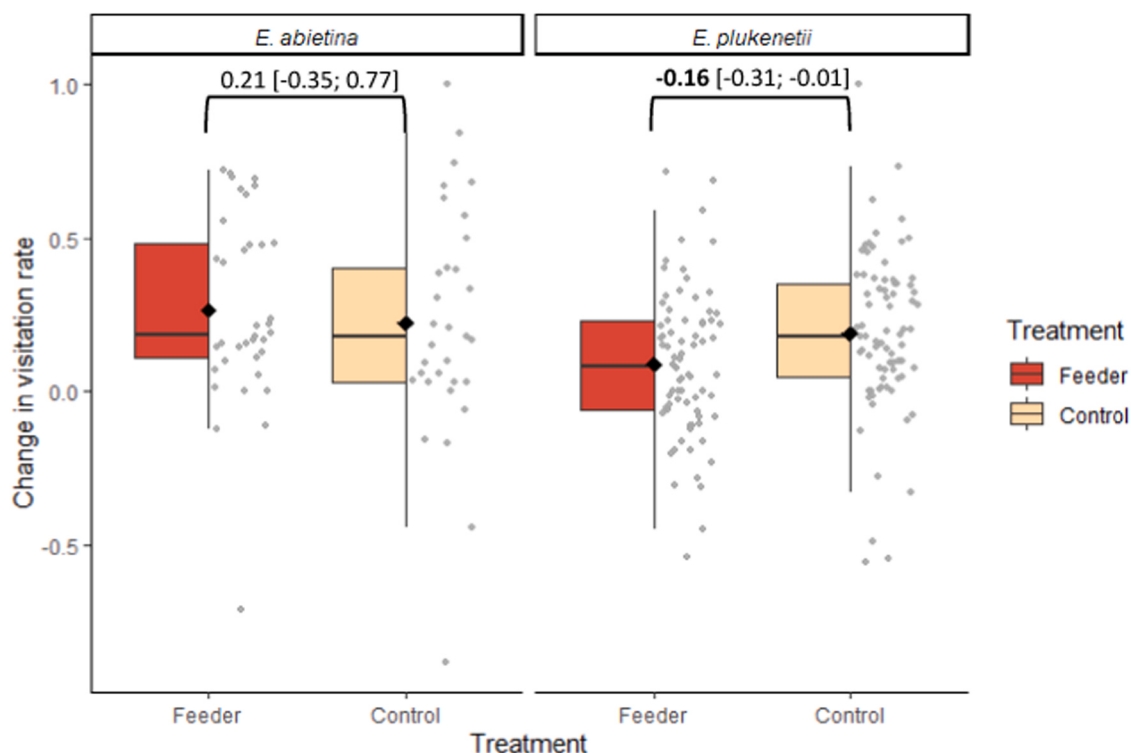


Fig. 7. Visitation rate to *E. abietina* and *E. plukenetii* flowers before and after a seven-day feeding experiment along the suburban edge of the Cape Peninsula for feeder and control treatments. Grey dots represent the difference between the proportion of flowers visited on an individual plant before and after the feeding experiment. Black diamonds indicate mean visitation rates and points outside the error bars are considered outliers. Unstandardized effect size is given as the difference between means of the treatment groups, with 95% confidence intervals in brackets.

4.1.3. Non-nectarivorous

Studies on nectar feeders seldom consider their effects on non-nectarivorous bird species. We found no significant effect of feeders on non-nectarivores in the short periods (one week) over which our experiments were run. However, it may be that over longer periods non-nectarivores could be negatively affected by increased abundance of nectarivores associated with feeders, owing to increased competition for non-nectar resources like nesting sites or other food sources.

4.2. Visitation rates

Experimental addition of nectar feeders negatively influenced bird visitation to *Erica plukenetii* flowers, an effect that did not vary with distance and was still detectable at 300 m. Reduced visitation rates likely translate into reduced seed set, since *E. plukenetii* relies on sunbird pollination (Arendse et al., 2021; Botha, 2017; Coetzee et al., 2020b).

This finding is consistent with two previous studies on hummingbirds (Arizmendi et al., 2007; Avalos et al., 2012) but contrasts with other studies which found neutral or positive effects of feeders on plant reproductive fitness (Brockmeyer and Schaefer, 2012; Sonne et al., 2016). These opposing results may be partly explained by duration of feeder availability. Feeders were present for only 7 days in this study, and only one day in Arizmendi et al. (2007), but present for several years in Brockmeyer and Schaefer (2012) and Sonne et al. (2016). Long-term exposure to nectar feeders could provide enough time for nectarivorous birds to form dominance hierarchies around feeders. As dominant individuals monopolize feeders, subordinate individuals may find surrounding flowers increasingly attractive, neutralizing the initial negative effect. Feeders may also increase “carrying capacity” of areas by supplementing available food sources, although Avalos et al. (2012) found that permanent feeder presence continued to disrupt pollination processes of hummingbird-pollinated species.

Unlike *E. plukenetii*, *E. abietina* experienced no detectable change in sunbird visitation. Our small sample size for *E. abietina* makes for large confidence intervals, which likely indicate a high level of uncertainty, and could mask a true effect of feeders on visitation. Alternatively, absence of an effect on *E. abietina* may reflect that it is a preferred food source at the site (Fig. A1), owing to its higher nectar concentrations (Fig. A2: $\Delta\mu = 5.85$, [3.77; 7.95]).

Our study focussed on long-tubed *Erica* species, but other plant families may also be affected by nectar feeders. Feeders not only influenced abundance and distribution of *A. violacea* (the main pollinator of *Erica* species), but also that of the two long-billed nectar-specialist species. *P. cafer* pollinates many Proteaceae, and *N. famosa* is the exclusive pollinator of many Iridaceae and Amaryllidaceae species (Geerts and Pauw, 2009). Furthermore, feeders also affected opportunist nectarivores, which pollinate several other plant species.

5. Conclusion

Nectar feeders facilitated crossing of urban-sensitive nectarivores into suburbia. From the perspective of enhancing biodiversity in city regions, attracting nectarivorous birds with nectar feeders may appear to be positive, increasing the capacity of suburban areas to support avian pollinators. However, nectar feeders altered local distribution ranges of nectarivores, regardless of floral abundance in neighbouring vegetation. This altered the visitation rates to at least one of two bird-pollinated species we considered, possibly with consequences for seed set.

Studies from a wider range of plant species and human-nature contexts could assess the generality of these effects, particularly for vulnerable plant species with specialized pollination systems. It would also be useful to determine which traits of plant species make them vulnerable to negative impacts of nectar feeders. Construction of pollinator networks (e.g., Simba et al., 2018) would allow identification of how plant and bird networks are affected by presence of nectar feeders, and which species are most impacted. Longer-term studies could determine whether prolonged exposure to nectar feeders have additional fitness consequences for bird communities (e.g., health and reproduction).

Despite remaining uncertainties regarding supplementary feeding, this study highlights the importance of considering its unintended effects on surrounding environments. Seemingly inconsequential human activities like attracting birds with feeders is unlikely to threaten entire plant populations but could exacerbate existing anthropogenic pressures on pollination systems at city edges, effectively reducing the size of neighbouring protected areas. This may be of particular concern in biomes where many endangered endemics and rare plants occur close to urban areas (Rebello et al., 2011) and numerous plants depend on birds for their reproductive success. However, these potential ecological effects should be considered along with the social value of supplementary feeding as a tool to connect people to nature (Jones and Reynolds, 2008; Seymour et al., 2020a).

Declaration of Competing Interest

All authors confirm that there is no conflict of interest in execution of this study or its submission to Global Ecology and Conservation.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01706](https://doi.org/10.1016/j.gecco.2021.e01706).

References

- Arena, G., Symes, C., Witkowski, E.T.F., 2013. The birds and the seeds: opportunistic avian nectarivores enhance reproduction in an endemic montane aloe. *Plant Ecol.* 214, 35–47.
- Arendse, B., Johnson, S.D., van der Niet, T., Midgley, J.J., 2021. Breeding systems and pollen-ovule ratios in *Erica* species (Ericaceae) of the Cape Floristic Region. *Int. J. Plant Sci.* 182, 151–160.
- Arizmendi, M.d.C., Constanza, M.S., Lourdes, J., Ivonne, F.M., Edgar, L.S., 2007. Effect of the presence of nectar feeders on the breeding success of *Salvia mexicana* and *Salvia fulgens* in a suburban park near Mexico City. *Biol. Conserv.* 136, 155–158.
- Avalos, G., Soto, A., Alfaro, W., 2012. Effect of artificial feeders on pollen loads of the hummingbirds of Cerro de La Muerte, Costa Rica. *Rev. Biol. Trop.* 60, 65–73.
- Thabethe, V., Downs, C.T., 2018. Citizen science reveals widespread supplementary feeding of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa. *Urban Ecosyst.* 21, 965–973.
- Barton, K., 2019. Mu-MIn: Multi-model inference, R package version 1.43.15.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.
- Botes, C., Johnson, S.D., Cowling, R.M., 2008. Coexistence of succulent tree aloes: partitioning of bird pollinators by floral traits and flowering phenology. *Oikos* 117, 875–882.
- Botha, P.W., 2017. The World Without Birds: An Experimental Test of the Ecological Significance of Pollinating Birds for Plant Communities (Doctoral dissertation). Stellenbosch University, Stellenbosch.
- Brockmeyer, T., Schaefer, H.M., 2012. Do nectar feeders in Andean nature reserves affect flower visitation by hummingbirds? *Basic Appl. Ecol.* 13, 294–300.
- Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400.
- Brown, M., Downs, C.T., Johnson, S.D., 2009. Pollination of the red hot poker *Kniphofia caulescens* by short-billed opportunistic avian nectarivores. *S. Afr. J. Bot.* 75, 707–712.
- Brown, M., Downs, C.T., Johnson, S.D., 2010. Concentration-dependent sugar preferences of the Malachite Sunbird (*Nectarinia famosa*). *Auk* 127, 151–155.
- Browne, W.J., Subramanian, S.V., Jones, K., Goldstein, H., 2005. Variance partitioning in multilevel logistic models that exhibit overdispersion. *J. R. Stat. Soc. Ser. A Stat. Soc.* 168, 599–613.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, 23–35.
- Calf, K.M., Downs, C.T., Cherry, M.I., 2003. Territoriality of cape sugarbirds (*Promerops cafer*) between and within breeding seasons. *Ostrich* 74, 125–128.
- Coetzee, A., Barnard, P., Pauw, A., 2018. Urban nectarivorous bird communities in Cape Town, South Africa, are structured by ecological generalisation and resource distribution. *J. Avian Biol.* 49, jav-01526.
- Coetzee, A., Barnard, P., Pauw, A., 2020a. Reliability and quality of artificial nectar feeders for birds in the Cape Floristic Region. *Ostrich* 92, 26–31.
- Coetzee, A., Spottiswoode, C.N., Seymour, C.L., 2020b. Post-pollination barriers enable coexistence of pollinator-sharing ornithophilous *Erica* species. *J. Plant Res.* 133, 873–881.
- Collins, B.G., Briffa, P., 1983. Seasonal and diurnal variations in the energetics and foraging activities of the brown honey eater, *Lichmera indistincta*. *Aust. J. Ecol.* 8, 103–111.
- Cox, D.T.C., Gaston, K.J., 2016. Urban bird feeding: connecting people with nature. *PLoS One* 11, 0158717.
- Cox, D.T.C., Gaston, K.J., 2018. Human–nature interactions and the consequences and drivers of provisioning wildlife. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 373, 20170092.
- Evans, K.L., Newson, S.E., Gaston, K.J., 2009. Habitat influences on urban avian assemblages. *Ibis* 151, 19–39.
- Ferraro, D.M., Miller, Z.D., Ferguson, L.A., Derrick Taff, B., Barber, J.R., Newman, P., Francis, C.D., 2020. The phantom chorus: birdsong boosts human well-being in protected areas. *Proc. Biol. Sci.* 287, 20201811.
- Fuller, R.A., Warren, P.H., Armsworth, P.R., Barbosa, O., Gaston, K.J., 2008. Garden bird feeding predicts the structure of urban avian assemblages. *Divers. Distrib.* 14, 131–137.
- Galbraith, J.A., Beggs, J.R., Jones, D.N., McNaughton, E.J., Krull, C.R., Stanley, M.C., 2014. Risks and drivers of wild bird feeding in urban areas of New Zealand. *Biol. Conserv.* 180, 64–74.
- Galbraith, J.A., Beggs, J.R., Jones, D.N., Stanley, M.C., 2015. Supplementary feeding restructures urban bird communities. *PNAS* 112, E2648–E2657.
- Galbraith, J.A., Jones, D.N., Beggs, J.R., Parry, K., Stanley, M.C., 2017. Urban bird feeders dominated by a few species and individuals. *Front. Ecol. Evol.* 5, 81.
- Geerts, S., 2016. Can short-billed nectar thieving sunbirds replace long-billed sunbird pollinators in transformed landscapes? *Plant Biol.* 18, 1048–1052.
- Geerts, S., Pauw, A., 2009. Hyper-specialization for long-billed bird pollination in a guild of South African plants: the Malachite Sunbird pollination syndrome. *S. Afr. J. Bot.* 75, 699–706.
- Geerts, S., Pauw, A., 2011. Easy technique for assessing pollination rates in the genus *Erica* reveals road impact on bird pollination in the Cape fynbos, South Africa. *Austral Ecol.* 36, 656–662.
- Geerts, S., Malherbe, S.D.T., Pauw, A., 2012. Reduced flower visitation by nectar-feeding birds in response to fire in Cape fynbos vegetation, South Africa. *J. Ornithol.* 153, 297–301.
- Geerts, S., Coetzee, A., Rebelo, A.G., Pauw, A., 2020. Pollination structures plant and nectar-feeding bird communities in Cape fynbos, South Africa: implications for the conservation of plant–bird mutualisms. *Ecol. Res.* 35, 1–19.
- Goldblatt, P., Manning, J., 2000. Cape Plants: A Conspectus of the Cape Flora of South Africa. National Botanical Institute.
- Greig, E.L., Wood, E.M., Bonter, D.N., 2017. Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. *Proc. Biol. Sci.* 284, 20170256.
- Hockey, P.A., Dean, W.R.J., Ryan, P.G., Maree, S., Brickman, B.M., 2005. Roberts' Birds of southern Africa. The trustees of the John Voelcker Bird Book Fund, Cape Town.
- Holmes, P.M., Rebelo, A.G., Dorse, C., Wood, J., 2012. Can Cape Town's unique biodiversity be saved? Balancing conservation imperatives and development needs. *E&S* 17, art28.
- Inouye, D.W., Calder, W.A., Waser, N.M., 1991. The effect of floral abundance on feeder censuses of hummingbird populations. *Condor* 93, 279–285.

- Jones, D.N., 2011. An appetite for connection: why we need to understand the effect and value of feeding wild birds. *Emu* i–vii.
- Jones, D.N., Reynolds, S.J., 2008. Feeding birds in our towns and cities: a global research opportunity. *J. Avian Biol.* 39, 265–271.
- Lawson, B., Robinson, R.A., Toms, M.P., Risely, K., Macdonald, S., Cunningham, A.A., 2018. Health hazards to wild birds and risk factors associated with anthropogenic food provisioning. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 373, 20170091.
- Lenth, R., 2020. *emmeans: Estimated Marginal Means, aka Least-Squares Means*, R package version, 1, 3.
- Leseigneur, C.D.C., Verburgt, L., Nicolson, S.W., 2007. Whitebellied sunbirds (*Nectarinia talatala*, Nectariniidae) do not prefer artificial nectar containing amino acids. *J. Comp. Physiol. B* 177, 679–685.
- Linder, H.P., 2005. Evolution of diversity: the Cape flora. *Trends Plant Sci.* 10, 536–541.
- Maguiña, R., Muchhala, N., 2017. Do artificial nectar feeders affect bat-plant interactions in an Ecuadorian cloud forest? *Biotropica* 49, 586–592.
- Maruyama, P.K., Bonizário, C., Marcon, A.P., D'Angelo, G., da Silva, M.M., da Silva Neto, E.N., Oliveira, P.E., Sazima, I., Sazima, M., Vizentin-Bugoni, J., dos Anjos, L., 2019. Plant-hummingbird interaction networks in urban areas: Generalization and the importance of trees with specialized flowers as a nectar resource for pollinator conservation. *Biol. Conserv.* 230, 187–194.
- McCaffrey, R.E., Wethington, S.M., 2008. How the presence of feeders affects the use of local floral resources by hummingbirds: a case study from southern Arizona. *Condor* 110, 786–791.
- Meehan, T.D., Dale, K., Lebaron, G.S., Rowden, J., Michel, N.L., Wilsey, C.B., Langham, G.M., 2020. Interacting with hummingbirds at home: associations with supplemental feeding, plant diversity, plant origin, and landscape setting. *Landsc. Urban Plan.* 197, 103774.
- Mnisi, B.E., Geerts, S., Smith, C., Pauw, A., 2021. Nectar gardens on school grounds reconnect plants, birds and people. *Biol. Conserv.* 257, 109087.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142.
- Nicolson, S.W., Fleming, P.A., 2003. Nectar as food for birds: the physiological consequences of drinking dilute sugar solutions. *Plant Syst. Evol.* 238, 139–153.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326.
- Orros, M.E., Thomas, R.L., Holloway, G.J., Fellowes, M.D.E., 2015. Supplementary feeding of wild birds indirectly affects ground beetle populations in suburban gardens. *Urban Ecosyst.* 18, 465–475.
- Pauw, A., Louw, K., 2012. Urbanization drives a reduction in functional diversity in a guild of nectar-feeding birds. *E&S* 17, art27.
- R Core Team, 2019. *R: A language and environment for statistical computing*, R Foundation for Statistical Computing.
- Rebelo, A.G., 1987. Bird pollination in the Cape flora. In: Rebelo, A.G. (Ed.), *A Preliminary Synthesis of Pollination Biology in the Cape Flora*. CSIR, Pretoria, pp. 83–108.
- Rebelo, A.G., Siegfried, W.R., Oliver, E.G.H., 1985. Pollination syndromes of *Erica* species in the south-western Cape. *S. Afr. J. Bot.* 51, 270–280.
- Rebelo, A.G., Holmes, P.M., Dorse, C., Wood, J., 2011. Impacts of urbanization in a biodiversity hotspot: conservation challenges in Metropolitan Cape Town. *S. Afr. J. Bot.* 77, 20–35.
- Reed, J.H., Bonter, D.N., 2018. Supplementing non-target taxa: bird feeding alters the local distribution of mammals. *Ecol. Appl.* 28, 761–770.
- Robb, G.N., McDonald, R.A., Chamberlain, D.E., Bearhop, S., 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Ecol. Environ.* 6, 476–484.
- Schumann, D., Kirsten, G., Oliver, E.G.H., 1992. *Ericas* of South Africa. Fernwood Press, Cape Town.
- Seymour, C.L., Gillson, L., Child, M.F., Tolley, K.A., Curie, J.C., Da Silva, J.M., Alexander, G.J., Anderson, P., Downs, C.T., Egoh, B.N., Ehlers Smith, D.A., Ehlers Smith, Y.C., Esler, K.J., O'farrell, P.J., Skowno, A.L., Suleman, E., Veldtman, R., 2020a. Horizon scanning for South African biodiversity: a need for social engagement as well as science. *Ambio* 49, 1211–1221.
- Seymour, C.L., Simmons, R.E., Morling, F., George, S.T., Peters, K., Justin O'riain, M., 2020b. Caught on camera: the impacts of urban domestic cats on wild prey in an African city and neighbouring protected areas. *Glob. Ecol. Conserv.* 23, e01198.
- Shutt, J.D., Trivedi, U.H., Nicholls, J.A., 2021. Faecal metabarcoding reveals pervasive long-distance impacts of garden bird feeding. *Proc. Biol. Sci.* 288, 20210480.
- Simba, L.D., Foord, S.H., Thébault, E., van Veen, F.J.F., Joseph, G.S., Seymour, C.L., 2018. Indirect interactions between crops and natural vegetation through flower visitors: the importance of temporal as well as spatial spillover. *Agric. Ecosyst. Environ.* 253, 148–156.
- Sonne, J., Kyvsgaard, P., Maruyama, P.K., Vizentin-Bugoni, J., Ollerton, J., Sazima, M., Rahbek, C., Dalsgaard, B., 2016. Spatial effects of artificial feeders on hummingbird abundance, floral visitation and pollen deposition. *J. Ornithol.* 157, 573–581.
- Taylor, L., Hahs, A.K., Hochuli, D.F., 2018. Wellbeing and urban living: nurtured by nature. *Urban Ecosyst.* 21, 197–208.