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Gardening on oceanic islands: the non-native Great Kiskadee *Pitangus sulphuratus* as a potential seed disperser of the alien invasive *Murraya paniculata* in Bermuda

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Abstract - On vulnerable oceanic island ecosystems, non-native species may form novel mutualistic interactions with one another and foster establishment. On Bermuda, the omnivorous Great Kiskadee *Pitangus sulphuratus* was introduced to control the invasive Anolis lizard population, but feeds on many other species of plants and animals. Here we investigated whether the Kiskadee may act as an effective seed disperser of the introduced alien plant, the Orange Jessamine *Murraya paniculata*. In 2022 and 2023 we collected pellets regurgitated by Kiskadees, and found that 96% (N=26) contained Jessamine seeds. In 2023 we carried out an experiment to compare the germination rates of whole Jessamine fruits with manually de-fleshed seeds and those extracted from Kiskadee regurgitates. Across groups, Jessamine seeds germinated 52.6% of the time. We found only a non-significant tendency for de-fleshed seeds to germinate more often than seeds with flesh (67% vs 49%). Our study highlights that Kiskadee can act as an effective seed disperser of Jessamine in an oceanic island ecosystem.

Keywords: Alien species, Bermuda, Invasive species, Kiskadee, Mutualism, *Murraya paniculata,* Oceanic island*,* Seed dispersal

INTRODUCTION

Oceanic islands are fragile ecosystems highly vulnerable to biological invasions which can have irreversible effects on local biodiversity (Vitousek 1988). Although some introductions of alien organisms occur unintentionally, there are numerous cases in which species have been introduced deliberately. For example, alien species have been often used as biological controls of previously introduced non-native species (with high invasive potential) with the aim of rebalancing ecological relationships within a disturbed ecosystem (Hoddle 2004). However, in highly modified ecosystems such as islands, species introductions (deliberate or accidental) are disproportionately impactful (Elton 1958). Species that appear in new environments may not survive but some thrive and become invasive, competing for resources with/feeding on native (frequently endemic) species ultimately leading to their decline or extinction (Wood et al. 2017).

Furthermore, previously non-existent ecological interactions between alien species can be expected. For instance, in the context of interspecific reproductive mutualism, such as seed dispersal, frugivorous/omnivorous alien bird species have the potential to establish novel interactions with non-native invasive plants (Gleditsch et al. 2019) performing as primary dispersal vectors of their seeds. Such ecological processes may have profound impacts on community dynamics (Traveset & Richardson 2006, Aslan et al. 2013, Gleditsch et al. 2019).

The Bermuda Islands, in the western North Atlantic, is a system where native terrestrial flora and fauna have been severely impacted by human activity since settlers established in the early 1600s (Wolsak et al. 2018). The original vegetation of this remote oceanic island was composed of a dense evergreen forest where Bermuda cedar *Juniperus bermudiana*, Bermuda palmetto (*Sabal bermudana*), and few native shrub species dominated (Britton 1918). After colonisation, the landscape was rapidly altered through burning and deforestation (Wingate 1990) as well as through massive introductions of alien plants as casuarina trees *Casuarina equisetifolia* (CABI 2020) (Wolsak et al. 2018). Further plants were used for ornamentation in gardens and public parks including the Orange Jessamine *Murraya paniculata* (hereafter Jessamine). The Jessamine is a tropical and subtropical plant listed as invasive in many regions of the world (CABI 2020). In Bermuda it is listed as a Category II invasive species (Bermuda's Plantfinder: Invasive and Indigenous Plants 2016) that has increased in abundance and occurrence but so far without altering Bermuda's plant community. It is a shrub to small tree that can reach 3 m of height (Dodson & Gentry 1978) producing orange-red fleshy fruits several times per year. Jessamine can be spread by seed, stem cuttings and air-layering (National Parks Board, 2020) but according to Gilman (1999), propagation is easiest with seeds. The seeds of Jessamine are usually dispersed by birds and other animals that feed on their fruits (White et al. 2006, Pikart et al. 2011, PIER 2018).

Along with plants, Bermuda recorded important introductions of alien fauna (Sterrer 1998). An iconic example is represented by the Great Kiskadee *Pitangus sulphuratus* a passerine bird from the New World flycatcher family (Tyrannidae) with a native range that extends from Texas to Argentina, including the island of Trinidad (Brush & Fitzpatrick, 2002) from which 200 individuals were caught and introduced to Bermuda in the 1950s (Bennett and Hughes 1959, Crowell & Crowell 1976). Kiskadees were released to control *Anolis* lizards, especially Jamaican Anole *Anolis graham* that had been brought to Bermuda at the beginning of the 20th Century to control fruit flies which were damaging local crops. The biological control plan failed because Kiskadees did not feed on lizards as expected, instead they preferred other items including eggs and chicks of smaller species, fruits, berries and marine/brackish fishes (Latino et al. 1999). As a consequence, the Kiskadee population quickly spread across the islands and in 1976 it was estimated to have reached 60,000 individuals (Crowell & Crowell 1976) being at present among the most abundant terrestrial birds on the island (Mejias & Nol 2020).

Anecdotal accounts from Bermudian birdwatchers suggest Kiskadee may act as seed-disperser of berries and fruits of native and invasive plants including Jessamine. However, to date, there is no published evidence supporting such a hypothesis, nor do we know whether Kiskadees can perform as a dispersal vector of viable seeds. To fill this knowledge gap, in the present study we investigated the inclusion of Jessamine fruits in the Kiskadee diet collecting pellets (i.e. hard, undigested materials that were compacted in the digestive tract and later ejected, da Paz Pereira & Melo 2012) from two breeding pairs (but birds were not ringed) nesting in a private garden in different years. Furthermore, we designed and implemented a germination experiment (Fig. 1) to evaluate whether seeds from ingested fruits ejected by Kiskadees through pellets were still viable and able to germinate. Finally, we compared the germinability of seeds found in pellets with that of seeds from fruits collected directly from trees.

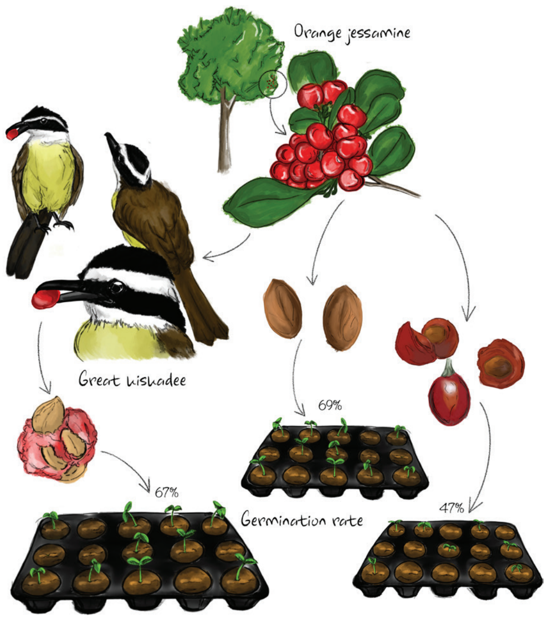

Figure 1. Overview of the experimental design we used to test whether Orange Jessamine *Murraya paniculata* seeds regurgitated by Great Kiskadee *Pitangus sulphuratus* germinated at the same rate as seeds naturally dispersed from trees. Model predicted germination rate averages are also shown. The illustration was produced by R. Reynaud.

MATERIALS AND METHODS

Study site and data collection

This study was carried out in the Bermuda Islands (western North Atlantic), which consist of more than 150 limestone islands with 5 main islands located along the southern margin of the Bermuda Platform. Bermuda is a low elevation subtropical island highly isolated from the continent, lying 1000 km from the coast of North America with an oceanic climate (Wolsak et al. 2018). It has an area of ca. 54 km^2 with the highest elevation point reaching 76 m. a.s.l. and with a total human population of 63,903 (2020), making Bermuda the two-hundredth most populous country in the world. The resident population is distributed within 9 parishes and Flatts Village, a small settlement, lying on the southern bank of Flatt's Inlet in Hamilton Parish (32° 19' 17.213"N, 64° 44' 10.464"W) is where data collection was conducted.

Data collection was carried out in 2022 and 2023. Between the 20th of January and the 10th of March 2022 we collected daily Great Kiskadee's pellets in a private garden, under a nest built within the garden and opportunistically at a dockyard (regurgitated on boats from unknown birds) within Flatts Village (i.e., 500 m from the private garden). The pellets were left on a tray for 3-4 days to ensure natural drying of the organic material present inside (Electronic Supplementary Material Fig. ESM1), then stored in paper bags. The bags were labelled including the following information: date and place of collection, observation on the state of the pellets (fresh/old, entire/fragments). Once in the laboratory, the pellets were opened by hand and the seeds therein were counted and stored in new paper bags. The seeds were identified through visual inspection and comparison with a small seed reference collection built when on the island. Most of the pellets contained seeds of the invasive plant Orange Jessamine that were used to set up a pilot germination experiment (Fig. ESM1). At the same time, we collected Jessamine fruits from a tree in a private garden in Flatts Village. Seed species and mean number of seeds found in pellets was calculated only for entire pellets (N=18).

In 2023, data collection was carried out between the 20th of January and 19th of February in the same private garden as 2022. We used the same protocol visiting the area under the nest which was built on a different palm tree each year (distance between palm trees ca. 21 m). Every day, in the morning and evening we checked and collected pellets found on the grass. This time Kiskadee pellets were much more fragmented, likely because of the tree branch they hit while falling. Therefore, in 2023 it was not possible to count the exact number of seeds in each pellet but we recorded the presence/absence of seed species.

Germination experiment (2023)

In 2023, the experiment was started on Feb 23rd when one seed was taken from each paper bag and sown, and concluded on May 7th. Six different experimental germination groups were used: Groups 1-5 were Jessamine seeds, and Group 6 were Fiddlewood *Citharexylum spinosum* seeds (another non-native invasive flowering plant). Seeds were planted with the flesh (1 & 3), after manual de-fleshing (2 & 4), or after removing from Kiskadee regurgitates ('bird de-flesh'; 5 & 6). Seeds were collected in two areas, either the 'nest area' (1, 2, 5, 6) or from a control area located several kilometres away from the 'nest area' (3 & 4). The nest area was a private garden where Kiskadees were observed nesting and feeding on Jessamine (only one tree present), and the control area was a separate garden with a Jessamine tree. Seeds were planted in two plastic germination trays, using Oris Universal Substrate (composed of composted forest matter, matured horse manure and sphagnum peat, >60% organic material, pH: 5.5-6.5). For each group, seeds were randomly selected, with a total of 57 planted. The trays were kept indoor, and out of direct sunlight, but were exposed to the natural light/dark regime (at 38.7° N latitude, Lisbon) and mean temperature of 18.8 °C (min-max 16-21 °C). Previous germination studies showed that different photoperiod regimes do not affect Jessamine germination rates (White et al. 2006). Seeds were initially watered with 7.5 ml of water, then, after the first week, all seeds were watered with 5 ml twice in the second week, then 3 ml was administered as needed to ensure the soil remained moist for the remainder of the experiment. Seeds were classified as germinated once a shoot emerged from the soil. Germination rate was calculated as the percentage of all seeds planted which germinated for each group (Traveset et al. 2001). The identity of species which germinated were confirmed by experts from the Bermuda Botanical Garden.

The germination rate of Jessamine seeds (Groups 1-5) were analysed in a generalised linear model (GLM) to assess the effects of seed origin (nest area or control area) and flesh state (with flesh, manual deflesh, bird deflesh). Germination was fitted as a binomial response variable, with seed origin and flesh state as two and three-state categorical predictors, respectively. Analysis was performed using the *lme4* package in the R statistical programming environment (Bates 2015, R Core Team 2023).

RESULTS

Seeds present in Great Kiskadee pellets

In 2022 we collected approximately 26 Kiskadees pellets (underestimated number, Figure ESM1) between the 26th of January and the 10th of March (Tab. 1). All pellets but one contained exclusively seeds of *Murraya paniculata* while the remaining one contained fragments of *Livistona chinensis* fruits and 4 unknown seeds that after germination were identified as *Citharexylum spinosum*. Eighteen out of 26 pellets were whole and had on average 6.6 ± 1.5 seeds of *M. paniculata* (range: 4 - 10, N = 18).

In 2023, we repeated the data collection in the same private garden (20th January - 19th February) but Kiskadee pellets were often fragmented therefore we pooled fragments by day. In total, we collected 17 daily samples, all of which presented only seeds of *M. paniculata* except one in which we found *Citharexylum spinosum* seeds (Tab. 1).

Germination rates

Jessamine seeds germinated 49.0% (24/49 seeds) of the time and Fiddlewood seeds germinated 75% (6/8 seeds) of the time (Tab. 2). There were significantly lower germination rates of Jessamine seeds collected in the control area compared to the nest area (GLM: P = 0.04, Fig. 2 and Fig. ESM3 for more details). Manual defleshing or bird defleshing did not significantly alter the germination rates of Jessamine seeds (GLM: P = 0.33, Fig. 2). However, the tendency was for de-fleshed seeds to germinate at a higher rate than seeds with flesh, which was consistent across groups (Tab. 2, Fig. 2).

Table 1. Pellets of Kiskadees and species of seeds found therein collected in a private garden (front and back yards) and under two nests built on palm trees within the garden. Several additional pellets were collected at Flatts dock. For pellets collected in 2023 we only reported seed species. Classification of the plant species according to CABI compendium on Invasive species (https://www.cabidigitallibrary.org/product/qi) is also shown. Samples in bold are those used to calculate the mean number of seeds found in pellets (see Results).

Sample	Date of collection	Place of collection	Total seeds	Seed species	CABI
1	26/01/2022	Front yard	8	*Murraya paniculata*	invasive
2	29/01/2022	Flatt's dock	na	*Livistona chinensis*	invasive
3	1- 4/02/2022	Back yard	30	*Murraya paniculata*	invasive
4	08/02/2022	Under the nest	7	*Murraya paniculata*	invasive
5	08/02/2022	Under the nest	5	*Murraya paniculata*	invasive
6	09/02/2022	Under the nest	7	*Murraya paniculata*	invasive
7	09/02/2022	Under the nest	7	*Murraya paniculata*	invasive
8	09/02/2022	Under the nest	7	*Murraya paniculata*	invasive
9	09/02/2022	Under the nest	5	*Murraya paniculata*	invasive
10	09/02/2022	Under the nest	6	*Murraya paniculata*	invasive
11	09/02/2022	Under the nest	5	*Murraya paniculata*	invasive
12	10/02/2022	Under the nest	5	*Murraya paniculata*	invasive
13	10/02/2022	Under the nest	4	*Murraya paniculata*	invasive
14	10/02/2022	Under the nest	6	*Murraya paniculata*	invasive
15	11/02/2022	Under the nest	7	*Murraya paniculata*	invasive
16	11/02/2022	Under the nest	7	*Murraya paniculata*	invasive
17	12/02/2022	Under the nest	7	*Murraya paniculata*	invasive
18	12/02/2022	Front yard	9	*Murraya paniculata*	invasive
19	12/02/2022	Under the nest	10	*Murraya paniculata*	invasive
20	12/02/2022	Under the nest	6	*Murraya paniculata*	invasive
21	12/02/2022	Flatt's dock	9	*Murraya paniculata*	invasive
22	12/02/2022	Front yard	8	*Murraya paniculata*	invasive
23	10/03/2022	Under the nest	6	*Murraya paniculata*	invasive
24	10/03/2022	Under the nest	4	*Murraya paniculata*	invasive
25	10/03/2022	Under the nest	5	*Murraya paniculata*	invasive
26	10/03/2022	Under the nest	na	*Murraya paniculata*	invasive
1	20/01-19/02/2023	Under the nest	16	*Murraya paniculata*	invasive
2	20/01-19/02/2023	Under the nest	1	*Citharexylum spinosum*	invasive

Table 2. Summary of seed germination experiment. Seeds were collected either from Kiskadee *Pitangus sulphuratus* regurgitates (Group 5, 6) or collected from Orange Jessamine *Murraya paniculata* trees near breeding Kiskadees (Groups 1, 2) or from a control area with no breeding Kiskadees present (Groups 3, 4). Percentages reflect the observed germination rates of each experimental group.

Group	Species	Origin	State	N planted	N germinated	%
1	Jessamine	Feeding tree	With flesh	8	4	50.0
2	Jessamine	Feeding tree	Defleshed	9	6	66.7
3	Jessamine	Control tree	With flesh	8	1	12.5
4	Jessamine	Control tree	Defleshed	9	3	33.3
5	Jessamine	Bird	Bird defleshed	15	10	66.7
			total	49	24	49.0
6	Fiddlewood	Bird	Bird defleshed	8	6	75.0

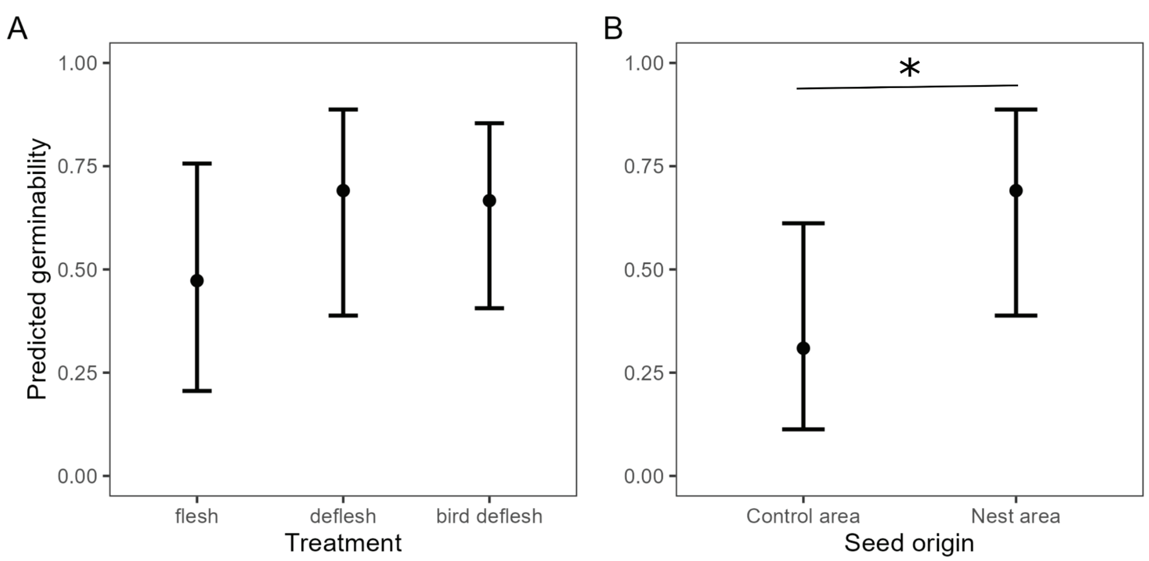

Figure 2. Plots showing the predicted germinability of Orange Jessamine seeds from each experimental group. Panel A shows the predicted effect of flesh state treatment on germination rate, where seeds were planted either with flesh, after manual defleshing, or defleshed as a result of ingestion by a Kiskadee. Panel B shows the predicted significant effect of the area of seed collection on seed germination rate, with seeds either being collected from a Jessamine tree in a control area, or in an area with a pair of nesting Kiskadees present. Predicted effects are derived from a generalised linear model with a binomial response.

DISCUSSION

Our results provided the first observational and experimental evidence showing that the introduced Great Kiskadee is acting as an effective seed disperser of the alien and invasive Orange Jessamine in Bermuda Islands. We also found that Kiskadees can feed on other two invasive plants and potentially disperse the seeds of the Fiddlewood. Such evidence highlights the great potential of Kiskadee to establish new interspecific interactions in novel environments.

Given the high vulnerability of oceanic islands to biological invitations (Vitousek 1988) and the large numbers of terrestrial flora and fauna species introduced in Bermuda (Wolsak et al. 2018), it is highly relevant for local conservation managers to understand the significance and extent of seed dispersal by predatory birds in highly modified ecosystems.

Although our work offers new insights on interactions between alien species, it has some limitations in terms of sample size. As such, our ability to extend the results from the individual to the population level is compromised. Indeed, we cannot exclude that the nesting pair(s) of Kiskadees we collected regurgitates from were specialised in feeding on Jessemine fruits. However, for a generalist and omnivorous predator such as Kiskadee, opportunistic feeding is more likely to occur than prey specialisation. Also, Jessemine fruit consumption may depend on the availability of more profitable prey which may vary with annual conditions. In contrast with the latter assumption, the observed frequency of occurrence of Jessemine seeds in Kiskadee pellets (ca. 99% of pellets) in both years suggests this species is a common fooditem at this time of the year (January-March). Other bird species such as the Figbird *Sphecotheres viridis* in Australia have been shown to act as seed dispersers of the invasive *M. paniculata* with their fruits forming 12-14% of its diet (White et al. 2006).

The results of the experiment suggest that there is no significant difference between the germination rate of seeds from the three experimental groups (Fig. 1, 2a). However, after controlling for the effects of seed origin, there remained a tendency for manually defleshed seeds (predicted rate: 69%) and those ingested by a Kiskadee (predicted rate: 67%) to germinate at a higher rate than whole fruits (predicted rate: 47%). Germination rate of seeds defleshed by birds (67%) was similar to the observed figure obtained in the pilot experiment in 2022 (80%) (see ESM2). The general trend is consistent with the germination rates resulting from a similar experiment with Jessamine fruits eaten by Figbirds in which seeds that had undergone gut passage germinated 75% of the time, manually depulped 78% and intact fruits 75% (White et al. 2016). Several studies investigated the hard and indigestible material of fruits including seeds ingested by birds that can be ejected as pellets (da Paz Pereira & Melo 2012) or excreted after being exposed to digestive fluids (Reed & Reed 1928, Wang et al. 2009). According to these studies, pulp removal after bird ingestion can provide advantages in terms of enhancing germination (Van der Pijl 1972, Lieberman & Lieberman 1986, Barnea et al. 1990). Seed germination is expected to be inhibited by pulp which contains germination inhibitors (Traveset et al. 2001 and reference therein).

Furthermore, in our experiment run in 2023 we found significant and lower germination rates for seeds from the control area than the nesting area. This can be due to the fact that we sampled seeds from one single tree in each area (intraspecific variability) or because seeds from the nesting area were fresher since collected a few days before starting the germination experiment, while seeds from the control area were collected approximately 1 week earlier. Indeed, Orange Jessamine has high germinability but low persistence in the seedbank due to the short life of seeds (White et al. 2006).

Finally, it is worth highlighting that the Kiskadee breeding behaviour in its introduced range is little known (Downs & Hart 2020), therefore the two nesting attempts we recorded in Bermuda between the end of January and February are to our knowledge the first published information of nesting at that time for the northern hemisphere, where nesting is expected to peak in spring and early summer (April–July) (Downs & Hart 2020).

Overall, despite minor shortcomings of our experiment we can still argue that the seeds of invasive plant species found in regurgitated pellets are viable, indicating that Great Kiskadees can be effective dispersers of Orange Jessamine, and potentially other invasive plants. In order to understand to what extent Kiskadees might be contributing to spread around Jessamine fruits, it would be interesting to investigate their foraging range, annual diet, as well as test seeds' germination capacity in the 'wild' on Bermuda.

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