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Såli (Micronesian starling – *Aplonis opaca*) as a key seed dispersal agent across a tropical archipelago

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Research Article

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Abstract

Seed dispersal is an important ecological process that structures plant communities and influences ecosystem functioning. Loss of animal dispersers therefore poses a serious threat to forest ecosystems, particularly in the tropics where zoochory predominates. A prominent example is the near-total extinction of seed dispersers on the tropical island of Guam following the accidental introduction of the invasive brown tree snake (*Boiga irregularis*), negatively impacting seedling recruitment and forest regeneration. We investigated frugivory by a remnant population of Såli (Micronesian starling – *Aplonis opaca*) on Guam and two other island populations (Rota, Saipan) to evaluate their ecological role as a seed disperser in the Mariana archipelago. Using a combination of behavioural observations, nest contents and fecal samples, we documented frugivory of 37 plant species. Native plants comprised the majority (66%) of all species and 90% of all seeds identified in fecal and nest contents. Diet was highly similar across age classes and sampling years. In addition, plant species consumed by Såli comprised 88% of bird-dispersed adult trees and 54% of all adult trees in long-term forest monitoring plots, demonstrating the Såli's broad diet and potential for restoring native forests. Overall, we provide the most comprehensive assessment to date of frugivory by the Såli and confirm its importance as a seed disperser on Guam and throughout the Marianas.

Introduction

Seed dispersal is a key ecological process that influences plant community structure (Levine & Murrell 2003) and helps maintain plant diversity (Wandrag *et al.* 2017). Mechanistically, dispersal allows seeds to escape their parent plant, reducing competition and density-dependent mortality and enhancing survival and recruitment of new individuals into the population (Harms *et al.* 2000, Schupp 1992). Furthermore, dispersal promotes colonization of new sites, gene flow among plant populations (Hamilton 1999) and regeneration of degraded habitats (Wunderle 1997). Thus, seed dispersers provide a function that is an essential to the ecology of forests (Kunz *et al.* 2011, Şekercioğlu 2006, Stratford and Şekercioğlu 2015, Whelan *et al.* 2008), especially in the tropics where zoochory is the predominant mode of seed dispersal (Howe & Smallwood 1982).

Loss of seed dispersers can have detrimental impacts on plant communities (Farwig and Berens 2012, Hansen and Galetti 2009, Melo *et al.* 2010). One of the most extreme examples of cascading effects of disperser loss on forest structure and function is from the tropical island of Guam in the Western Pacific. Virtually all of Guam's native frugivores were extirpated by the invasive, predatory brown tree snake (*Boiga irregularis*) following its introduction to the island shortly after the First World War (Fritts & Rodda 1998, Rodda *et al.* 1992, Savidge 1987). Cascading impacts of frugivore loss on Guam include reduced seedling survival and recruitment, altered spatial distributions of native tree species, reduced local species richness and slower rates of forest regeneration relative to neighbouring islands with intact bird communities (Rogers *et al.* 2017, Wandrag *et al.* 2017).

The only remaining native avian frugivore on Guam is the Såli (Micronesian starling – *Aplonis opaca*), a medium-sized (~80g) passerine bird in the family Sturnidae. The Såli has a broad geographic distribution across Micronesia, with resident subspecies unique to each of the major island groups of Palau, the Mariana Islands and the Caroline Islands (Craig & Feare 2018). They have large home-ranges (Rehm *et al.* 2018*a*), use a variety of habitat types and cross ecotones frequently (Rehm *et al.* 2018*b*), and disperse seeds at relatively large spatial scales (Rehm *et al.* 2019), illustrating their capacity to move seeds around the landscape, particularly from native forests to degraded habitats. Although their diet has never been described quantitatively, Såli are thought to be omnivorous and have been observed eating arthropods,

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small vertebrates and even seabird eggs (Engbring & Ramsey 1984, Reichel & Glass 1990). However, fruit is a primary component of the diet (Craig & Feare 2018), and anecdotal feeding observations have identified at least 19 plant species consumed by Såli (Baker 1951, Craig 1996, Engbring & Ramsey 1984, Jenkins 1983, Marshall 1949, Marshall & Fosberg 1975). Furthermore, they have been recorded eating both native and exotic fruits (e.g. Jenkins 1983), although the prevalence of native vs non-native fruits in their diet is unknown. A comprehensive look at frugivory and seed dispersal by the Såli will shed light on its ecological role in the forests of the Mariana archipelago. Furthermore, because small or restricted populations often exhibit cryptic function loss (McConkey & O'Farrill 2015), understanding the Såli's diet on Guam may help elucidate whether or not the island's remnant population is contributing seed dispersal services to Guam's otherwise defaunated forests.

In this study, we employed a combination of systematic and opportunistic observations of Såli at fruiting trees, fecal samples collected from wild-caught birds, and seeds found within nests to investigate frugivory by Såli on three islands (Saipan, Rota, Guam) in the Mariana archipelago. Our primary goal was to provide a more complete picture of its role as a frugivore, with a particular focus on native versus non-native fruits in the diet. We compared dietary information collected in behavioural observations to that based on fecal samples and nest contents to provide a more complete characterization of dietary breadth. Finally, on Guam, we explored seasonal and age-specific (i.e. nestling vs adult) dietary patterns to determine if the Såli's functional role as a disperser varied between years or among age classes.

Methods

Study sites

We investigated Såli diet on three islands (Saipan, Guam, Rota) in the Mariana archipelago (Figure 1). Guam is the largest of the three (541 km^2), followed by Saipan (115 km^2) and Rota (85 km^2). The islands are all within 200 km of each other and experience similar temperature and rainfall regimes, with little annual temperature variation and pronounced dry (December–June) and wet seasons (July–November). Unlike Guam, Saipan and Rota have not been invaded by the brown tree snake and still have relatively intact bird communities (Rogers *et al.* 2017, Wiles 2005). On Saipan and Rota, we observed Såli in limestone karst forests of similar plant community composition (see Rehm *et al.* 2018*a* and Fricke *et al.* 2018 for details). We studied Såli on Andersen Air Force Base in northern Guam, an 8100-ha military installation where the majority (>99%) of the island's remaining Såli population is concentrated. Our study area included limestone forest along the eastern edge of the base and an urban housing area comprised of large tracts of lawn with isolated trees and a golf course (see Pollock *et al.* 2019 for details).

Literature review

To assess the current state of knowledge on Såli frugivory, we conducted a literature search on Web of Science and Google Scholar in March 2019 using all combinations of the keywords 'Såli', 'Micronesian Starling' or '*Aplonis opaca*', with 'Mariana Islands', 'diet', 'fruit', 'frugivory' and 'seed dispersal'. We then compiled dietary information (based exclusively on behavioural observations of Såli at fruiting trees – the only data available in the literature) into a summary table (Table 1), which we used as a reference to contextualize our own dietary characterization.

Diet sampling

We used three complementary approaches to characterize the diet of the Såli. First, we collected behavioural observations of Såli consuming fruit. On Guam, we recorded opportunistic observations in limestone forest and developed areas on Andersen Air Force Base from 2017–2018. On Saipan and Rota, we collected timed behavioural observations of fruiting trees from 20 fleshy-fruited tree species (see Table 1, Fricke *et al.* 2019) in limestone forest from 2013–2015. Following methods described in Fricke *et al.* (2017, 2019), observers recorded interactions where seeds were consumed or taken away from the canopy at fruiting trees, with an average of 400 hours of observation per tree species (Fricke *et al.* 2017). Because we did not account for sampling effort in our behavioural observations on Guam, we present these data as presence-absence of a given tree species in the Såli diet on each island, and refrain from quantitative comparisons between islands.

Second, we collected fecal samples on Saipan in 2015–2016 and Guam in 2017–2018 to identify seeds dispersed through endozoochory. To obtain fecal samples, we captured Såli using mist-nets erected on trails within native limestone forest and at forest ecotones where forest transitions into non-native habitats (e.g. grasslands or urban areas). Mist-nets were double-high (i.e. 6 m) and we used a pulley system to raise nets level with the forest canopy. We opened between 2–4 nets at sunrise and closed nets no later than 1100h to avoid capturing birds in the heat of the day. We used speakers to broadcast playback of conspecific vocalizations and attract juvenile and adult birds. Following capture, we placed birds in cloth bags and waited for them to defecate. If birds did not defecate within 30 min, we released them at the site of capture. We collected fecal samples in glass vials and transported them back to the laboratory for sorting. On Guam, we also obtained fecal samples by trapping both breeding adults and nestlings in nest boxes (n = 31 boxes), which were deployed throughout the urban area as part of an effort to improve nest survival. Såli exhibit some breeding seasonality (i.e. active nests are less common in the months of October–December) but have been recorded breeding in every month of the year on Guam (J.A. Savidge, unpublished data). We trapped incubating adults at dawn by covering the entrance of the nest box with a hand net and flushing them, while nestlings were removed from the nest by hand during daylight hours. We also surveyed for presence-absence of arthropods in all fecal samples.

Third, we collected and sorted through nest box contents on Guam following each completed nesting attempt from July–September 2018 to identify the seeds that had been defecated or regurgitated inside the box. We removed entire nests from boxes and froze them to kill feather mites and other nest parasites. We then used a sieve to remove all non-seed nesting material and sorted the dry seeds. We also surveyed for presence-absence of arthropods in all nest contents. To identify seeds from fecal samples and nest contents, we collected voucher samples from the wild to create a seed library, which we used along with the help of botanists to cross-reference with seeds that we found in our samples.

Statistical analysis

All statistical analyses were conducted in R version 3.3.3 (R Core Team 2017). We combined all plant species detected in our tripartite approach (i.e. behavioural observations, fecal samples, nest contents) across all islands with the list of plant species compiled

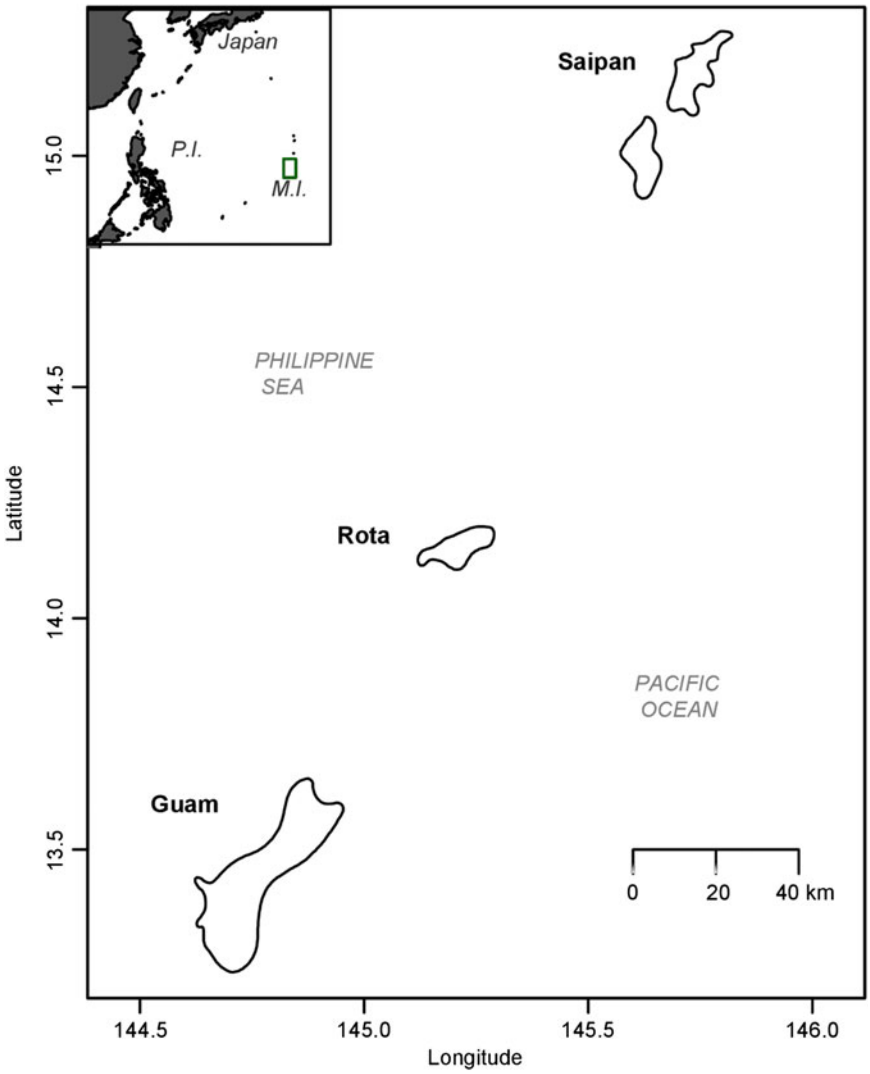

Figure 1. Map of the southernmost islands of the Mariana archipelago where the study was conducted. Inset indicates the location of the Mariana Islands (M.I., delineated by the green rectangle) relative to the closest land masses, Japan and the Philippine Islands (P.I.).

from the literature review to create a comprehensive list of species dispersed by Sâli. We also compared the observed Sâli diet to plant species assemblages from 60 × 60 m long-term census plots located on Saipan (n = 3) and Guam (n = 4; see Rogers *et al.* 2017 for details) to determine the proportion of fleshy-fruited plant species consumed by Sâli in limestone forest.

To explore variation in diet across age classes (nestlings versus juveniles/adults) and years (2017 versus 2018), we focused on fecal samples from Guam, the only island where we had sufficient data to quantitatively assess these patterns. We excluded nest box contents given that they were only collected in 2018 and were not able to be classified to age due to shared use of nest boxes by nestlings and adults. To quantify year and age-specific variation in diet, we first calculated proportional presence of each species in fecal samples (i.e. total number of samples with species present/total number of samples) for each year and age class. We ran linear regressions using the proportional data for year (i.e. proportional presence of a given species in 2017 as the predictor variable and proportional presence in 2018 as the response variable) or age class (i.e. proportional presence of a given species in adult/juvenile diet as the predictor variable and proportional presence in nestling diet as the response variable). We verified that residuals for both regression were normally distributed. We then plotted the proportional data for (1) 2017 vs 2018 and (2) adults/juveniles vs nestlings to explore shifts in frequency of occurrence between years and age classes of the different plant species in the fecal samples. We used the coefficient of determination (R^2) as a metric of diet similarity, with the unity line (i.e. slope = 1, $R^2 = 1$) representing identical diets between the years or age classes. We then visually inspected plots for deviations from unity to detect dietary differences between years and age classes. We also generated bar charts using the proportional metric to visually compare diets between years and age classes.

Results

Overall dietary characterization

From existing literature, we compiled a list of 19 (eight native, 42%; 11 non-native, 58%) plant species that Sâli have been observed consuming throughout Micronesia (Table 1). All but one of these species (*Crateva speciosa*) is present in the Mariana Islands. Combining our three different approaches (behavioural observations, fecal samples, nest contents), we documented frugivory of 37 (22 native, 15 non-native) plant species (22 trees, 10 shrubs, five vines; Table 1). Of these 37 species, 15 were previously recognized as part of the Sâli diet based on our literature review. We thus report the first record of Sâli frugivory for 22 plant species

Table 1. List of plant species consumed by Sâli (*Aplonis opaca*) based on historical observations from throughout Micronesia (n = 19) and in this study (n = 37) based on behavioural observations, fecal samples and nest contents from three islands (Saipan – S, Guam – G, Rota – R) in the Mariana archipelago. Historical observations were compiled from the published literature and include the locality where the observation occurred and the reference in which observational data were presented. Plant species identified in this study from behavioural observations of Sâli are indicated with a "+" under the island where observations occurred. Seeds identified from fecal samples on Saipan (n = 20 samples, 354 seeds) and Guam (n = 403 samples, 25 967 seeds) and nest contents on Guam only (n = 49 samples, 728 seeds) include the proportion of samples in which the given species was present

Plant species (common name)	Functional group	Historical observation locality	Historical reference	Behavioural			Fecal		Nest contents
				S	G	R	S	G	G
Native									
Aglaia mariannensis[a,c,d]	tree		–	+	+	+			
Aidia cochinchinensis[d]	tree		–	+			0.10	0.02	0.02
Artocarpus mariannensis (breadfruit)[d]	tree	Guam	Jenkins 1983		+	+			
Casuarina equisetifolia	tree	Guam	Jenkins 1983						
Clerodendrum speciosissimum	shrub		–						0.04
Eugenia spp.[b,c,d]	shrub/tree	Chuuk	Marshall & Fosberg 1975						0.08
Ficus spp.[d]	tree	Guam; Saipan	Jenkins 1983; Craig 1996	+	+	+	0.52	0.39	0.20
Flagellaria indica	vine		–					0.01	0.53
Ixora triantha[c]	tree		–					<0.01	0.04
Macaranga thompsonii[b,c,d]	tree		–		+			0.19	0.39
Maytenus thompsonii[b,c,d]	shrub		–						0.04
Meiogyne cylindrocarpa[b,c,d]	tree		–					<0.01	0.02
Melanolepis multiglandulosa[d]	tree	Guam	Jenkins 1983	+	+	+		0.36	0.73
Morinda citrifolia[d]	tree	Chuuk	Marshall & Fosberg 1975		+			0.09	0.60
Phyllanthus mariannensis	tree		–		+			0.04	0.33
Pipturus argenteus[d]	tree		–	+	+	+	0.05	0.21	0.02
Planchonella obovata[d]	tree		–	+					
Polyscias grandifolia	shrub		–			+		0.02	0.06
Premna serratifolia[d]	tree	Guam; Saipan	Jenkins 1983	+	+	+	0.10	0.51	0.61
Psychotria mariana[c,d]	tree		–	+			0.14		0.10
Scaevola taccada	shrub	Guam	Jenkins 1983					<0.01	0.02
Tabernaemontana rotensis[a,c]	tree		–						0.14
Wikstroemia elliptica[c]	shrub		–					<0.01	0.06
Non-native									
Annona squamosa[a]	tree		–						0.12
Areca catechu (betelnut)[a]	tree		–		+				
Capsicum frutescens (donne Sâli pepper)	herbaceous	Guam; Saipan; Rota; Tinian	Egerer *et al.* 2018					0.01	0.12
Carica papaya (papaya)[d]	tree	Chuuk; Guam; Saipan;	Baker 1951; Marshall & Fosberg 1975; Jenkins 1983; Craig 1996	+	+	+	0.05	0.07	0.33
Cestrum diurnum	shrub	Guam	Jenkins 1983					0.02	0.04
Coccinia grandis (ivy gourd)	vine		–		+		0.29	0.05	0.02
Cocos nucifera (coconut)[a]	tree	Chuuk	Marshall & Fosberg 1975 (pet)		+				
Crateva speciosa	shrub	Chuuk	Marshall & Fosberg 1975						
Lantana camara	shrub		–					0.01	0.02
Momordica charantia	vine	Guam	Jenkins 1983					<0.01	0.06
Muntingia calabura	tree	Guam	Jenkins 1983						

(*Continued*)

Table 1. (*Continued*)

Plant species (common name)	Functional group	Historical observation locality	Historical reference	Behavioural			Fecal		Nest contents
				S	G	R	S	G	G
Musa sp. (banana)[a]	herbaceous	Chuuk	Marshall & Fosberg 1975		+				
Passiflora foetida	vine		–		+			0.06	0.12
Passiflora suberosa	vine		–		+			0.09	0.37
Pithecellobium dulce	tree	Guam; Saipan	Jenkins 1983; Craig 1996						
Schefflera actinophylla	tree		–					0.01	0.08
Triphasia trifolia[d]	shrub/tree	Guam	Jenkins 1983					<0.01	0.29
Vitex parviflora	tree	Guam	Jenkins 1983		+			0.03	0.59

[a] Plant species with seedless fruit or seeds that are too large to be dispersed via endozoochory (i.e. gut-passage or regurgitation). On Guam, we observed Sâli consuming the flesh of broken *Cocos nucifera* fruits that had fallen to the ground.
[b] Fruiting trees of these species were monitored on Saipan and Rota from 2013–2016 but were never observed being visited by Sâli.
[c] Plant species that are endemic to the Mariana Islands. We were not able to distinguish between the seeds of the three *Eugenia* species (*E. palumbis*, *E. reinwardtiana*, *E. bryanii*), but *E. palumbis* and *E. bryanii* are endemic.
[d] Fleshy-fruited plant species present in 60 × 60 m long-term census plots on Saipan, Guam and Rota.

(Table 1), including 15 (68%) native (of which nine are endemic) and seven (32%) non-native species. Finally, Sâli consumed the majority of fleshy-fruited species in limestone forests in the Marianas; plant species observed to be dispersed by Sâli comprised 88% of bird-dispersed adult stems and 54% of all adult stems in the forest monitoring plots (Table 1).

Behavioural observations

We observed frugivory of 21 species (13 native, eight non-native) in our combined behavioural observations of Sâli from Guam (n = 17), Saipan (n = 9) and Rota (n = 8), including 11 previously undocumented species (Table 1). Seven species (*Aglaia mariannensis*, *Artocarpus mariannensis*, *Ficus* spp., *Melanolepis multiglandulosa*, *Pipturus argenteus*, *Premna serratifolia*, *Carica papaya*) were seen being consumed on multiple islands (Table 1).

Fecal samples

On Saipan, we collected fecal samples from 28 individuals (23 adults, 5 juveniles), 20 (71.4%) of which contained seeds (Supplementary Table 1). On Guam, we collected fecal samples from 403 individuals (384 nestlings, 12 adults, seven juveniles; Supplementary Table 1), 375 (93.1%) of which contained seeds. We positively identified all seeds (n = 354 seeds, seven species) found in fecal samples on Saipan. On Guam, we positively identified 97.5% (n = 25 967 seeds, 25 species) of total seeds. The vast majority of identified seeds on Guam (96.7% by seed number; 56% by species) and Saipan (86.1% by number; 71% by species) were from native plants, including nine species endemic to the Mariana Islands (Table 1). All seven species found in fecal samples on Saipan were nested within samples from Guam (Table 1). However, commonness of species in the diet varied between Guam and Saipan. On Guam, the three most common species were the native trees *P. serratifolia* (51%), *Ficus* spp. (39%) and *M. multiglandulosa* (36%), compared with *Ficus* spp. (52%), the invasive vine *Coccinia grandis* (29%) and the native tree *Psychotria mariana* (14%) on Saipan (Table 1).

Nest contents

We collected nesting material from 49 Sâli nests (collected from 31 nest boxes) on Guam, all of which contained seeds. We positively identified 97.0% (n = 728 seeds, 31 species; Supplementary Table 1) of all seeds, of which 400 seeds (60.4%) and 19 species (61.2%) were native (Table 1; Supplementary Table 1). The most common native species based on frequency of occurrence were *M. multiglandulosa* (present in 73% of nest boxes), *P. serratifolia* (61%), *Morinda citrifolia* (60%) and *Flagellaria indica* (53%) and the most common non-native species was *Vitex parviflora* (59%).

Method comparison

Combining data from all three islands, we documented 31 species (19 native, 12 non-native) in nest contents and 25 species (14 native, 11 non-native) in fecal samples, as well as frugivory of 21 species (13 native, eight non-native) through behavioural observations. The 25 species identified in fecal samples were nested within the 31 species found in nest contents, all of which were dispersed via endozoochory (i.e. gut passage or regurgitation). The size (i.e. seed volume) threshold for gut passage was ~150 mm^3 – the size of the largest seed found in fecal samples (*Meiogyne cylindrocarpa*). We were unable to determine the size threshold for regurgitation, but the largest seed found in nest boxes was *Annona squamosa* (~230 mm^3). Despite the species nestedness of fecal samples with respect to nest contents, frequency of occurrence of seeds differed considerably between the two sampling methods for many plant species (e.g. *V. parviflora* on Guam: 59% in nest contents, 3% in fecal samples; *F. indica* on Guam: 53% in nest contents, 1% in fecal samples). Furthermore, on Guam arthropods occurred more frequently in fecal samples (83.9% in 2017, 69.2% in 2018) than in nest contents (n = 3 nests; 6.1%). Finally, behavioural observations revealed a unique component of the diet – plant species (n = 6) with edible pericarps whose seeds were too large to be dispersed via endozoochory (Table 1).

Seasonal, annual and age-specific patterns of frugivory

We found little evidence of seasonality in diet based on fecal samples from Guam. Most species of seeds occurred idiosyncratically in fecal samples throughout a given year. For example, in 2017, *Macaranga thompsonii* occurrence peaked in May and then declined to zero in July and did not occur again until October. In contrast, in 2018, this pattern was reversed, with *M. thompsonii* increasing steadily throughout the season and peaking in August

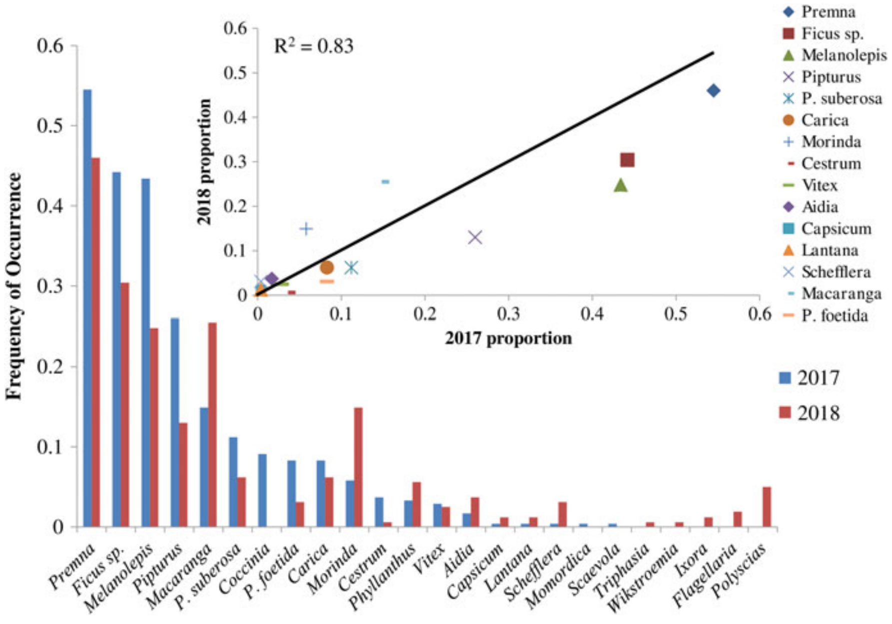

Figure 2. Frequency of occurrence of seeds of tree species found in fecal samples of Sâli (Micronesian starling – *Aplonis opaca*) on Guam, USA in 2017 (n = 242 samples, blue bars) and 2018 (n = 161 samples, red bars). Inset is a linear regression of 2017 *vs* 2018 proportions, including a line with slope of 1 (indicating a 1:1 ratio of frequency of occurrence between years).

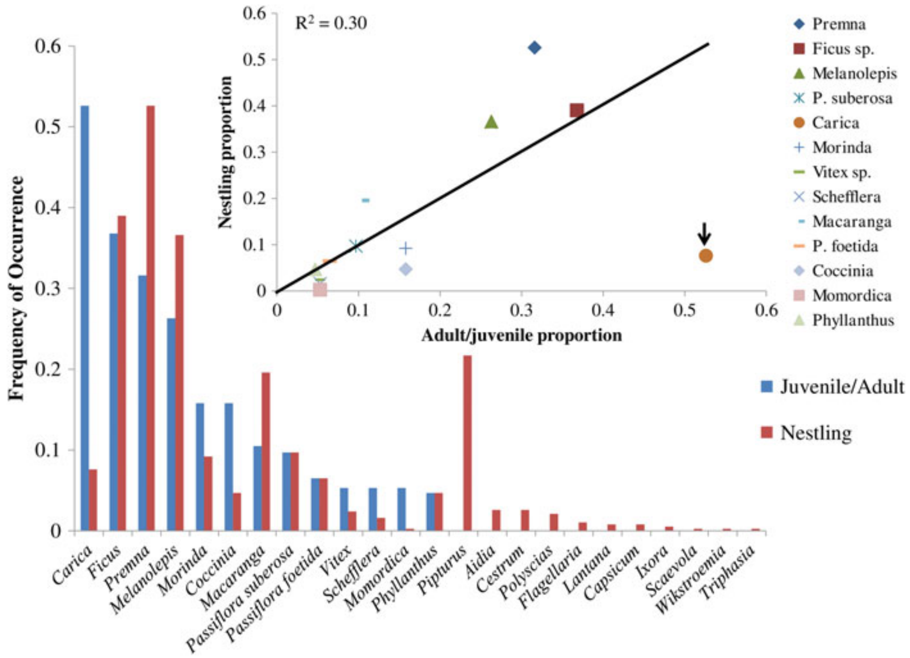

Figure 3. Frequency of occurrence of seeds of tree species found in fecal samples of adult/juvenile (n = 19) and nestling (n = 382) Sâli (Micronesian starling – *Aplonis opaca*) on Guam, USA in 2017–2018. Inset is a linear regression of juvenile/adult vs nestling proportions, including a line with slope of 1 (indicating a 1:1 ratio of frequency of occurrence between age classes). One outlier species (*Carica papaya*) is indicated by the black arrow.

(Supplementary Figure 1). However some species did exhibit consistent seasonal changes, such as *P. serratifolia*, which peaked in April with a secondary peak in July in both years (Supplementary Figure 1). Diet remained highly consistent on Guam between the two sampling years ($R^2 = 0.83$, Figure 2), with four of the same five native species (*P. serratifolia*, *M. multiglandulosa*, *Ficus* spp., *M. thompsonii*) among the most common in both years (Fig. 2). With respect to age class, the juvenile/adult diet was fully nested within and also similar to the nestling diet ($R^2 = 0.30$, Figure 3), although several exotic species (e.g. *C. papaya*, *C. grandis*) were more common and several native species were less common (e.g. *P. argenteus*, *M. thompsonii*) in the adult diet compared with the nestling diet. *Carica papaya* was a particularly extreme exception, as it was consumed frequently by adults/juveniles and rarely by nestlings; when *C. papaya* was excluded from the data, the coefficient of determination between adult/juvenile and nestling diets increased to $R^2 = 0.82$, indicating a highly consistent diet between age classes.

Discussion

We present the first systematic characterization of frugivory by Sâli in the Mariana Islands. Using a combination of behavioural observations, fecal samples and nest contents, we demonstrated that Sâli consume fruits from a broad variety of herbaceous, shrub, vine and tree species. Moreover, we found that Sâli eat and likely act as dispersers for at least three-quarters of the fleshy-fruited plant species present in long-term forest plots across the islands. Finally, diet was similar across years and age classes. Our data suggest that Sâli are generalists whose dietary patterns are influenced by abundance and/or phenology of plant species on the landscape. Despite this cosmopolitan diet, both the majority of species and the total number of seeds consumed by Såli were native. Different methods yielded complementary dietary information – behavioural observations revealed frugivory of plant species whose fruits and/or seeds were too large for gut passage or regurgitation and therefore not detected in fecal samples or nest contents. Together, these complementary methods produce an integrative picture of Såli frugivory and highlight the importance of its role as a seed disperser and its potential for restoring native forests in the Marianas.

Overall, we documented frugivory of 37 tree species (22 native, 15 non-native) across the three islands, nearly doubling the previously known plant-based diet. Såli were dietary generalists and consumed the majority of bird-dispersed tree species present in limestone forest plots. The diet breadth of the Såli is consistent with recent evidence demonstrating that among frugivorous birds, tropical species tend to be more highly specialized on fruit and therefore require a greater variety of food plant species than temperate species (Dalsgaard *et al.* 2017). Similarly, other species of starlings (family Sturnidae) have cosmopolitan diets and consume large quantities of fruit (e.g. LaFleur *et al.* 2009, Yoshikawa & Isagi 2012). Importantly, the vast majority of total seeds found in fecal samples were from native plants on Guam (97%) and Saipan (86%), and our combined methodologies revealed nine previously undocumented species endemic to the Marianas. Indeed, one of these species, *Tabernaemontana rotensis*, is a federally listed, threatened species in the Marianas (Marler *et al.* 2015) yet was moderately common (14% of samples) in nest contents. In contrast, previous research has highlighted the propensity of other starling species to consume and disperse invasive plants (Jordaan *et al.* 2011, LaFleur *et al.* 2007, 2009). To our knowledge, this is the first study demonstrating the importance of a starling as a mutualist for rare plant species.

Nevertheless, Såli are also consuming and dispersing a variety of non-natives and invasives. For example, on Guam, several highly invasive plant species were fairly common in nest contents, including *V. parviflora* (59%), *Passiflora suberosa* (37%) and *Triphasia trifolia* (29%; Pacific Island Ecosystems at Risk (PIER), US Forest Service 2018). Similarly, on Saipan, 29% of fecal samples contained *C. grandis*, a widespread invasive that has had detrimental impacts on native plant communities in the Marianas (Raman *et al.* 2007, Space & Falanruw 1999). Thus, the Såli's ecological role as a seed disperser is not wholly positive, but rather nuanced and likely dependent on the abundance of non-natives across the islands. However, the Såli is not unique in this matter, since all native frugivores in the Marianas also consume and disperse non-native plants (Craig 1996, Jenkins 1983, Wiles & Johnson 2004). Overall, their broad diet, long-range movements (Rehm *et al.* 2019), positive impact on gut passage (Fricke *et al.* 2018), and frequent ecotone crossings (Rehm *et al.* 2018*b*) would make Såli an excellent candidate for restoring dispersal to Guam's forests if their range on the island could be expanded through the implementation of existing or novel brown tree snake control methods.

Age-specific and annual dietary patterns of Såli on Guam indicate that all age classes are at least partially frugivorous throughout the year. However, Såli also consumed arthropods, which were present in most fecal samples (84% in 2017; 70% in 2018). The adult/juvenile diet was fully nested within nestling diet (likely an artifact of small sample size of adult/juvenile fecal samples; n = 19, Figure 3). The fruit-based diet was qualitatively (i.e. overall species richness) and quantitatively (i.e. frequency of occurrence) similar across years both, with the same native species (*P. serratifolia*, *Ficus* spp., *M. multiglandulosa*, *P. argenteus*, *M. thompsonii*) dominating the diet (Figure 2). These data suggest that Såli are tracking abundant and reliable sources of fruit, a common behaviour of tropical frugivorous birds (Saracco *et al.* 2004). Indeed, Såli have minimal competition for food resources on Guam and thus may be able to select their preferred food plants, so their diet on Guam is likely unconstrained relative to their diet on nearby islands. However, testing this hypothesis would require detailed information on variation in fruiting tree abundance and/or phenology on a landscape level across multiple islands (Kimura *et al.* 2001), and we do not currently have those data for this system.

Behavioural observations, fecal samples and nest contents allowed us to more fully characterize patterns of frugivory and provided complementary information about different components of the Såli diet. Fecal samples and nest contents shed light on the food plants that Såli disperse via endozoochory. Seeds found in fecal samples were defecated, whereas seeds found in nest boxes were either defecated or regurgitated. Regardless of the mechanism, gut passage has been shown to improve seedling germination success, especially in the tropics (Traveset 1998, Traveset *et al.* 2007) and in the Marianas (Fricke *et al.* 2019), further contextualizing the importance of Såli as seed dispersers. Nevertheless, we also documented important differences in plant species' frequency of occurrence between fecal samples and nest contents. For example, all but one (*C. grandis*) of the 11 non-native species found in both fecal samples and nest contents on Guam occurred more frequently in the nest contents. These patterns were driven by seed size – many of the non-natives consumed by Såli have larger seeds and were therefore more likely to be regurgitated than gut-passed (e.g. *V. parviflora*, which was present in 1% of fecal samples versus 59% of nest contents). Conversely, arthropods occurred far more frequently in fecal samples (>70%) than in nest contents (~6%), further highlighting the differences between the methods. Perhaps most importantly, nest contents (n = 31 species) provided more dietary information than fecal samples (n = 25 species) in a shorter period of time (i.e. months *vs* years), demonstrating their utility as a sampling method (Wheelwright *et al.* 1984). Even so, both of these methods omitted a subset of plant species with seeds too large to be dispersed via endozoochory (e.g. *Cocos nucifera*, *Areca catechu*), which were only detected in behavioural observations. Our behavioural approach using direct observation of focal tree canopies could determine interactions with seeds of any size, but can only reveal interactions between frugivores and the subset of plant species that are the focus of the observations. Our results reinforce the notion that no single method provides a complete picture of a frugivore's diet (Rosenberg & Cooper 1990) and highlight the need for complementary sampling approaches to fully characterize diet breadth and understand a frugivore's ecological role as a seed disperser.

Our findings bolster the emerging picture of Såli as a key disperser in forests of the Mariana Islands. Såli have the largest home-range of any of the archipelago's avian frugivores (Rehm *et al.* 2018*b*) and the greatest potential for long-distance dispersal (Rehm *et al.* 2019). Furthermore, Såli cross ecotones more than other frugivorous birds and are thought to contribute disproportionately to restoration of degraded habitats (Rehm *et al.* 2018*a*). Finally, they have generally positive impacts on germination on a broad array of native plant species (Fricke *et al.* 2019). With their broad diet and propensity to disperse native and endemic plant species, Såli are a critical agent for restoring seed dispersal to Guam's forests and maintaining ecosystem functioning throughout the Marianas and Micronesia as a whole.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467419000361

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