Quantifying drivers of supplementary food use by a reintroduced, critically endangered passerine to inform management and habitat restoration

Gwen Maggs [a, b *], Ken Norris [a], Nicolas Zuël [c], David J. Murrell [b], John G. Ewen [a], Vikash Tatayah [c], Carl G. Jones [c, d], Malcolm Nicoll [a]

[a] Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom

[b] Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, Darwin Building, Gower Street, London WC1E 6BT, United Kingdom

[c] Mauritian Wildlife Foundation, Grannum Road, Vacoas, Mauritius

[d] Durrell Wildlife Conservation Trust, Les Augrès Manor, Trinity, Jersey JE3 5BP, Channel Islands, United Kingdom

* Corresponding author - email: gbmaggs@hotmail.co.uk

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Abstract

The provision of supplementary food is widely used in the management of endangered species. Typically, food is provided *ad libitum* and often without a planned exit strategy, which can be costly. The role supplementary food plays within population demography can be challenging to identify and therefore any reduction must be carefully considered to avoid negative impacts. Here we investigate the role supplementary food plays within a reintroduced population of a Critically Endangered passerine species by quantifying its use alongside intrinsic and extrinsic factors. Specifically, we illustrate how the provision of supplementary food could be refined in response to breeding stage and the time of food provisioning and, via habitat restoration, create a long-term exit strategy based on influential plant species. The consumption of supplementary food increases during energetically expensive phases of the breeding cycle, during the morning provision of food and when natural plant resource availability is low. We also show a pattern whereby supplementary food could act as a buffer during periods of low natural resource availability during breeding. Based on these findings short-term management could take a reactive approach; refining supplementary food supply in response to breeding stages of pairs and potentially removing the provision of food in the afternoon. In the long-term key plant species, found to correlate with a decrease in supplementary food consumption, could be incorporated into habitat restoration efforts which could create a continuous natural food supply and contribute to creating a self-sustaining population and a potential exit strategy.

1. Introduction

Species conservation often requires intensive management to reduce population limiting factors (Blanco et al. 2011; Jones & Merton 2012). The reintroduction of endangered species has been an effective technique for many decades, with the goal of creating self-sustained populations (Soorae 2011; Jones & Merton 2012; IUCN/SSC 2013). In cases where critically endangered species are reintroduced to habitats outside their natural range, or habitats which are compromised or undergoing restoration, it is difficult to know if a viable population can be sustained; especially as small populations are vulnerable to stochastic events (Shaffer 1981; Armstrong & Ewen 2001; Chauvenet et al. 2012). To counter this, the provision of supplementary food can buffer the impacts of environmental stochasticity and limited natural resource availability (Houston & Piper 2006; Rodriguez-Hidalgo et al. 2010; Correia et al. 2015).

Providing supplementary food is a well-established conservation tool but is applied with varying degrees of success (Boutin 1990; Newton 1998; Ruffino et al. 2014). Studies investigating the effect of feeding on bird populations have found it can induce earlier laying dates and longer breeding seasons, increase egg size, clutch size, fledgling success and survival (Newton 1998; Robb *et al.* 2008); but can also cause increased aggression, create ecological traps, encourage higher rates of predation, chick sex-bias and reduced health (Robertson et al. 2006; Robb et al. 2008; Blanco et al. 2011; Oro et al. 2013). This means that the net effect of feeding should be monitored and quantified when possible to avoid counterintuitive management outcomes.

In most conservation management programmes using supplementary feeding, it is provided *ad libitum* and without an exit strategy (Chauvenet et al. 2012; Ewen et al. 2015). The IUCN Guidelines for Reintroductions and other Conservation Translocations, proposes an exit strategy is an integral part of any reintroduction plan, and enables a defensible and orderly exit when investing further resources is no longer justifiable or if the reintroduction is thought unsuccessful (IUCN/SSC 2013). In most cases exit strategies are planned in the event of a failed reintroduction, but rarely for reintroductions that are succeeding, therefore, the provision of supplementary food could increase exponentially alongside population growth, becoming costly or logistically unsustainable (Chauvenet et al. 2012; Ewen et al. 2015).

The role of supplementary feeding needs to be understood together with how this is modified by the availability of natural plant resources. Identifying patterns between intrinsic and extrinsic drivers and supplementary food consumption, gives an understanding of the relationship between species, supplementary food and their habitat.

Here we explore patterns in the consumption of supplementary food by a reintroduced population of the Mauritius olive white-eye (*Zosterops chloronothos*). Specifically, we examine if the daily consumption rates are impacted by breeding stage, the timing of provisioning, and the availability of nectar and fruit from native plants, to enable the refinement of current *ad libitum* management and devise a potential exit strategy through targeted habitat restoration.

2. Materials and Methods

2.1. Study Site and Species

The study site, Ile aux Aigrettes (20˚42′S 57˚7′E) (Figure 1), is a 26 hectare coralline limestone island 0.7km off the south-east coast of Mauritius and has one of the last surviving, and best, examples of native coastal forest (Figure 1; Parnell et al., 1989). The island experienced high levels of deforestation during the 20th century, however, this ceased following the initiation of a conservation programme by Mauritian Wildlife Foundation in 1985 after which habitat restoration commenced (Parnell et al. 1989). By 1991 ship rats *Rattus rattus* and feral cats *Felis catus* were eradicated allowing the island to be used for the establishment of Mauritian plant, reptile and bird communities (Jones & Merton 2012).

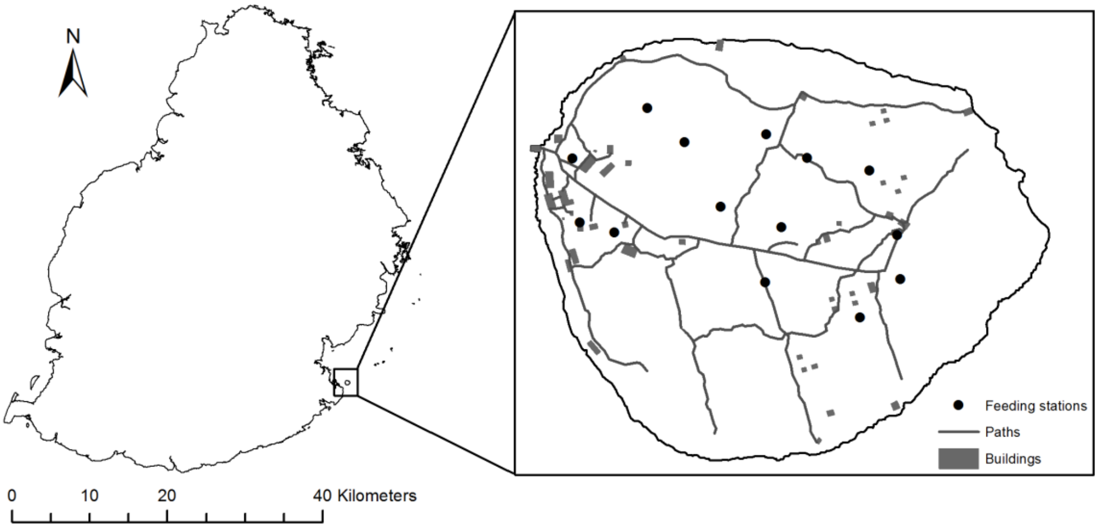

Figure 1. Mainland Mauritius (left) illustrating the location of Ile aux Aigrettes in south-east Mauritius. Ile aux Aigrettes (right) showing the distribution of Mauritius olive white-eye supplementary feeding stations in relation to paths and buildings in March 2013.

The Mauritius olive white-eye is a Critically Endangered passerine species endemic to Mauritius and is in the top 10% of the Evolutionary Distinct and Globally Endangered (EDGE) bird species list (IUCN 2014, Jetz et al. 2014). The species is part of an ancient Indian Ocean lineage having evolved from Asian progenitors (Warren et al. 2006). The species has the longest bill of all white-eyes and is a specialised nectar feeder showing convergence with sunbirds (Moreau et al. 1969). Currently, the rarest of the Mauritius passerines it is declining, currently estimated at <150 pairs, and a restricted to <25km^2 in the upland habitat of the Black River Gorges National Park (Nichols et al. 2005). Drivers in this decline are habitat loss and nest predation by invasive rat species (*R. rattus* and *R. norvegicus*), causing an estimated decline of around 14% per annum (Maggs et al. 2015, Nichols et al. 2004).

In response to population decline a recovery project was started in 2005 by Mauritian Wildlife Foundation to establish a population on Ile aux Aigrettes (Cole et al. 2007, 2008, Maggs et al. 2009, 2010). The historical range of the olive white-eye is unknown, with the first systematic survey in 1975 finding the species restricted to south-west Mauritius in habitat above 1000ft (Cheke 1987). With no record of olive white-eye behaviour and feeding ecology within lowland coastal habitats a soft-release technique was used, accompanied by the provision of supplementary food (2006-2010) which continued post-release. All individuals within the population are ringed with unique identification rings and a colour band combination enabling individual-based data collection. The species is highly territorial and monogamous, defending territories on the island of c.0.6ha and breeding in the austral summer between the months of September and March (Maggs et al. 2011).

2.2. Supplementary Food Programme

Three types of supplementary food are provided to replicate their natural diet; (i) Aves® commercial nectar; (ii) fresh fruit (grapes); and (iii) insectivorous mix (commercial insectivorous mix, grated boiled egg, grated carrot and finely chopped apple). The population is provided with *ad libitum* food which is replaced once in the morning (approx. 6am) and once in the early afternoon (12-1pm). The food is provided from feeding stations that exclude all other bird species and are suspended on wires in open habitat to exclude reptiles with the food inside the feeding station positioned on stands within a water dish to exclude ants (Figure A1). The feeding equipment is sterilised daily to minimise disease risks. During the reintroduction, feeding stations were established across the island (Figure 1) and as the population increased the number of feeding stations provided matched (or exceeded) the number of known breeding pairs. For example nine breeding pairs and 10 feeding stations in 2010-11, 10 breeding pairs and 10 feeding stations in 2011-12 and 13 breeding pairs and 14 feeding stations in 2012-13 (Figure 1; Maggs et al. 2011; Hotopp et al. 2012; Ferrière et al. 2013).

2.3. Supplementary Food Consumption

In order to understand what affects the consumption of supplementary food the amount eaten was recorded 2-3 days a week for three consecutive years (January 2010 to March 2013). Consumption of each food type provided was recorded; fruit and insectivorous mix were weighed, in grams, using digital scales and nectar was measured, in millilitres, using a syringe before and after each morning and afternoon feed, with the difference in these values representing the consumption. A control feeding station, which excluded olive white-eyes, was established at the start of the study to account for daily natural fluctuations in food weight caused by evaporation or saturation. These control values were subtracted from the individual feeding station values to gain the net consumption. Data were excluded if other bird species, reptiles or invertebrates were found consuming the food.

To confirm all individuals within the population had access to, and used, the supplementary food, feeding station monitoring was conducted (see *Breeding Behaviour* in Section 2.4). This showed that all individuals used the supplementary food and that no individuals were monopolising feeding stations.

2.4. Factors Impacting the Consumption of Supplementary Food

We used data collected on the consumption of supplementary food to explore if it was related to (i) breeding behaviour, (ii) the time of day when food was provisioned or (iii) the availability of natural plant resources.

Breeding Behaviour

Data on breeding behaviour were collected daily for all pairs and classified according to the key stages; (i) non-breeding; (ii) nest building; (iii) incubating eggs; (iv) rearing nestlings; (v) fledgling young, left nest but still dependant; and (vi) periods between nesting attempts. To investigate the impact of breeding behaviour on supplementary food consumption, feeding stations were assigned to breeding pairs. Olive white-eye breeding pairs are territorial and do not allow others to use their feeding stations. Pairs were identified through territory searches as part of the wider monitoring programme, observations during feeding times, and by monitoring birds visiting feeding stations. Feeding stations were monitored for 30-60 minutes twice a month at varying times during both the morning and afternoon (2009-2013, n=602). Breeding pairs accounted for a minimum of 58-89% of visits to the feeding stations within their territories, therefore considered the main consumer of the supplementary food; dependant fledglings, floaters or unidentified birds accounted for the remaining 11-42% of visits. Breeding stage was then assigned to daily consumption rates from the relevant feeding station.

On Ile aux Aigrettes there are “floaters” which are either juvenile or single adult birds that also use feeding stations. Daily sightings data, collected throughout the study period shows the proportion of floaters within the population is around 8% (± 7%) but varies throughout the year in response to the breeding period. The use of feeding stations by floaters, observed through feeding station observations, is consistently low and does not have a marked impact upon the recorded consumption rates assumed to be by the pairs. When there is no resident pair using a feeding station, the use by floaters increases. These periods have been classed as “no breeding pair” so that they are investigated independently to breeding stages.

Feeding Time

The consumption of nectar, fruit and insectivorous mix was recorded during both the morning and afternoon feed to note any within day variation.

Natural Plant Resource Availability

The availability of natural plant resources was calculated using plant phenology data collected monthly on Ile aux Aigrettes throughout the study period. The flowering and fruiting of plants were recorded as either present/absent, with 10-20 plants monitored per species, distributed evenly across the island. Due to the variation in sample sizes across the study period, the percentage of the plants flowering or fruiting per month was calculated for each species to make them comparable.

Feeding observations show that both endemic/native and exotic plant species act as natural plant resources for the olive white-eye (Ile aux Aigrettes, 2007-2013; (Cole et al. 2008; Maggs et al. 2009, 2010, 2011; Hotopp et al. 2012; Ferrière et al. 2013). However, exotic plant species makeup a small proportion of the nectar, fruit and invertebrate feeding observations at 11%, 1% and 7% respectively and reflects the low use of exotic plants by the olive white-eye. The phenology data only includes endemic and native species and it is assumed is representative of natural plant resource availability throughout the year.

Using feeding observations on olive white-eye, fifteen endemic/native plant species were identified on Ile aux Aigrettes. These plants are all available within the breeding territories of olive white-eye (except *Ficus rubra* which was absent from three of fourteen territories), but are utilised in different proportions with some forming only 1% of observations. The latter may be due to the low abundance of some species across the island. Nonetheless, these could be important plant resources and so all endemic/native species, where phenology data are available, were included in the analysis. The only plant species for which phenology data were unavailable was *Aloe lomatophyllum*.

2.5. Statistical Analysis

All analysis was conducted in R version 3.5.3. (R Core Team 2019)

Plant Phenology Hierarchical Clustering

To reduce the number of explanatory variables and account for colinearity within the final analysis plant species were clustered, based on seasonal patterns of their flowering and fruiting phenology; clustering flowering and fruiting patterns separately. This was to investigate the impact of natural nectar and fruit resources on the consumption of supplementary food. For each plant species the percentage of monthly flowering and fruiting plants were calculated (see *Natural Plant Resource Availability* Section 2.4) and separate matrices created. Hierarchical cluster analysis was then conducted on the matrices using Ward's minimum variance method, which aims to form hierarchical groupings of mutually exclusive subsets each of which has members that are maximally similar with respect to specific characteristics; which in this study are flowering and fruiting patterns (Browning et al. 2018; Ward 1963).

The hierarchical clustering method grouped plant species based on their squared Euclidean distance using an agglomerative approach with the 'dist' and 'hclust' functions and the default complete linkage method. The final cluster groupings used for the plant phenology explanatory variables were displayed in a dendrogram and highlighted with borders using the 'cutree' function. For each cluster the flower or fruiting percentages were averaged across the species.

Generalised Linear Mixed-effects Models

To investigate what factors drive the consumption of supplementary food, generalized linear mixed-effects models (GLMM) were run using the package 'Lme4' to allow for fixed factors and account for repeated data via random factors (Bates et al. 2019, Bolker et al, 2009). Separate models were run for the different types of food to understand what impacts the different food groups, all models had a response variable of net daily consumption (nectar, fruit or insectivorous mix), Gaussian family for normal errors and maximum likelihood; data were checked for normal distribution. Fixed factors included breeding stage (non-breeding season, nest building, incubation, nestling, fledgling, between nesting attempts and no breeding pair), time of feed (morning/afternoon), and plant phenology clusters based on monthly flowering and fruiting patterns (Figure 2). Random factors included feeding station number and year. The latter factors account for repeated data from feeding stations and within years accounting for spatial and temporal autocorrelation, respectively. All explanatory variables within each supplementary food type GLMM were checked for colinearity using variance inflation factors (VIF) with the function vif from the package 'car' (Fox and Weisberg 2011); variables with a value higher than five were removed (Table A1). The high level of response variables prevented model convergence for the insectivorous mix GLMM and so fixed factors were systematically removed based on their relative importance until the global model fit the data using the package 'relaimpo' (Groemping and Matthias 2018).

The most parsimonious models for nectar, fruit and insectivorous mix were selected based on the lowest Akaike information criterion (AIC) values conducting all-subsets model selection using the function dredge from the package 'MuMIn' (Bartoń 2019). Where top models had a difference in AIC (ΔAIC) of two or less, and therefore equally plausible, model averaging was used to estimate predicted parameter values using the function modavg also from the package 'MuMIn' (Bartoń 2019, Burnham and Anderson 2002). In order to identify the goodness-of-fit for the top AIC models the R^2 values were calculated through the function dredge.

Results

In total 6762, 6218 and 6303 records of supplementary food consumption were collected for nectar, fruit and insectivorous mix respectively, over 361 days, across 10-14 feeding stations, between January 2010 – March 2013. Table 1 presents the ranking of the top 10 models for nectar, fruit and insectivorous mix based on AIC values and Table 2 presents the top model or model averaged output for the three supplementary food types. All of the top AIC models for nectar, fruit and insectivorous mix showed high goodness-of-fit with R^2 values of 0.28, 0.52 and 0.38 respectively.

Plant Phenology Hierarchical Clustering

Hierarchal clustering of plant phenology data identified six clusters of seasonal flower phenology and eight clusters of seasonal fruit phenology (Figure 2). The clusters were determined using the chosen height criterion of 1. As there is no definitive answer to where to set the height criterion, as cluster analysis is essentially an explanatory approach, the height criterion selected here was chosen based on where the branches are short, and therefore more highly correlated, and where clustering is biologically meaningful. Due to fluctuations in data collection and inconsistency of flowering and fruiting events within the plant phenology data two species (*Morinda citrifolia* and *Dracaena concinna*) were removed from the analysis. These plant species combined equated to only 2% of feeding observations by olive white-eye.

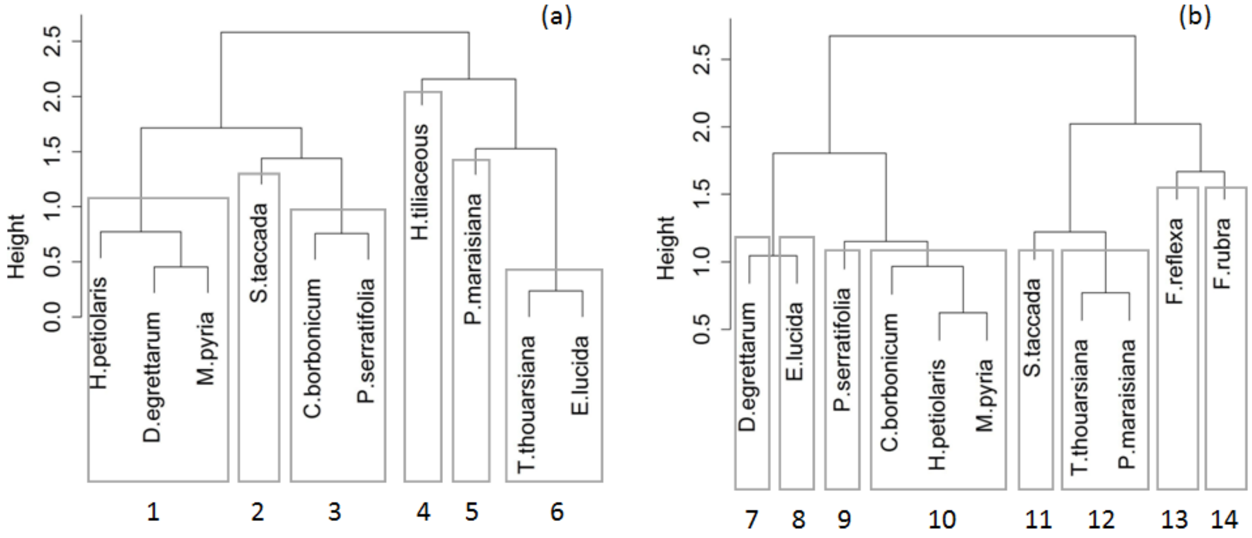

Figure 2. Hierarchical clustering dendrogram illustrating clusters of endemic/native Mauritian plant species based on their seasonal flower (a) and fruit (b) phenology patterns on Ile aux Aigrettes, January 2010 to March 2013. Grey boxes indicate clusters defined at the height = 1 criterion, and the numbers correspond with the fixed factors used in the generalized linear mixed-effects models

Breeding Behaviour

We have identified a relationship between the consumption of nectar, fruit and insectivorous mix and breeding stage, being present in all the top AIC models (Table 1). There was a positive relationship between an increase in nectar and fruit consumption and the fledgling stage and an increase in insectivorous mix and the whole breeding period, between first egg date and last fledgling; except during the no breeding pair stages (Figure 3). However, the relative importance of the predictor variable was low for all three supplementary feeding types (Table 2).

Feeding Time

The relationship between feed time and supplementary food consumption was apparent for all the food types, being present in all the top AIC models (Table 1), with the consumption of all three supplementary food types decreasing during the afternoon feed. The relative importance values were high for insectivorous mix and nectar, at 0.56 and 0.12 respectively, indicating a strong relationship, but low for fruit at 0.03 indicating a weaker relationship in comparison to other variables (Table 2).

Natural Plant Resource Availability

Due to colinearity, clusters 7, 8, 9, 10, 11 and 12 were removed from the nectar and fruit global models with cluster 1 also being removed for nectar and clusters 3, 4, 6, 9, 10, 11 and 14 were removed for the insectivorous mix global model; with VIF values above five or model complexity preventing model convergence for insectivorous mix (Table A1). All of the clusters within the global models were present in the top AIC models (Table 1).

Strong relationships were found between the availability of natural plant resources and the consumption of supplementary food. For nectar, flowering clusters 4, 6 and fruiting clusters 13 and 14 were correlated with a decrease in consumption, especially 13 and 14 with relative importance values of 0.19 and 0.25 respectively, and flowering clusters 2, 3 and 5 with an increase in consumption. For fruit, flowering clusters 3, 4, 6 and fruiting clusters 13 and 14 were correlated with a decrease in consumption, especially cluster 4 with a relative importance value of 0.10, and flowering clusters 1, 2 and 5 with an increase in consumption, especially clusters 2 and 5 with relative importance values of 0.37 and 0.21 respectively. For insectivorous mix, flowering cluster 1 and fruiting clusters 8 and 13 correlated with a decrease in consumption and flowering clusters 2 and 5 and fruiting clusters 7 and 12 with an increase in consumption, all with relatively low relative importance values.

Table 1. Results using a generalised linear mixed-effects model (GLMM) examining daily consumption of supplementary food (SF) by the Mauritius olive white-eye in relation to breeding stage (BS), time of feed (F) and natural plant resource availability (CL1-14; Figure 2). GLMMs were run separately for the three types of supplementary food provided; nectar, fruit and insectivorous mix. Models were ranked in order of decreasing AIC value, and Δ is the difference in AIC from that of the top ranked model. The top ten models and the null model for each supplementary food type are shown.

Rank	Model	K	Log Likelihood	AIC	ΔAIC	AIC weights	R^2
Nectar							
1	BS + F + CL2 + CL3 + CL5 + CL6 + CL13 + CL14	17	-15039.29	30112.6	0	0.39	0.28
2	BS + F + CL2 + CL3 + CL5 + CL6 + CL13	16	-15040.78	30113.6	0.99	0.24	0.28
3	BS + F + CL2 + CL3 + CL4 + CL5 + CL6 + CL13 + CL14	18	-15039.2	30114.4	1.83	0.16	0.28
4	BS + F + CL2 + CL3 + CL4 + CL5 + CL6 + CL13	17	-15040.73	30115.5	2.88	0.09	0.28
5	BS + F + CL2 + CL5 + CL6 + CL13	15	-15044.26	30118.5	5.94	0.02	0.28
6	BS + F + CL3 + CL5 + CL6 + CL13	15	-15044.31	30118.6	6.05	0.02	0.28
7	BS + F + CL2 + CL5 + CL6 + CL13 + CL14	16	-15043.6	30119.2	6.62	0.01	0.28
8	BS + F + CL2 + CL3 + CL5 + CL6	15	-15044.75	30119.5	6.93	0.01	0.28

9	BS + F + CL2 + CL4 + CL5 + CL6 + CL13	16	-15043.9	30119.8	7.23	0.01	0.28
10	BS + F + CL2 + CL3 + CL5 + CL6 + CL14	16	-15044.03	30120.1	7.48	0.01	0.28
Null		4	-15500.01	31008	895.4	0.00	0.12
Fruit							
1	BS + F + CL1 + CL2 + CL3 + CL4 + CL5 + CL6 + CL13 +CL14	19	-5924.9	11887.8	0	1	0.52
2	F + CL1 + CL2 + CL3 + CL4 + CL5 + CL6 + CL13 +CL14	13	-5946.7	11919.3	31.56	0	0.52
3	BS + CL1 + CL2 + CL3 + CL4 + CL5 + CL6 + CL13 +CL14	18	-5945.2	11926.4	38.66	0	0.52
4	BS + F + CL1 + CL2 + CL3 + CL5 + CL6 + CL13 +CL14	18	-5955.9	11947.9	60.11	0	0.52
5	CL1 + CL2 + CL3 + CL5 + CL6 + CL13 +CL14	12	-5966.1	11956.2	68.39	0	0.51
6	BS + F + CL1 + CL2 + CL3 + CL4 + CL5 + CL13 +CL14	18	-5963.3	11962.6	74.81	0	0.51
7	F + CL1 + CL2 + CL3 + CL5 + CL6 + CL13 +CL14	12	-5978.5	11981	93.23	0	0.51
8	BS + CL1 + CL2 + CL3 + CL5 + CL6 + CL13 +CL14	17	-5977.4	11988.9	101.14	0	0.51
9	F + CL1 + CL2 + CL3 + CL4 + CL5 + CL13 +CL14	12	-5984.2	11992.4	104.63	0	0.51
10	BS + F + CL1 + CL2 + CL3 + CL5 + CL13 +CL14	17	-5980.3	11994.5	106.77	0	0.51
Null		4	-7513.5	15035	3147.22	0	0.02
Insectivorous Mix							
1	BS + F + CL1 + CL2 + CL5 + CL7 + CL8 + CL12 + CL13	18	-6353.4	12742.7	0	0.71	0.38
2	BS + F + CL1 + CL5 + CL7 + CL8 + CL12 + CL13	17	-6355.3	12744.5	1.78	0.29	0.38
3	BS + F + CL1 + CL2 + CL5 + CL7 + CL8 + CL12	17	-6360.7	12755.5	12.71	0.00	0.38
4	BS + F + CL1 + CL5 + CL7 + CL8 + CL12	16	-6362.3	12756.7	13.93	0.00	0.38
5	BS + F + CL1 + CL2 + CL5 + CL7 + CL8 + CL13	17	-6367.0	12768	25.25	0.00	0.38
6	BS + F + CL1 + CL2 + CL5 + CL7 + CL12 + CL13	17	-6368.5	12771	28.28	0.00	0.38
7	BS + F + CL1 + CL5 + CL7 + CL12 + CL13	16	-6370.7	12773.4	30.7	0.00	0.38
8	BS + F + CL1 + CL2 + CL5 + CL7 + CL8	16	-6370.8	12773.7	30.92	0.00	0.38
9	BS + F + CL1 + CL2 + CL5 + CL7 + CL12	16	-6372.9	12777.7	35	0	0.38
10	BS + F + CL1 + CL5 + CL7 + CL12	15	-6374.8	12779.7	36.93	0	0.38
Null		4	-7260.9	14529.9	1787.14	0	0.07

Table 2. Top AIC model summaries for generalised linear mixed-effects models (GLMM) examining daily consumption of supplementary food by the Mauritius olive white-eye in relation to breeding stage (BS), time of feed and natural plant resource availability. Separate models were run for the different food types offered; nectar, fruit and insectivorous mix. Model output for nectar and insectivorous mix are model averaged summaries of top AIC models with ΔAIC ≤ 2 (Table 1). NPRs are grouped into clusters based on flowering and fruiting phenology patterns (Figure 2)

Predictor Variable	**Estimate**	**SE**	**z-value**	**Relative Importance**
Nectar				
BS - Non-breeding period (Intercept)	0	0	0	
BS - Nestling	-0.029336	0.01316	2.229	0.00
BS - Fledgling	0.047661	0.013669	3.486	0.05
BS - Incubation	-0.030906	0.01436	2.152	0.01
BS - In between nesting attempts	-0.006298	0.015408	0.409	0.05
BS - Nest building	-0.05642	0.013889	4.061	0.01
BS - No breeding pair	-0.002013	0.024293	0.024	0.03
Feed - afternoon	-0.340158	0.012162	27.962	0.12
Cluster 2	0.045509	0.015993	2.845	0.12

Cluster 3	0.040163	0.014351	2.798	0.04
Cluster 4	-0.001587	0.009177	0.173	0.02
Cluster 5	0.174988	0.015508	11.281	0.10
Cluster 6	-0.092678	0.013654	6.786	0.02
Cluster 13	-0.051933	0.017448	2.976	0.19
Cluster 14	-0.019099	0.018281	1.045	0.25

Predictor Variable	**Estimate**	**SE**	**t-value**	**Relative Importance**
Fruit				
BS - Non-breeding period (Intercept)	3.3969	0.1006	33.75	
BS - Nestling	-0.0407	0.0761	-0.54	0.00
BS - Fledgling	0.0932	0.0625	1.49	0.01
BS - Incubation	-0.1317	0.0587	-2.24	0.00
BS - In between nesting attempts	-0.1762	0.0486	-3.63	0.01
BS - Nest building	-0.3077	0.0756	-4.07	0.00
BS - No breeding pair	-0.1766	0.0440	-4.01	0.02
Feed - afternoon	-0.1805	0.0282	-6.39	0.03
Cluster 1	0.0142	0.0010	13.73	0.04
Cluster 2	0.0307	0.0007	41.24	0.37
Cluster 3	-0.0307	0.0011	-28.54	0.06
Cluster 4	-0.0089	0.0011	-7.91	0.10
Cluster 5	0.0304	0.0011	28.89	0.21
Cluster 6	-0.0065	0.0007	-8.80	0.06
Cluster 13	-0.0240	0.0009	-25.86	0.04
Cluster 14	-0.0232	0.0009	-26.26	0.05

Predictor Variable	**Estimate**	**SE**	**z-value**	**Relative Importance**
Insectivorous Mix				
BS - Non-breeding period (Intercept)	0	0	0	
BS - Nestling	0.04524	0.01289	3.509	0.01
BS - Fledgling	0.11522	0.01324	8.701	0.05
BS - Incubation	0.04423	0.01401	3.155	0.01
BS - In between nesting attempts	0.06699	0.01483	4.516	0.03
BS - Nest building	0.0252	0.01333	0.01334	0.01
BS - No breeding pair	-0.03647	0.02267	1.608	0.01
Feed - afternoon	-0.49067	0.01182	41.498	0.56
Cluster 1	-0.14563	0.01757	8.285	0.07
Cluster 2	0.02111	0.01865	1.132	0.03
Cluster 5	0.1173	0.01654	7.089	0.04
Cluster 7	0.1352	0.0171	7.905	0.08
Cluster 8	-0.08707	0.01566	5.557	0.02
Cluster 12	0.12707	0.02311	5.497	0.07
Cluster 13	-0.06112	0.01603	3.812	0.01

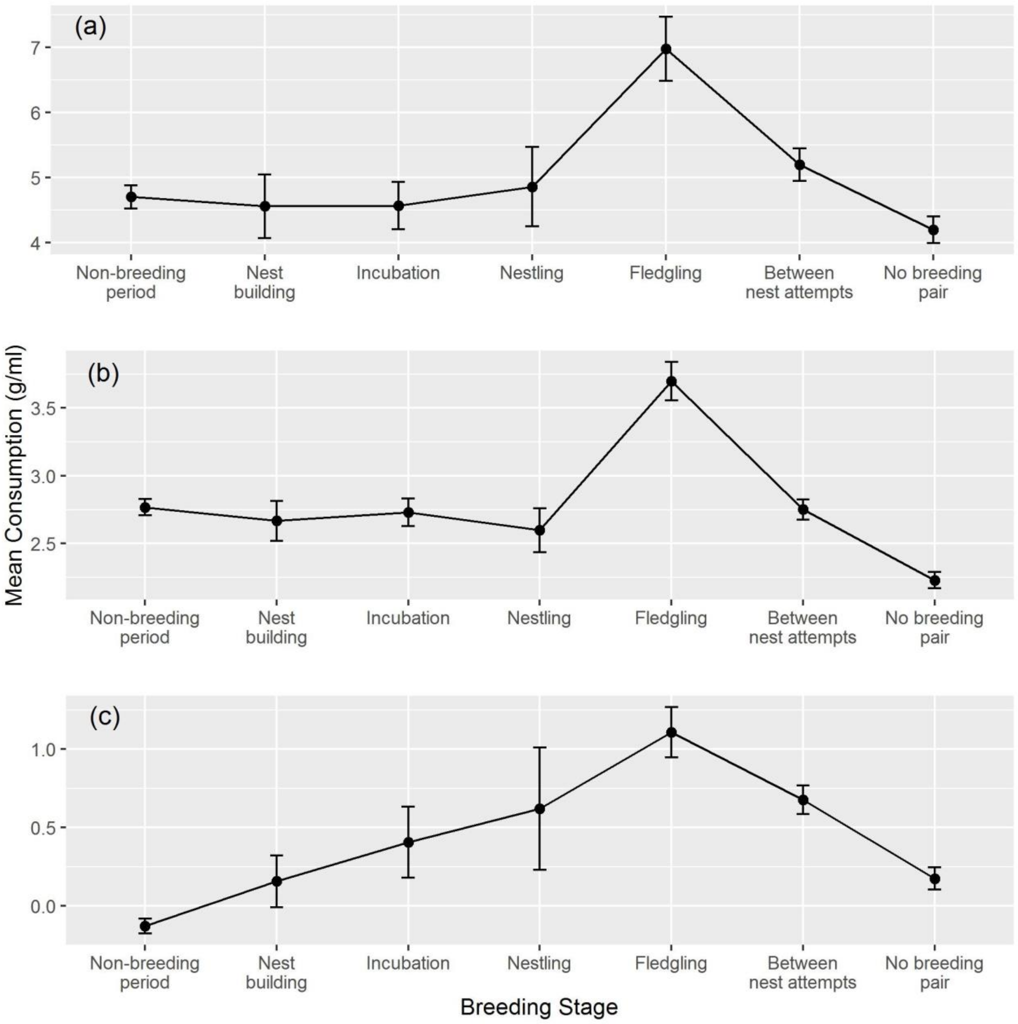

Figure 3. Mean daily consumption of nectar (a; ml), fruit (b; g) and insectivorous mix (c; g) at individual feeding stations by Mauritius olive white-eye during different breeding stages; Ile aux Aigrettes, January 2010 to March 2013. Bars represent standard error

3. Discussion

Our findings indicate that supplementary food consumption peaked in the morning, and during energetically expensive phases of the breeding cycle, particularly when the availability of natural plant resources was low. This can guide the refinement of current *ad libitum* provisioning and make a significant contribution to long-term management strategies by designing a potential exit strategy through habitat restoration.

Management Refinement

The reintroduced olive white-eye population use supplementary food, and through this study we have been able to identify key relationships between behaviour and consumption. These findings could enable a more flexible approach to the provisioning of supplementary food that more closely tracks consumption across the seasons. This could be achieved through a reactive management approach, optimising the timing of supply in response to requirements and reducing management without jeopardising species recovery.

Short-term reactive management could focus on feeding times and breeding activity. Supplementary food supply could be reduced, potentially removing the afternoon feed, ensuring enough supplementary food is provided in the morning to match expected consumption patterns throughout the day. This is supported by Hansen et al. (2002) who found that olive white-eye on mainland Mauritius are most active during the early morning; behaviour which is seen in other nectar feeding passerines (Paton 1993). This action could halve the current workload.

Since the consumption of supplementary food peaked during energetically expensive phases of the breeding cycle, the supply of all three food types could be modified in response. Our results suggest that outside the breeding period insectivorous mix could be greatly reduced and during the breeding period nectar and fruit could be reduced except when fledglings are present. The increased consumption of all three food types, when fledglings are present, indicates high energy requirements suggesting that supplementary food could be important for post fledging survival; although further work would need to quantify this possible effect. Other studies on supplementary feeding and its impacts on nesting success have also found high consumption during the nestling and fledging periods (Meijer & Drent 1999; Schoech et al. 2008; Heath et al. 2008; Ruffino et al. 2014).

A reduction in consumption does not necessarily mean supplementary food is not needed, and a low level of consumption could be important, so removing food all together could cause unexpected negative impacts. It is necessary that any alterations made to current management are carried out using an adaptive management approach, conducting continuous monitoring and evaluation of survival and productivity alongside supplementary food availability to identify any potential negative impacts of management changes (Armstrong et al. 2007; Westgate et al. 2013). Invertebrate availability was not included in this study, and so further research is required to investigate the impact of invertebrate availability on the consumption of supplementary food.

Habitat Restoration

The consumption of supplementary food increased during certain breeding stages, however, during these periods increases in natural plant resources resulted in a decrease in supplementary food consumption. When plotted together it can be seen that during these key breeding stages there are two phases of high and low natural plant resource availability (Figure 4). This indicates that for the olive white-eye natural plant resources may take preference over supplementary food. However, the provisioning of food may act as a buffer when natural plant resources are low, such as during high energy breeding stages, patterns which have been observed in other studies (Elliott et al. 2001; Siriwardena et al. 2008).

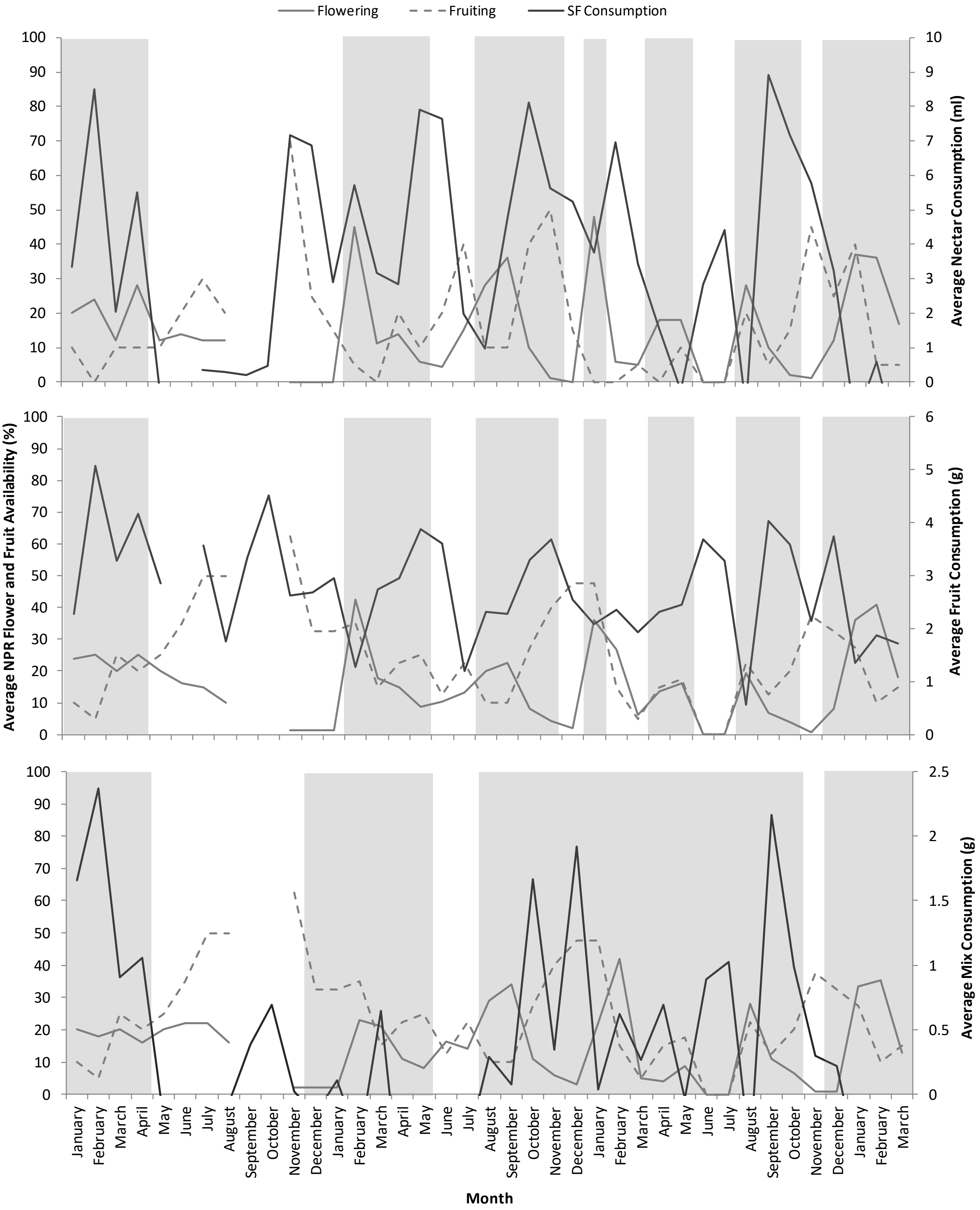

Figure 4. Average monthly consumption of nectar, fruit and insectivorous mix supplementary food by Mauritius olive white-eye (Ile aux Aigrettes, January 2010 – March 2013) in relation to average natural plant resource availability of key plant species identified in the respective top AIC models; illustrating flowering and fruiting plants separately (Table 2). Also shown are the time periods for the breeding stages (grey areas), taken from raw data, where there is an increase in the consumption

of the respective supplementary food types, identified based on a relative importance value of above zero (Table 2).

Due to the variable seasonality of plant phenology, caused by environmental stochasticity, using a reactive management approach based on natural plant resource availability would be difficult. Instead focus should be put into habitat manipulation, planting additional key species on Ile aux Aigrettes, thereby increasing the availability of natural plant resources and reducing olive white-eye dependency on supplementary food. Plant species found to correlate with a decrease in consumption of supplementary food can potentially provide continuous resources throughout the year, however, their availability fluctuates and plant abundance may not currently be high enough to support the population. Ile aux Aigrettes is still being restored following historical deforestation, therefore, the habitat will only increase in coverage and maturity over time. The current habitat restoration work should focus on increasing the abundance and distribution of the key plant species identified in this study to support the population and create continuity in natural food supply: *Coptosperma borbonicum, Diospyros egrettarum, Eugenia lucida, Ficus reflexa, Ficus rubra, Hibiscus tiliaceous, Hilsenbergia petiolaris, Maytennus pyria, Premna serratifolia* and *Turraea thouarsiana.* Of those plant species clusters not included in the analysis due to colinearity or the prevention of model convergence for insectivorous mix, further research is required to investigate the relationship of these natural plant resources and the consumption of supplementary food.

The availability of certain plant species is positively related to an increase in the consumption of nectar, fruit, and insectivorous mix. This suggests that although certain plant species are used by olive white-eye as natural plant resources they may not fulfil all of their energy or nutritional requirements and therefore olive white-eye may rely on supplementary food to boost their intake. At present the nutritional content of plant species and daily nutritional requirements of the olive white-eye are unknown and habitat mapping of plant species across olive white-eye breeding territories and Ile aux Aigrettes is unavailable. Opportunistic feeding observations of olive white-eye show that all key plant species are available within the breeding territories (except *F. rubra* which was absent from three of 14 territories). However, these key plant species are utilised by the olive white-eye in different proportions with *H. petiolaris* forming 26% and *T. thouarsiana* 14% of all feeding observations and others less than 1%, *M. pyria* (n=2782, 2007-2013). We suggest that more observational studies be carried out to verify the importance of natural plant resources and research into the plant species abundance required to meet olive white-eye nutritional requirements.

Conclusion

Conservation programmes often have to utilise all the tools and resources at their disposal to recover populations from the brink of extinction, but this level of effort may not be sustainable in the long-term (Komdeur 1996; Heath et al. 2008). Therefore refining management actions in the long-term is a priority. Supplementary feeding is often viewed as important in the recovery of threatened species but can be costly in terms of conservation resources. This study quantifies the use of supplementary food by a reintroduced population and investigates how this use is shaped by a range of factors including breeding activity and seasonal fluctuations in natural plant resources. By exploring the link between various factors and supplementary food consumption we are able to identify management options which can refine current management techniques and be incorporated into habitat restoration. Potentially, these options could allow the effective allocation of finite conservation resources and lead to the reduction or even removal of supplementary food, providing an exit strategy for successful threatened species management; something which has been rarely achieved.

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