Reduced diet breadth in the Scarlet Macaw *Ara macao* of the Área de Conservación Osa (ACOSA), Costa Rica: Implications for conservation and ecotourism

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Summary

The Área de Conservación Osa (ACOSA) contains the largest population of Scarlet Macaws *Ara macao* in Costa Rica. Despite their influence on ecosystem dynamics and status as a flagship species, empirical data on the foraging patterns of this population is lacking. This information is crucial in implementing effective conservation strategies, particularly reintroduction attempts. Observations of feeding behaviour were made systematically over a 12-month period to provide the first direct examination of Scarlet Macaw diet within the ACOSA region. Scarlet Macaws feed on various items including seeds, flowers, bark, and leaf-gall larvae. Key findings included a demonstration of a smaller dietary niche breadth than that recorded for other Central American populations, use of button mangrove *Conocarpus erectus*, a species not previously recognised as a food source for Scarlet Macaws, and a heavy reliance on an exotic non-native species, *Terminalia catappa*. We argue that whilst human-modified coastal locations may present viable habitat for Scarlet Macaws, anthropogenic influences including the removal of native food sources and proliferation of exotic and cultivated species have left the Scarlet Macaws of the ACOSA particularly dependent on a small number of species.

Resumen

El Área de Conservación Osa (ACOSA) contiene la mayor población de Guacamayos Rojos *Ara* macao de Costa Rica. Pese a su influencia en las dinámicas del ecosistema y su estatus de especie bandera, faltan datos empíricos sobre los patrones de búsqueda de alimento de esta población. Esta información es crucial para implementar estrategias de conservación efectivas y, particularmente, para llevar a cabo intentos de reintroducción. Observaciones del comportamiento alimentario fueron realizadas de manera sistemática durante un período de 12 meses para proporcionar el primer examen directo de la dieta del Guacamayo Rojo dentro de la región de ACOSA. Los guacamayos rojos se alimentan, entre otros, de semillas, flores, de la corteza de los árboles y de larvas en las agallas de las hojas. Los hallazgos clave incluyeron una demostración de que la amplitud del nicho alimentario es menor que la registrada para otras poblaciones centroamericanas, el uso del mangle botón *Conocarpus erectus*, el cual es una especie previamente no reconocida como fuente de alimento de los guacamayos rojo, y una gran dependencia de una especie exótica no nativa, *Terminalia catappa*. Nuestro argumento es que, aunque las localizaciones costeras modificadas por el hombre pueden representar un hábitat viable para los guacamayos rojo, ciertas influencias antrópicas entre las que se encuentran la eliminación de fuentes de alimento nativas y la proliferación de especies exóticas y cultivadas han dejado a los guacamayos rojo de ACOSA particularmente dependientes de un pequeño número de especies.

Keywords: Scarlet Macaw, diet, ecotourism, exotic, non-native, Terminalia catappa, Costa Rica

Palabras Clave: guacamayo rojo, dieta, ecoturismo, exótico, no nativo, *Terminalia catappa*, Costa Rica

Introduction

The Scarlet Macaw *Ara macao* of Central America was once widespread across the lowland neotropical forests but is now restricted to small, isolated populations (Wiedenfeld 1994, Renton 2000). An iconic social psittacine, they are threatened throughout much of their range by habitat loss, increasing rural human pressure, and chick poaching for the pet trade (Enkerlin-Hoeflich *et al.* 2000, Vaughan *et al.* 2005, Dear *et al.* 2010, Berkunsky *et al.* 2017). Between 1940 and 1977 the Scarlet Macaws of Costa Rica lost an estimated 37% of their forest habitat (Vaughan 2011). It is due to such anthropogenic pressures that *A. macao* are one of 20 psittacid species in Central America and Caribbean - 48% of the total - that are considered threatened and listed under Appendix I of the Convention on International Trade of Endangered Species (CITES) (Renton *et al.* 2015). Scarlet Macaws are a target for conservation efforts due to their status as a flagship species and resulting role in promoting ecotourism (Marineros and Vaughan 1995, Guedes 2004). Despite historically having been viewed as seed predators, large macaws are also important actors in ecosystem functioning, with recent studies demonstrating their importance in shaping forest landscapes via seed dispersal (Blanco *et al.* 2015, 2016, Baños-Villalba *et al.* 2017).

Attempts have been made to reintroduce groups of macaws across their historic range with the hope that after identifying and mitigating the causes of extirpation, new populations can be sustained (Brightsmith *et al.* 2005, Estrada 2014, Figueras 2014). Knowledge of species' dietary behaviour is required to accurately identify high-quality habitat, a factor that nearly triples the success of psittacine reintroduction attempts (White *et al.* 2012). Such studies are particularly relevant in assisting the conservation of threatened species in areas undergoing environmental change and anthropogenic development, such as the Osa Peninsula (Sutherland 1998, Caro 1999, Minca and Linda 2000, Buchholz 2007). The environmental impact of increased ecotourism in the region remains unclear, as does the viability of these areas in supporting populations of Scarlet Macaw (Stem *et al.* 2003). A further concern is the potential for dependency on cultivated or non-native species in human-altered landscapes (Vaughan *et al.* 2006, Matuzak *et al.* 2008). Whilst these may represent a useful resource when faced with a scarcity of native food sources, questions have been raised regarding the ecological value of exotic species in the context of sustaining threatened populations (Stromberg *et al.* 2009, Davis *et al.* 2011).

Here we consider the population of Scarlet Macaws found in the Área de Conservación Osa (ACOSA) in Costa Rica, which is the largest of two viable populations in the country, with between 800 and 1,200 individuals (Dear *et al.* 2010). The other is found in the Área de Conservación Pacífico Central (ACOPAC), and has been subject to frequent monitoring since 1990, including

studies of diet (Vaughan *et al.* 2006), fledgling dispersal and behaviour (Myers and Vaughan 2004), nesting (Vaughan *et al.* 2003), and population size (Marineros and Vaughan 1995, Vaughan *et al.* 2005). These two Costa Rican populations comprise the northernmost viable populations of the South American subspecies, *Ara macao macao* (Wiedenfeld 1994).

Early genetic work had suggested minimal levels of genetic differentiation between the Costa Rican populations; however, this result was obtained from the sampling of only 16 captive and confiscated individuals and is therefore unlikely to accurately reflect the genetic status of these populations (Nader *et al.* 1999, Monge *et al.* 2016). A more comprehensive recent examination found a significant level of population-level isolation, despite the small (\approx 80 km) distance between the two groups (Monge *et al.* 2016). The authors argue that this finding supports treating each population as a separate management unit, with associated local conservation strategies. Despite this, and their status as the largest national population, the ACOSA Scarlet Macaws remain largely unstudied (Guittar *et al.* 2009).

Studies of *A. macao* diet conducted across Central and South America have documented a wide dietary breadth that includes fruits, seeds, flowers, vegetable matter and nuts (Renton 2006, Vaughan *et al.* 2006, Matuzak *et al.* 2008, Lee *et al.* 2014, Amaya-Villarreal *et al.* 2015). Attempts to examine *A. macao* diet and foraging behaviour within the ACOSA have however been limited to just one study, where information on foraging ecology was obtained through interviews with local residents only (Dear *et al.* 2010). Here we begin to address this knowledge gap, by presenting a systematic examination of Scarlet Macaw diet within the ACOSA region, to provide a basis on which conservation strategies including reintroduction attempts can be more effectively implemented. We observed foraging Scarlet Macaws on systematic transects to determine which plant species were being consumed, estimate dietary niche breadth, and how this varied seasonally. We also recorded the number of individuals within each foraging group as a potential measure of the extent of social cohesion associated with different food resources and seasons, as this is considered an important factor in reintroduction attempts (Brightsmith *et al.* 2005).

Materials and methods

Study site

The study site is centred on Carate ($8.442651^{\circ}N$, $83.445007^{\circ}W$), a small village located on the southern coast of the Osa Peninsula, Costa Rica. Carate is located within the Golfo Dulce Forest Reserve, and the Área de Conservación Osa (ACOSA). It is situated ≈ 3 km east of Corcovado National Park, one of the largest remaining tracts of lowland Pacific forest in Central America (Dear *et al.* 2010, Vaughan 2011). The peninsula is predominantly (> 90%) comprised of tropical wet forest, with smaller areas of tropical moist and premontane wet forests (Holdridge 1967). Annual rainfall on the peninsula is high, with a mean of 6,000 mm per year (Carrillo *et al.* 2008), with a dry season from December to May and a wet season June to November (Janzen 1967, Lobo *et al.* 2008). This distinction is used for all analyses concerning seasonality.

Sampling methodology

Studies of Scarlet Macaw diet in Costa Rica have employed either opportunistic sampling (e.g. Vaughan *et al.* 2006), or opportunistic sampling combined with transects (e.g. Matuzak *et al.* 2008). Whilst these methods have the potential to dramatically increase the number of observations – particularly as the study site has one of the highest mean daily sightings of Scarlet Macaws within the ACOSA (Dear *et al.* 2010) – it does not allow for accurate seasonal comparisons to be made. It was therefore decided that surveys would be conducted systematically, with transects selected to represent the differing biotic and abiotic factors within the study area. To avoid pseudoreplication, surveys were conducted unidirectionally along transects and only once per morning, midday, or evening session (i.e. a maximum of three surveys per transect per day). Plant

species were identified with reference to *A field guide to plants of Costa Rica* (Gargiullo 2008). Identification of insect leaf-gall larvae consumption was made possible through the presence of a conspicuous foraging behaviour, sample collection, and reference to Hanson *et al.* (2014).

Three 1-km transects were selected in an effort to sample habitats representative of lowland Pacific rainforest. These were chosen primarily on the basis of different levels of human disturbance and varied biogeography, including the presence of both coastal and freshwater features. Transect 1 utilises a dirt road track that runs through the forest next to a large lagoon before dissecting a localised lowland palm forest. Transect 2 is a 1-km stretch of beachfront, an area popular with ecotourists. The third and final transect is the river mouth and lower course of Rio Carate. This route runs perpendicularly from the coast and transects a cline of habitats away from the coast and into old-growth primary forest. Pilot surveys began in October 2017, with transects completed in the early morning (o6hoo) and early afternoon (14hoo). These times were chosen with reference to Gilardi and Munn's (1998) observation that *Ara* spp. are most active at these times. Anecdotal evidence soon demonstrated no such local major activity peaks. Consequently, the survey schedule was altered in favour of a more comprehensive sunrise-to-sunset approach, permitting more surveys to be conducted throughout the day. The study commenced in November 2017 and continued for 12 months.

Gilardi and Munn (1998) have found that large *Ara* spp. can be reliably counted at a distance up to 300 m, however as this study required collection of data such as the presence of foraging behaviour, data collection was restricted to macaws judged to be within 100 m of the transect line. We used 8 x 42 binoculars for all observations. Foraging bouts were defined with reference to Matuzak *et al.* (2008). An observation of a macaw or group of macaws feeding was considered a single foraging bout, but if any flew to and fed upon a different plant of the same or different species, a further feeding bout was recorded. The number of individuals within each foraging group was recorded. Foraging behaviour was marked as absent when perched *A. macao* were observed but not seen actively foraging within an immediate five-minute window. During foraging it could often be difficult to accurately discern which plant parts were being consumed, resulting in this information being collected for some, but not all observations.

Dietary niche breadth was calculated from the proportion of macaws observed feeding on each resource across all transects and seasons. This enables an examination of the level of discrimination demonstrated across food resources, assuming equal relative abundance. The standardised dietary index of Levins (1968) was applied, with a score close to 1 suggestive of a generalist diet and values closer to 0 indicative of dietary specialisation (Colwell and Futuyma 1971). Five foraging bouts occurred on plant species that could not be accurately identified and were excluded from analyses. In total, 266 transects were conducted.

To examine the extent of social cohesion across different contexts, the size of feeding groups across the four-most foraged plant species was subject to a non-parametric analysis of variance, whilst a Wilcoxon rank-sum test was conducted to test for the effect of season on both group size and feeding group size. Chi-squared tests were used to determine the independence of season and foraging rate, and of season and observation rate. Surveys were led by individuals with prior experience of ornithological surveys in the area and were assisted by up to five individuals. A further non-parametric analysis of variance was used to determine if there were any confounding effects of observer number on macaw observation rate. Three surveys lacked this information on surveyor number and were omitted from analysis. Statistical analysis was conducted in the software R (3.1.2) (R Core Team 2014).

Results

Diet

Across the 266 transects, we recorded a total of 283 Scarlet Macaw groups. Over the 12-month study period Scarlet Macaws consumed 11 different species from seven families, with flowers,

Table 1. Species and family foraged upon, number of recorded feeding bouts, percentage total of all feeding bouts, total number of foraging macaws, and plant parts eaten for Scarlet Macaws in the ACOSA, Costa Rica (2017–2018).

Family/Species	No. feeding bouts	% of total bouts	Mean group size \pm 1SE	Months fed upon	Plant part commonly eaten
Combretaceae/ <i>Terminalia</i> <i>catappa</i>	127	70.9	$2.5\pm\!0.1$	Nov-Oct	Fr/S, Lv
Bombacaceae/Ochroma pyramidale	17	9.5	2.4 ±0.2	Dec-Mar	Fl
Palmae/Attalea butyracea	12	6.7	3.7 ± 0.7	Dec-Feb, Oct	Fr, S
Anacardiaceae/Anacardium excelsium	8	4.5	3.5 ±0.8	Feb-Mar, June	S, B
Homoptera: leaf-gall larvae of <i>Astronium graveolens</i>	4	2.2	6.0 ±2.2	May-June	LgL
Moraceae/Brosimum alicastrum	4	2.2	3.0 ±0.4	June	Fr/S
Combretaceae/Conocarpus erectus	3	1.7	2.3 ±0.7	Feb, July	Fr/S
Anacardiaceae/Mangifera indica	1	0.6	5	June	Fr
Moraceae/Ficus insipida	1	0.6	3	Mar	Fr/S
Caesalpiniaceae/Cassia grandis	1	0.6	2	Mar	Unclear
Meliaceae/Cedrela odorata	1	0.6	1	Mar	Unclear
Total:	179	100.0			

Plant part eaten key: Fr-fruit, S-seeds, Lv-leaves, Fl-flowers, B-bark, LgL-insect leaf-gall larvae.

seeds, bark and insect leaf-gall larvae all utilised as food sources (n = 179 foraging bouts; Levins' diet breath = 0.123) (Table 1). A high proportion of all flock foraging bouts (71%) occurred on *T. catappa*, with this proportion being similar across seasons ($\chi^2 = 0.0001$, df = 1, P = 0.99).

Social cohesion and seasonality

Feeding group size did not vary significantly across the four most-commonly eaten plant species (Kruskal-Wallis rank-sum test: H = 2.8, df = 3, P = 0.41). There was also no effect of seasonality on measures associated with social cohesion, with neither group size (Wilcoxon rank sum test with continuity correction: W = 8361, P = 0.06), nor size of groups observed foraging (W = 3279, P = 0.25) varying significantly across seasons.

There were no seasonal differences in terms of how frequently macaws were observed (Pearson's Chi-squared test: $\chi^2 = 1.1$, df = 1, P = 0.30), however, when observed, macaws were significantly more likely to be observed feeding during the dry season (81%) compared to the wet season (52%) ($\chi^2 = 10.7$, df = 1, P = 0.001). Finally, there was no effect of surveyor number on total macaws observed (H = 2.4, df = 6, P = 0.87), nor on the number of macaws observed feeding (H = 7.9, df = 6, P = 0.25).

Discussion

As the first systematic dietary examination of the largest viable Scarlet Macaw population in Costa Rica, it is hoped that these findings can help to inform conservation strategies, particularly regarding the selection of suitable sites for release during reintroduction attempts. In total,

Table 2. Comparison table of various examinations of Scarlet Macaw diet across the Neotropics, listed by study length. Diet breadth is indicated via the total number of species foraged upon and the Levins dietary niche breadth index. The present study is highlighted in bold text. Locations, total number of recorded foraging bouts, and proportion of diet contributed by *T. catappa* are included for context.

Study Length	Location	Total spp.	Levins′ Index	% T. catappa	No. Foraging Bouts
5 months ¹ Chiquibul National Park, Belize		16	0.39*	0	49
6 months ²	Palenque, Mexico	31	0.24	3	283
1 year	ACOSA, Costa Rica	11	0.12	71	179
2 years ³	ears ³ Tambopata National Reserve, Peru		0.49	0	178
2 years ⁴	Nicoya Peninsula, Costa Rica	32	0.12	38	600
4 years ⁵	ACOPAC, Costa Rica	43	N/A	6	160

¹Renton 2006; ²Amaya-Villareal *et al.* 2015; ³Lee *et al.* 2014; ⁴Matuzak *et al.* 2008; ⁵Vaughan *et al.* 2006. * This value calculated from only the dry season, March-May.

11 different species were utilised as food resources across this 12-month study in the Área de Conservación Osa in Costa Rica, with seeds, fruits, flowers, bark and insect leaf-gall larvae all consumed. Consumption of insect leaf-gall larvae is thought to provide extra protein in the diet but is only infrequently observed in studies of Neotropical parrot diets (Martuscelli 1994, Renton 2001, 2006, Amaya-Villarreal *et al.* 2015).

The total of 11 species is a far smaller number utilised for food than has been reported in other studies of Scarlet Macaw diet in Costa Rica. Macaws in the Nicoya Peninsula have been reported as using 32 species for food (Matuzak *et al.* 2008), and 43 in the ACOPAC (Vaughan *et al.* 2006). This difference is unlikely to solely be the result of differing study site habitats or plant availability, as the ACOPAC, located only 80 km away, shares many bioclimatic similarities with the ACOSA (Holdridge 1967, Cifuentes *et al.* 1983).

As these studies took place across multiple years, the observed narrow dietary breadth may be an artefact of the comparatively shorter length of this study. As Renton *et al.* (2015) noted, in studies of psittacine diets, the number of species recorded as sources of food significantly correlates with the length of the study. The authors argue that this is likely the result of the tendency for longer studies to better reflect intra- and inter-annual variations in food-resource exploitation patterns. Despite this, however, other short-term (< 1 year) studies from elsewhere in the Neotropics have also demonstrated wider dietary breadths, with a reintroduced population in Mexico recorded using 31 different species over just a six-month period (Amaya-Villareal *et al.* 2015), and Renton (2006) noting the use of 16 different species over five months by the Scarlet Macaws of Belize. These results imply that even if the dietary breadth of the ACOSA macaws is wider than the results here suggest, the population is still likely to utilise a smaller number of species as food resources than other Neotropical populations studied to date (Table 2).

Whilst useful metrics for understanding foraging behaviour, dietary breadth indices do not account for the relative abundance of potential food sources in the area, and thus provide no insight as to the level of selectivity exhibited by the population (Feinsinger *et al.* 1981). Insufficient vegetational and phenological data preclude a selectivity analysis, therefore a list of potential food sources in the study area is provided instead (Table 3). The species listed therein are known to be foraged upon by Scarlet Macaws in Central America, present within 100 m of at least one transect (J. H. pers. obs.), and yet not observed to have been eaten during this study period. Whilst unlikely to be exhaustive, this information is useful in contextualising the decisions made during foraging by the Scarlet Macaws of the ACOSA.

Seven individuals were observed feeding on the small, cone-like fruits of *Conocarpus erectus*, a terrestrial mangrove-associate commonly found along shorelines (Schoener 1988). Whilst it has been noted as food source for other parrot species (Snyder *et al.* 1982), it has not previously been

Table 3. Species foraged upon by Scarlet Macaws in Central America but not observed to be eaten during the study period, listed by family. Species shown are known to be present within 100 m of at least one transect (J. H. pers. obs.). Data compiled from 1. Renton 2006, 2. Amaya-Villareal *et al.* 2015, 3. Matuzak *et al.* 2008, and 4. Vaughan *et al.* 2006.

1	2	3	4	Family / Species
			Х	Anacardiaceae / Anacardium occidentalis
Х	Х	Х	Х	Anacardiaceae / Spondias mombin
		Х	Х	Bombacaceae / Ceiba pentandra
Х			Х	Bromeliaceae / Bromeliad spp.
Х			Х	Burseraceae / Bursera simarouba
			Х	Combretaceae / Terminalia oblonga
			Х	Euphorbiaceae / Hura crepitans
		Х		Fabaceae / Cassia grandis
		Х	Х	Fabaceae / Inga spp.
Х		Х	Х	Fabaceae / Schizolobium parahybum
			Х	Moraceae / Brosimum utile
Х				Moraceae / Cecropia obtusifolia
		Х	Х	Moraceae / Ficus spp.
	Х	Х		Myrtaceae / Psidium guajava
		Х		Palmae / Cocos nucifera
		Х		Rhizophoraceae / Rhizophora mangle
	Х			Urticaceae / Cecropia peltata
			Х	Verbenaceae / Gmelina arborea

recorded as a food source for Scarlet Macaws. This finding suggests that some human-modified coastal areas may represent viable habitats for macaws, as other food sources, including *T. catappa*, grow well in these conditions (Vaughan *et al.* 2006). Myers and Vaughan (2004) have noted the high value of coastal regions in the early post-fledging period of Scarlet Macaws in Costa Rica and propose that such sites be given a degree of protection when they exist outside of national park boundaries. Revenue from ecotourism could act as an incentive for lodges and government to preserve such habitats and has been credited with increases in the number of large macaws in Peru (Brightsmith *et al.* 2008).

A greater proportion of macaws were recorded actively feeding during the dry season (81%) than the wet season (52%), likely due to the need to provide extra food for nestlings between February and May (Grenier and Beissinger 1999, Vaughan et al. 2009). Another likely contributing factor is that seed production of the most commonly eaten species, T. catappa, peaks in the dry season and is selectively foraged upon by Scarlet Macaws (Matuzak et al. 2008; Henn et al. 2014). Native to South-East Asia, T. catappa is now widespread throughout the tropics, including Costa Rica. Fast-growing and largely tolerant of salt-stress, it is commonly found in coastal areas and has increasingly been used in reforestation efforts and in areas of ecotourism (Vaughan et al. 2006). In these disturbed areas it has become a common food source for Scarlet Macaws: a study conducted on seven Costa Rican beaches found that 49% of all fallen *T. catappa* seeds - totalling 50,832 - had been preved upon by Scarlet Macaws (Henn *et al.* 2014). Representing 71% of all foraging bouts (n =127) and 65% of total foraging individuals (n = 313), T. catappa comprises a very large part of the ACOSA population's diet. This level of dependency is not reflected in other populations in Costa Rica. For example, T. catappa in the Nicoya Peninsula accounts for a reduced 38% of the macaw diet (Matuzak et al. 2008), and only 6% of the diet of the nearby ACOPAC population (Vaughan et al. 2006). Elsewhere in the Neotropics *T. catappa* rarely features, comprising only 3% of the diet of a reintroduced population in Mexico (Amaya-Villareal et al. 2015), and was not recorded as a food source at all for populations in Belize (Renton 2006) and Peru (Lee et al. 2014).

There exist concerns regarding the level of dependency on exotic and cultivated species exhibited by Scarlet Macaws. In the Nicoya Peninsula, non-native and cultivated species, including

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T. catappa, comprise 76% of the Scarlet Macaw diet compared to a mean of just 28% for other psittacine species (Matuzak *et al.* 2008). Whilst not observed here, Scarlet Macaws are known to frequently feed on teak *Tectona grandis* and melina *Gmelina arborea*, species widely cultivated across Costa Rica (Vaughan *et al.* 2006; Matuzak *et al.* 2008, Dear *et al.* 2010). There has been a reported instance from Rancho Quemado, in the heart of the ACOSA, of a large group of macaws (n = 85) becoming accustomed to feeding on exotic cultivated melina only to have their numbers decimated when the plantation is harvested (Dear *et al.* 2010). With large teak plantations only \approx 40 km east of the study site (J. H. pers. obs.) there is a concern that should these plantations spread westwards, reliance on this resource could leave macaws vulnerable to sudden anthropogenic changes including routine harvests. There is also the risk that they become perceived as agricultural pests, as Red-fronted Macaws *Ara rubrogenys* have in Bolivia (Bucher 1992, Pitter and Christian-sen 1995).

Nevertheless, Vaughan *et al.* (2006) have suggested that cultivated and exotic species could be used to support Scarlet Macaws in areas where ongoing habitat loss has resulted in a lack of native food sources, such as has seemingly occurred in Australia with the endangered Orange-bellied Parrot *Neophema chrysogaster* feeding on commercially grown sunflowers *Helianthus annus* (Eckert 1990). Furthermore, an increase in exotic trees has been postulated as a possible factor in the growing size of the ACOSA macaw population (Dear *et al.* 2010). This suggests that characterisation of high-quality habitat, whether for potential release sites or ongoing protection efforts, requires explicit definition. Our results show that sites containing an abundance of certain non-native species can provide valuable year-round food sources for Scarlet Macaws, however the level to which this is mitigated by resultant narrow dietary breadth and dependence on exotic or cultivated species requires careful consideration by policymakers and landholders. Further research is required before the viability of anthropogenically-influenced landscapes can be reliably assessed, including the requirement for mature roosting tree species such as *Caryocar costaricense, Schizolobium parahyba* and *Ceiba pentandra* (Vaughan *et al.* 2003, Guittar *et al.* 2009).

A further component vital for the success of reintroduction efforts is the social integration of macaws with pre-established flocks upon release (Brightsmith *et al.* 2005, White *et al.* 2012). In our results, however, neither group size or foraging group size, included as potential measures of sociality, showed any significant changes across commonly foraged plant species or season. This suggests that release programmes are unlikely to be able to augment social integration through the identification of prevalent food sources or timing of releases alone. Consideration should be given to the potential of other approaches to promote the social structuring of released birds, such as post-release supplementary feeding. This technique, by providing foci for socialisation, has been found capable of more than doubling the success of psittacine reintroductions (White *et al.* 2012).

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