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Research Article

Use of wild foods during the rainy season by a reintroduced population of scarlet macaws (*Ara macao cyanoptera*) in Palenque, Mexico

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Abstract

The scarlet macaw (*Ara macao cyanoptera*) is an endangered species in Mesoamerica due to illegal traffic, habitat loss, and hunting. In Mexico, its range has been reduced by 98%. Between April 2013 and June 2014, a population of 96 individuals of *A. m. cyanoptera* was reintroduced (six releasing events), in the tropical rainforests of Palenque, southeast Mexico, where this macaw had been extinct for the last 70 years. This study documents the use of wild foods and range use by the reintroduced macaws for the rainy season period June to November, 2014. The macaws used 140 trees of 31 species (19 families; 84% native species) as a source of food. Seeds and fruit accounted for 70% of their diet. The remaining 30% consisted of bark, stems, leaves, insect galls, flowers and shoots. A subset of five tree species was highly dominant in their diet (regarding number of trees used, months used and feeding records). Spatial data showed that food trees used by the macaws were dispersed over 36 ha and had a highly clumped distribution. The macaws used an additional 23ha for non-feeding activities. The dietary diversity and breadth (as indicated by Levin´s Index) of the reintroduced macaws closely approaches that of wild macaws. The capacity of the reintroduced macaws to use wild foods, a very low mortality in the released population (9%), and the occurrence of nine successful nesting events, attests to a short-term success of the reintroduction. We discussed the observed patterns of use of wild foods and habitat by the reintroduced scarlet macaws in the context of the soft-release protocol used and of behavioral flexibility, accumulated social learning and a high cognitive capacity typical of psittacines, aspects essential for a successful adaptation to the wild.

Keywords: frugivory, reintroduction, foraging ecology, Neotropics, Psitacids

Resumen

En Mesoamérica, la guacamaya roja (*Ara macao cyanoptera*) está amenazada debido al tráfico ilegal, la pérdida de hábitat, y la cacería. En México, su distribución original se ha reducido en 98%. Entre abril de 2013 y junio de 2014, se reintrodujeron 96 individuos de *A .m. cyanoptera* (seis eventos de liberación), en las selvas de Palenque, México, en donde este psitácido se extinguió hace 70 años. Este estudio documenta, para el periodo de la época de lluvias junio-noviembre 2014, el uso de alimento silvestre y rango de acción de las guacamayas reintroducidas. Las guacamayas usaron 140 árboles de 31 especies (19 familias, 84% especies nativas) como fuente de alimento. Las semillas y frutas constituyeron el 70% de su dieta, el 30% restante consistió de corteza, tallos, hojas, agallas de insectos, flores y rebrotes. Cinco especies dominaron su dieta (en cuanto a número de árboles usados, número de meses en que se usaron y número de registros). El análisis espacial mostró que los árboles usados por las guacamayas como fuente de alimento se encontraron dispersos en 36ha y mostraron un patrón agregado. Otras 23ha fueron usadas para otras actividades. La diversidad y amplitud en la dieta en las guacamayas reintroducidas se aproximan a los valores reportados para poblaciones silvestres. La capacidad de las guacamayas reintroducidas para usar alimento silvestre, una mortalidad particularmente baja (9%) y la ocurrencia de nueve eventos de anidación, atestiguan el éxito de la reintroducción a corto plazo. Se discuten los patrones observados de uso de alimento silvestre y uso del hábitat en el contexto del generalismo ecológico, aprendizaje social acumulado y una alta capacidad cognitiva, típicos en psitácidos y esenciales para una adaptación exitosa al medio silvestre.

Palabras clave: reintroducción, ecología de forrajeo, Neotrópico, psitácidos

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Introduction

Reintroductions of species, which are locally or globally extinct, have proven to be effective for the restoration/conservation of many threatened fauna [1,2]. For example, the red-necked ostrich in Saudi Arabia, the southern ground Hornbill in South Africa, and the vinaceous Amazon parrot in Brazil (see these and other case studies in [3]). Although its use as a conservation tool remains controversial [2, 3], reintroduction to restore or reinforce populations in its indigenous range is nonetheless a valuable approach [1].

The family Psittacidae encompasses 374 extant species worldwide, but 52% are reported by the IUCN Red List, with populations decreasing (http://www.iucnredlist.org/by; consulted May 3, 2015). A recent assessment of the common denominators of success in psittacine reintroductions indicates that a first-year survival >0.50 and released birds breeding with conspecifics is an important measure of success. In addition, habitat quality and post-release supplementation are important predictors of successful psittacine reintroductions [4].

Eighteen extant species of macaws are recognized for the Neotropics, most of them found in South America (http://www.iucnredlist.org/by; consulted May 3, 2015). The IUCN Red List categorizes the scarlet macaw (*Ara macao*) as Least Concerned due to its broad geographic distribution in the Neotropics (Mexico to the east of the Andes in Colombia, Ecuador, Peru, Bolivia, Brazil, French Guiana, Guyana, Suriname, Trinidad and Tobago and Venezuela), but classifies populations as decreasing. Two subspecies are distinguished in Mesoamerica: *Ara macao cyanoptera*, found from Mexico to central Nicaragua and *Ara macao macao*, from southern Nicaragua to South America. The conservation status of *A. macao cyanoptera* is dire in its indigenous range. For example, this macaw is regionally extinct in El Salvador and occurs in very low numbers in Mexico and in a few localities in Guatemala, Belize, Honduras and Nicaragua [5]. Illegal traffic, habitat loss and hunting have resulted in the local and regional extinction of this macaw within its historical range. The species is listed on Appendix I of CITES because it is threatened with extinction due to illegal traffic [6].

In Mexico, the scarlet macaw historically occurred from southern Tamaulipas through the lowlands of the states of Veracruz, Tabasco, Campeche, Oaxaca and Chiapas [7]. Currently, illegal traffic, hunting and habitat loss have reduced its range in Mexico by 98% [8]. Only about 150-200 scarlet macaws exist in the southern Lacandon forest in the state of Chiapas, close to the border with Guatemala, and about 50 individuals apparently occur in the Chimalapas mountain region shared by the states of Oaxaca and Chiapas [8]. This macaw is classified as “Endangered” by the official environmental norm of the government of Mexico [9]. Recent studies have shown that the scarlet macaw population in the Usumacinta River Basin shared by Mexico, Guatemala and Belize consist of only about 400 breeding individuals [10,11].

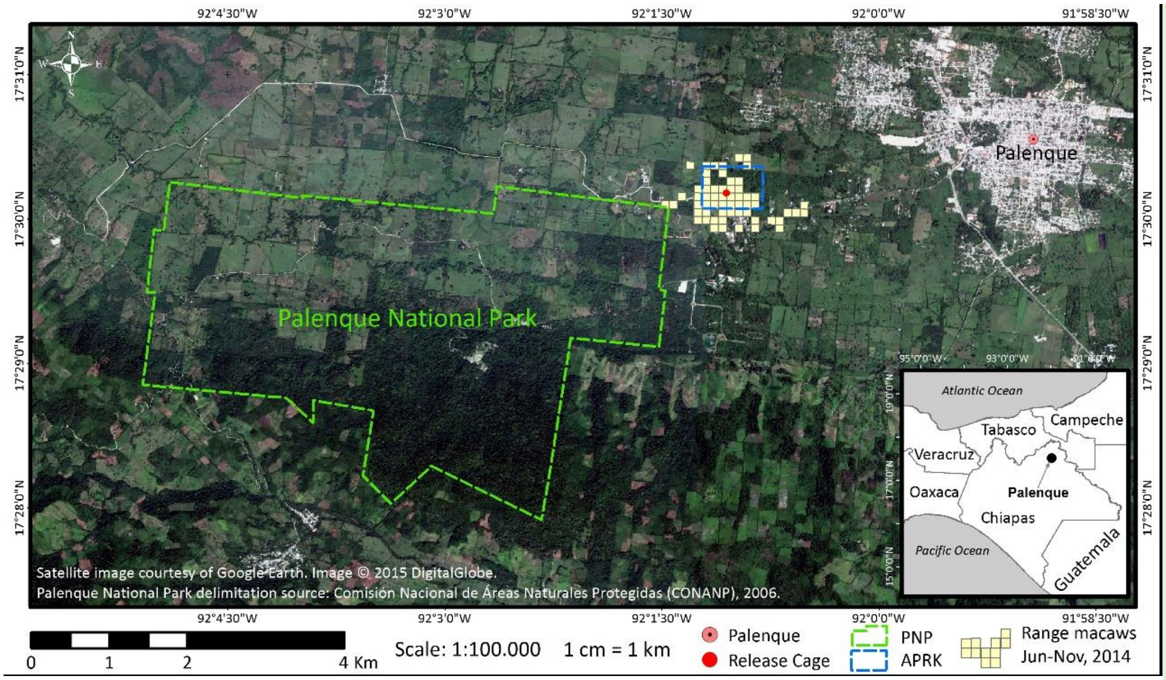
Such concern led to the design and implementation of a reintroduction program for the scarlet macaw in the region of Palenque, Chiapas, in southeast Mexico, where this macaw had been extinct for 70 years [12, 13]. This initiative brought together three institutions: Aluxes Ecopark of Palenque (Aluxes, hereafter; provider of the release site), Xcaret Ecopark (donor of captive bred scarlet macaws) and the Institute of Biology of the National Autonomous University of Mexico (provider of the scientific planning, execution and follow up for the project) [13]. The release program followed a soft-release protocol, which included pre and post release monitoring and post-release food provisioning. Between March of 2013 and June of 2014, 96 captive bred adult scarlet macaws were released in the forest of Aluxes, located near Palenque National Park [13] (Fig. 1).

This paper documents the use of wild foods and range use for the rainy season months of June to November 2014 by the reintroduced population of scarlet macaws in the protected rainforest of Aluxes and in adjacent land in Palenque, southeast Mexico. We assumed that one key measure of adaptation to the wild by the captive-bred scarlet macaws released in Palenque would be their capacity to discover and use wild foods to satisfy metabolic and nutritional requirements, and that this would be accompanied by an expansion of their range within and beyond the release site. An additional question framed by our study was to what extent the captive bred reintroduced macaws would develop a dietary diversity and breadth similar to those observed in wild scarlet macaws.

Methods

Study site

Implementation of the reintroduction project began in April 2013 with a first release of macaws in the forested grounds of Aluxes, a rescue and rehabilitation center for wildlife (17°30'10.9"N; 92°1'4.3"W). The land of Aluxes encompasses *ca* 44ha with extensive forest cover, several lagoons and about 7ha consisting of seasonally flooded wetlands. The site is only about 0.5 km from the forest that extends toward Palenque National Park (*ca* 1,800 ha; Fig. 1), which we expect that the reintroduced macaws will eventually add to their range.



Satellite image courtesy of Google Earth. Image © 2015 DigitalGlobe.
Palenque National Park delimitation source: Comisión Nacional de Áreas Naturales Protegidas (CONANP), 2006.

Fig. 1. Location of Aluxes Ecopark (APRK; square polygon with broken blue line). Yellow squares are 1ha cells, illustrating the range of the scarlet macaws from June to November 2014. Broken green line is the polygon of Palenque National Park (PNP).

Released population

All scarlet macaws released were captive bred at Xcaret [14] and were divided into groups for a scheduled set of sequential releases. Between March of 2013 and June of 2014, 96 adult scarlet macaws were released in six releasing events (April, June, August and December 2013; March and June 2014) in the forest of Aluxes [13]. Mean age of individuals at the time of release was 35.1±17.7 months; range 11–86 months (only two individuals were 11 months old and only two individuals were $\geq$ 80 months old). Thirty five percent of the released macaws consisted of individuals between 11 and 24 months of age, 43% between 25 and 48 months of age and 22% were $\geq$ 48 months. The released population consisted of 56 females and 40 males. All reintroduced macaws had a subcutaneous microchip and a numbered leg band. In addition, each individual had an external mark painted on the beak or tail feathers. Such external marks lasted about 60 days (see [13]). All aspects of pre and post-release soft protocols complied with regulations and ethics of the government of Mexico.

Overall mortality of macaws since the first release was restricted to nine of 96 individuals released. These events occurred between May 2013 and September 2014. The cadaver in all nine cases of death was recovered. Causes of death were crocodile predation (4 cases; individual macaws falling into a lagoon), newly released macaws hitting branches while flying (3 cases) and unknown (2 cases). Necropsies conducted on the cadavers by the veterinary staff at Aluxes indicated as causes of death, physical trauma and unknown. The latter due to the high degree of decomposition of the body. No additional mortalities have been detected between October 2014 and May 2015.

Pre-release diet and pre-release wild foods training

In Xcaret, the macaws were fed a diet consisting of soft commercial fruits such as bananas, papaya, and others, boiled and broken corn, parrot food pellets and corn dough mixed with beets and other vegetables [14]. This diet was continued while macaws were in the aviary at the release site, but with two important changes: (1) corn was replaced by sunflower seeds (*Helianthus annuus;* Asteraceae) and (2) weekly offering of wild foods. Sunflower seeds are rich in energy (580 kcal/100g dry weight), protein and vitamins and contain many trace metals (calcium, potassium and sodium, among others) [20], and, importantly, are not grown in the area. Wild foods consisted of fruits of tree species consumed by scarlet macaws in the wild in Belize and northern Guatemala [5], and present in the forest of Aluxes as well as in Palenque National Park and surrounding forested areas. The species used were *Ficus insipida* and *Ficus benjamina* (Moraceae), *Brosimum alicastrum* (Moraceae), *Cecropia peltata* (Urticaceae), *Spondias mombin* (Anacardiaceae), *Enterolobium cyclocarpum* (Fabaceae) and *Guazuma ulmifolia* (Malvaceae). We offered wild foods to the macaws in each flock 2–3 times a week in the form of small branches pruned from large trees. We expected the offering of branches with fruits, would motivate the macaws to learn not only to recognize the fruits, but also to learn how to harvest them, as different plants offer fruits in different ways (http://www.theplantlist.org/). Training lasted from 3–4 months, a time during which they were in the pre-release aviaries.

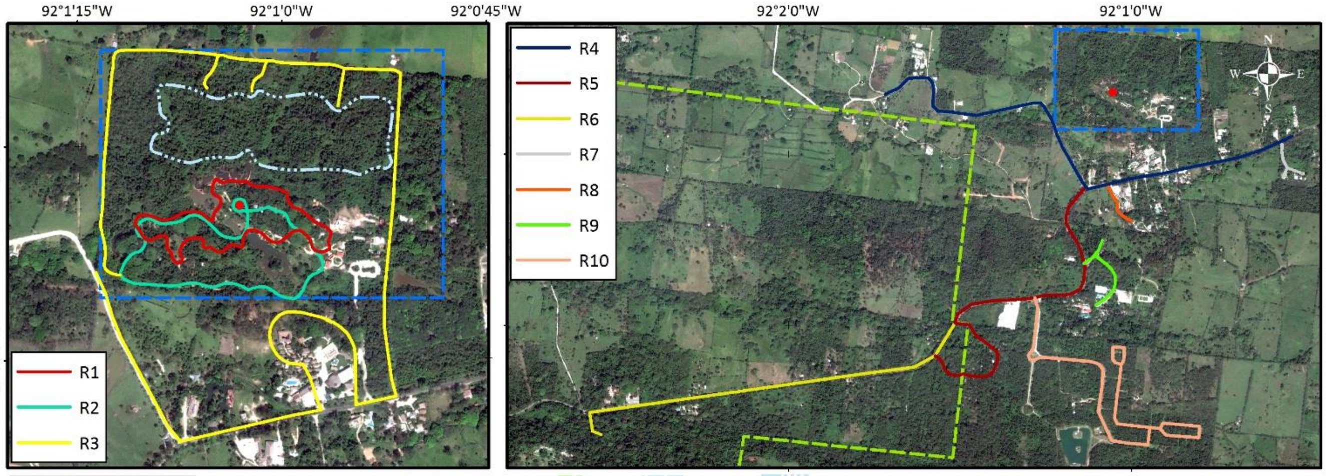
Post-release food provisioning

After release, a daily ration of 50g of sunflower seeds per macaw (about 5.8kcal/g) and water was offered in a single 6m x 3m feeding platform located in the release cage. The upper gates of the cage where the feeding platform was located remained open 24hrs a day [13]. Half of the ration was provided in the early morning (7-8 am) and the other half in the late afternoon (5 pm). The ration of sunflower seeds per macaw was estimated from published information on caloric requirements of macaws in free-ranging conditions [15]; requirement based on $BW^{0.73}$; 200–250kcal/day). Because the feeding platform located in the release cage was adjacent to the pre-release cage, it promoted familiarity between the released flocks and flocks waiting for release [13]. Post-release food provisioning was implemented with each of the six scarlet macaw flocks released to encourage a gradual adaptation to the wild by promoting site fidelity of released birds, increased social interactions, and enhanced integration of subsequently released flocks [4,13]. There are no plans to suspend or gradually reduced food supplementation, as a measure to ensure the survival of the macaws.

Observations of feeding and ranging behavior

We conducted irregular observations on the use of wild foods and ranging after the release of the first and of subsequently released flocks. However, due to time and personnel constraints and to the need to prepare each flock for its release [13], we decided to wait until after the release of the last flock to run a systematic monitoring of the use of wild foods and ranging behavior. Our observations thus reflect the gains made by the six flocks in adopting wild foods and in expanding their range within and beyond the release site, up to the end of the study period reported here.

All surveys and observations reported here were carried out by the first author and one field assistant. Between June 15th and November 15th, 2014, we spent five days a week surveying the presence and feeding activities of macaws along a network of walkways and trails at the release site. Two of these survey routes traversed the forested areas of Aluxes, except a permanently flooded area (*ca* 7ha; Fig. 2), and one ran along the entire perimeter of the land (routes 1, 2 and 3; Fig 2). These routes had a total accumulated length of 6km. Towards the middle of the study period, we added seven additional routes, when we observed macaws flying in forested areas outside of Aluxes to use food resources (Fig. 2). The additional routes had an accumulated length of 12.1km. All routes were walked at a speed of 1km/hr. Surveys were conducted from 6:00 to 10:00 am and from 4:00 pm to 6:30 pm between June and August and from 7:00 to 11:00 am and from 3:30 to 5:30 pm from September to November, to adjust for differences in the length of the day in these two time blocks. We made additional *incidental* observations in non-survey days when we traversed some of the routes. We used survey routes to access as much area as possible within the grounds of the release site and adjacent areas. When we detected macaws along the routes by sound or sight, the observers moved into the forest to reach their location. We used 10 x 42 binoculars for observations.



Satellite images courtesy of Google Earth. Images © 2015 DigitalGlobe. Palenque National Park delimitation source: Comisión Nacional de Áreas Naturales Protegidas (CONANP), 2006.

Fig. 2. Left, routes 1–3 (red, aquamarine, yellow lines) in the grounds of Aluxes Ecopark (APRK). Broken light blue polygon within the yellow route is a flooded area. Right, routes outside of the release site (4–10, blue, crimson, yellow, gray, orange, green and pink lines).

Once with the macaws, we recorded a GPS waypoint and proceeded to run an instantaneous scan sampling, noting the number of individuals present and their activities. Two major activities were recorded: feeding (manipulation and ingestion of plant parts) and non-feeding (perching, social interactions, locomotion along tree branches, short flights between trees, and beak manipulation of dry branch sticks and leaves without evidence of ingestion). If a feeding bout was observed, we noted the number of macaws involved in this activity, the plant life form, the plant parts consumed (seeds, ripe and unripe fruit, young or mature leaves, shoots, stems, flowers and tree bark) and the taxonomic identity of the plant. We defined a feeding bout following Renton [16], as one or more macaws feeding on a food source. If the macaws shifted to another food source during the period of observation, we considered this as a second feeding bout [16,17]. This method does not provide independence between foraging events recorded sequentially, but it emphasizes the diversity of items consumed by birds [18]. The category “seeds” refers to records of macaws eating only the seed and to the records of macaws eating seeds mixed with pulp. The category “fruit” includes the consumption of pulp, shell or both, discarding the seed.

At the end of each feeding bout, we collected samples and took photographs of food items and of the tree. All trees used by the macaws as a source of food were GPS located and marked with a numbered tag, their DBH measured and their height estimated. While we were able to identify several tree species in the field, others required collecting herbarium specimens. A plant taxonomist at the National Herbarium of Mexico in Mexico City identified these samples.

We used ArcGIS® 10.2 ESRI (http://www.esri.com) to plot the GPS records of trees used as a source of food by the macaws onto a Google Earth satellite image. Also, using ArcGIS®, a grid consisting of 1ha cell was overlaid on the image and the feeding trees found within the cells were counted. Such grid encompasses an area about 190ha in size, and had as its origin the geographic location of the release cage.

Data analysis

We calculated monthly dietary species richness from feeding records and estimated the number of potential species richness in the diet using the software EstimateS (version 9.1.0) [19,20]. We used the JACK1 estimator from EstimateS [19], considered an accurate predictor of species richness [21]. This estimator has been used in other studies documenting the diet species richness in several species of parrots, including macaws [22]. To estimate the degree of uncertainty with predicted species richness, we used the Abundance-based Coverage Estimator (ACE; [23,24]) and the coverage sample was estimated in iNext Online [23,25].

In order to test if the recurrent use of specific tree species in the diet of the macaws was due to their temporal proximity, we used the Mantel test [26] to test the correlation between beta diversity and the temporal distance between months. We used Rank Abundance Curves, given by the number of trees used per species, to assess relative dominance of tree species in the monthly diet of macaws. On this curve, species are plotted for the six sampling months from the most abundant (left) to the least abundant (right) along the X axis and the proportional abundance along the Y axis [27]. To determine the breadth of the macaws’ diet for the study period, we used the standardized Levin’s niche breadth index. Values close to 0 indicate a specialized diet and values close to 1 indicate a broad diet [28]. We calculated the Morisita index of dispersion [29] to determine if the spatial distribution of trees used by the macaws as a source of food presented a uniform or a clumped pattern. If the value of the index falls between 0 to 1, it suggests a uniform distribution and if it falls between 1 and n, it suggests a clumped pattern. The deviation from random expectation was tested using critical values of the Chi-squared distribution with *n-1* degrees of freedom [30]. Means and standard deviations are expressed as mean±sd throughout.

Vegetation survey

To estimate the relative dominance of tree species used by the macaws as a source of food in the tree community, we sampled the tree vegetation using 10 randomly located 50 x 2m transects [31] in the forested area of the release site, avoiding the flooded area (*ca* 7ha; Fig. 2). This procedure is logistically simple to implement and it is a standard method used worldwide for sampling vegetation in tropical forests, as it allows for comparable units and the resulting data is an accurate statistical representation of the structure and composition of the vegetation of the surveyed area [31, 32]. Within each transect, we identified and measured all trees with a DBH of ≥ 10cm and a height of ≥ 3m. A plant taxonomist (Alvaro Campos MSc) from the National Autonomous University of Mexico, and expert in the flora of tropical rainforests, assisted in the census of the vegetation and provided the taxonomic identification of each tree in the field or via herbarium samples. From the transect data, we quantified species richness, density, and basal area for all tree species. For each tree species in the survey, we calculated an importance value index (IVI). The IVI is an indicator of the species importance in the tree community and is calculated by the sum of the species density (number of individuals of species x / area sampled), frequency (number of transects in which species x occurs / total number of transects) and dominance (total basal area of the species in the sampled area). The higher the value of the IVI, the higher the importance of species in the tree community [33].

Range estimate

We do not report the area of habitat used by the macaws as a home range estimate, but rather as a total range estimate for the duration of the sampling period [34]. We estimated total range use by the macaws by recording the geoposition of the central mass of each stationary flock intercepted along the survey routes. The GPS location data were transferred and plotted onto the gridded (1ha cells) digital map of the release site and of areas beyond using ArcGIS® 10.2. The number of cells in which macaws were present during the surveys provided a general assessment of the size and shape distribution of the range used in each month and for the entire study period.

Habitat use estimate

We estimated overall and monthly habitat use by combining records for feeding and non-feeding activities in each of the cells in which macaws were present. We made the same estimate separately for feeding records. We calculated intensity of use of each cell for each month as the percentage of records contributed by each cell to the total foraging records scored for all cells. Based on the proportional distribution of records, we classified cell use by the released macaws into three categories: heavy use (>15% records), moderate use (> 5<15% records) and light use (<5%). We used ArcGIS® 10.2 to illustrate range and habitat use by the macaws, using these categories.

RESULTS

Sampling effort achieved

During the study period, we completed 262 survey sessions, of which 91% were on the grounds of the release site (routes 1-3; Table 1). The sampling effort resulted in an accumulation of 2,087 records of the presence of macaws along surveyed routes, but 96% of these were on the three principal routes in the grounds of Aluxes. We recorded 283 feeding bouts, 82% logged in the three main survey routes (Table 1). The value of the coverage sample was 0.9217, that is, our coverage sample was 92%.

Table 1. Sampling effort completed during the study period.

Routes	Field hours	Length (km) of routes	Cumulative km	Sessions am	Sessions pm	Total sessions	Feeding records	Total records
1–3	436	6	408	147	92	239	233	2,012
4–10	66	12	43	15	8	23	13	26
Incidental	7						37	49
Total	502	18	451	162	100	262	283	2,087
Routes 1–3 as % of total	87			91	92	91	82	96

Plant taxa used and niche breadth index

Trees were the only plant life form recorded in the diet of macaws during the study period. The macaws used 140 trees as a source of food. These represented 31 species of 19 families (Appendix 1). Five plant families accounted for 55% of the tree species recorded in the macaws' diet (Fig. 3). Of these, the Fabaceae and Malvaceae stand out with 32% of the tree species followed by the Anacardiaceae, Boraginaceae and Myrtaceae (Fig. 3). Five of the 31 tree species used as a source of food by macaws were non-native species. These were *Tectona grandis* (Lamiaceae), *Terminalia catappa* (Combretaceae), *Eucalyptus robusta* (Myrtaceae), *Ficus benjamina* (Moraceae) and *Zanthoxylum panamense* (Rutaceae). These species accounted for 8.5% of feeding records and for 8.6 % of the trees used as a source food (Appendix 1). Mean monthly dietary niche breadth index (standardized Levin's index) for the study period was 0.24±0.12, and it ranged from 0.07 in October to 0.36 in August, indicating a narrow dietary breadth. Mean DBH and height of trees used by the macaws as a source of food were 45.3±43.2cm (range 6–298 cm) and 12.8±5.9 m (range 3–35 m), respectively.

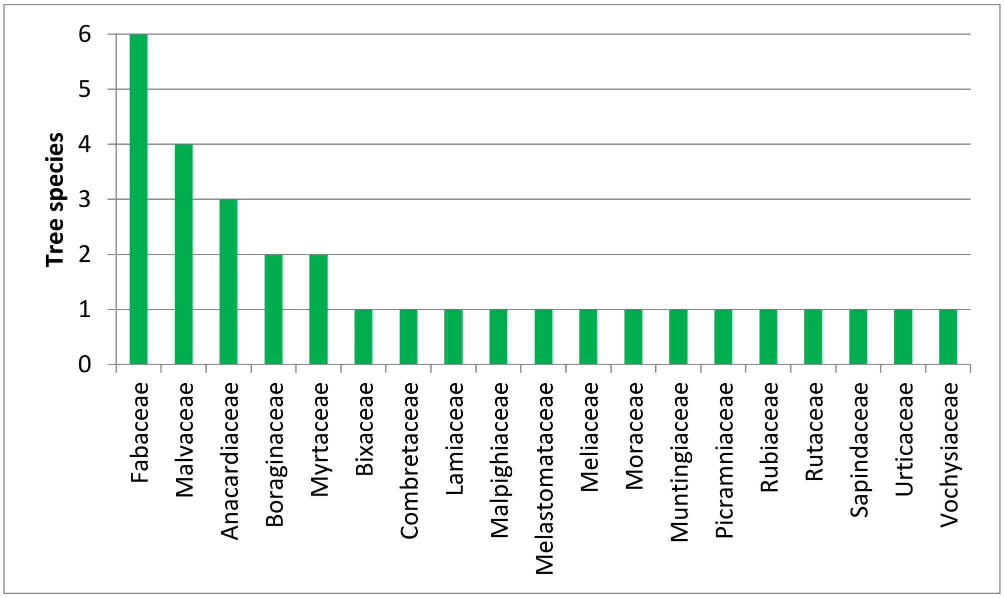


Fig. 3. Plant families represented in the diet of the scarlet macaws for the period June-November 2014.

Predicted dietary species richness and relative importance of tree species in the diet

Curves for the three estimators of species richness showed steep species accumulation curves indicating, as expected, incompleteness in our sample. However, it also suggested that the scarlet macaws are expected to add about 10–13 more tree species in their diet (Fig. 4a). Mean monthly predicted dietary species richness using the Jack1 estimator was 30.89±12.5. Mean monthly Abundance Coverage Estimator (ACE) was 32.54±9.1. Five tree species (*Cordia stenoclada, Muntingia calabura, Entorolobium cyclocarpum, Psidium guajava* and *Cupania glabra*) were particularly important in the macaws' diet, accounting for 56.5% of feeding records (Appendix 1). These species also accounted for 51.4% of the trees used as a source of food and were used by the macaws for an average of four months. In contrast, the macaws used the rest of the tree species as a food source for an average of 1.7 months (Appendix 1). The relative dominance of tree species in the diet of macaws, given by the number of trees used per species over the study period, varied from month to month, with a subset of tree species dominating their diet in each month (Fig. 4b). Number of feeding records and number of trees used per species were correlated ($r_s = 0.896$ $p<0.001$) and number of months species were used was associated with the number of trees recorded ($r_s = 0.797$ $p<0.001$).

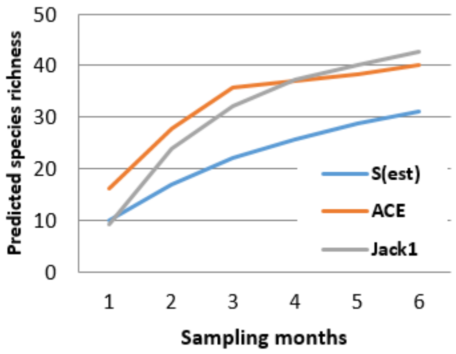


Fig. 4a. Predicted species richness in the diet using three estimators (see methods).

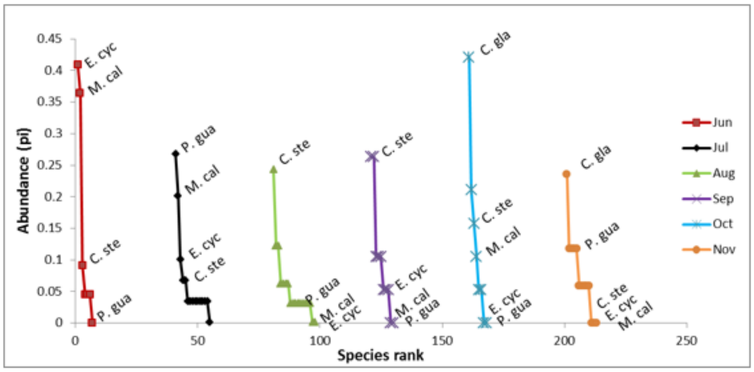


Fig.4b. Monthly abundance curves, given by the number of trees used per species in the diet of scarlet macaws. Species codes: C. ste: *Cordia stenoclada;* M. cal: *Muntingia calabura;* E. cyc*: Entorolobium cyclocarpum;* P.gua: *Psidium guajava* and C. gla: *Cupania glabra.*

Plant parts consumed

Consumption of seeds and fruit accounted for 70% of feeding records (n = 283), but the consumption of seeds alone accounted for 56%. Other food items (bark, stems, leaves, insect galls, flowers and shoots accounted for the remaining 30% of the feeding records (Table 2). Nineteen tree species were the macaws' source of seeds and they accounted for 80% of the trees used as a food source. The macaws ate the bark and shoots of 14 and 12 tree species, respectively. These species contributed to about 14% of the trees used (Table 2).

Table 2. Plant parts and insect galls (ranked by number of feeding records) in the diet of scarlet macaws for the period June-November 2014.

Plant parts and insect galls consumed	Feeding records	%	Cumulative %	Tree species	Number of trees	Number of months used
Seeds	159	56.2	56.2	19	112	6
Fruits	38	13.4	69.6	5	22	6
Bark	29	10.2	79.9	14	21	6
Stems	24	8.5	88.4	12	22	4
Leaves	10	3.5	91.9	5	9	5
Insect Galls	10	3.5	95.4	1	7	2
Flowers	8	2.8	98.2	7	8	4
Shoots	5	1.8	100	4	4	2
TOTAL	283					

Monthly variations and overlap in use of tree species as a source of food

The mean number of tree species used per month as a source of food by the macaws were 12±4.3 (range 6–19). Mean number of trees used per month was 31.5±10.5 (range 22–49). The macaws added new tree species to their diet at an average rate of five species per month. Monthly accumulation of new tree species in their diet was associated with monthly increments in the number of trees used as a source of food (Rs = 0.972 p< 0.001).

Eight species of trees were used as a source of food for 4–5 months, 10 were used from 2–3 months and the remaining 13 for one month (Appendix 1), indicating a recurrent use of selected sets of tree species as a source of food from month to month. The macaws used three tree species (*C. stenoclada*, *M. calabura* and *E. cyclocarpum*) as a source of food for five months. These three species also accounted for 49% of the trees used as a source of food (n = 140) and for 45% of the feeding records (n = 283). In the sixth month of the study period, another four tree species (*Cedrela odorata*, *Guazuma ulmifolia*, *Luehea speciosa* and *Picramnia antidesma*) became predominant in their diet *(*Appendix 1). The Mantel test showed a lack of a correlation between the beta diversity matrix and temporal distance matrix (p>0.05, where the Ho = matrix are not correlated), indicating that the use of some species of trees between consecutive months was not due to temporal proximity.

Size of foraging flocks

Size of foraging flocks at feeding trees ranged from 1 to 35 individuals, but 92% of the flocks was composed of six or less individuals (Fig. 5). Three tree species (*Pachira aquatica*, *L. speciosa* and *G. ulmifolia*) had the largest flock size recorded in a single foraging event, 35, 31, and 21 individuals, respectively. However, these flock sizes were only recorded once during the study period. Three additional tree species (*Cupania glabra*, *Cordia collococca* and *C. stenoclada*) had foraging flocks ranging in size from 10 to 16 macaws.

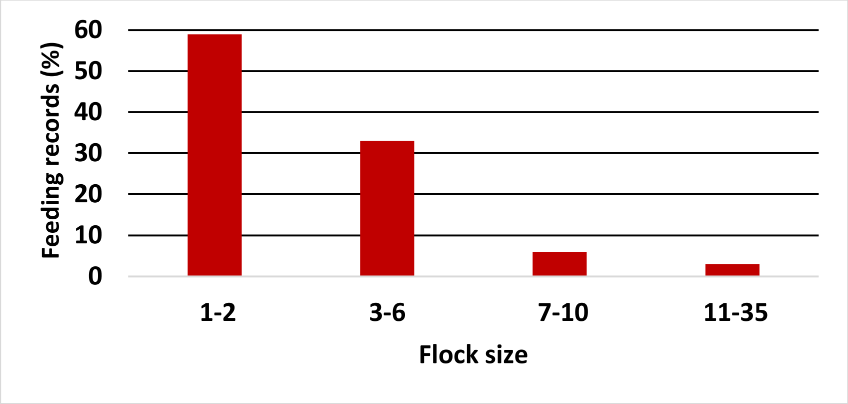


Fig.5. Size distribution of scarlet macaw foraging flocks at feeding trees.

Vegetation survey

We recorded 80 trees of 32 species of 17 families in the vegetation survey. Thirteen of the tree species detected in the surveys were species used by the macaws for food. These included three of the eight top species in their diet, *C. stenoclada*, *E. cyclocarpum* and *M. argentea* (Appendix 1). The mean IVI value of the thirteen species used for food by macaws was 0.154±0.130 (range 0.033–0.455). For the nineteen tree species not recorded in the macaws´ diet, but which appeared in the vegetation census, for the study period, the mean IVI was 0.053± 0.029 (range 0.033–0.148).

Spatial distribution of feeding trees

The trees used as a source of food by the macaws during the study period were found in 36 cells in the release area (Fig. 6a). Spatial analysis of concentration of food trees in the release area showed that 50% of the trees (n = 140) were found in seven cells, six of which were located within the grounds of the release site (Fig. 6b). The rest of the trees displayed a more dispersed spatial patterns and located in areas within Aluxes and beyond (Fig. 6b). Calculation of Morisita's index showed that the spatial distribution of trees used for feeding by the macaws was clumped (iMor = 1.63) and did not follow a random pattern (X^2 = 123.31, df = 35, p <0.001).

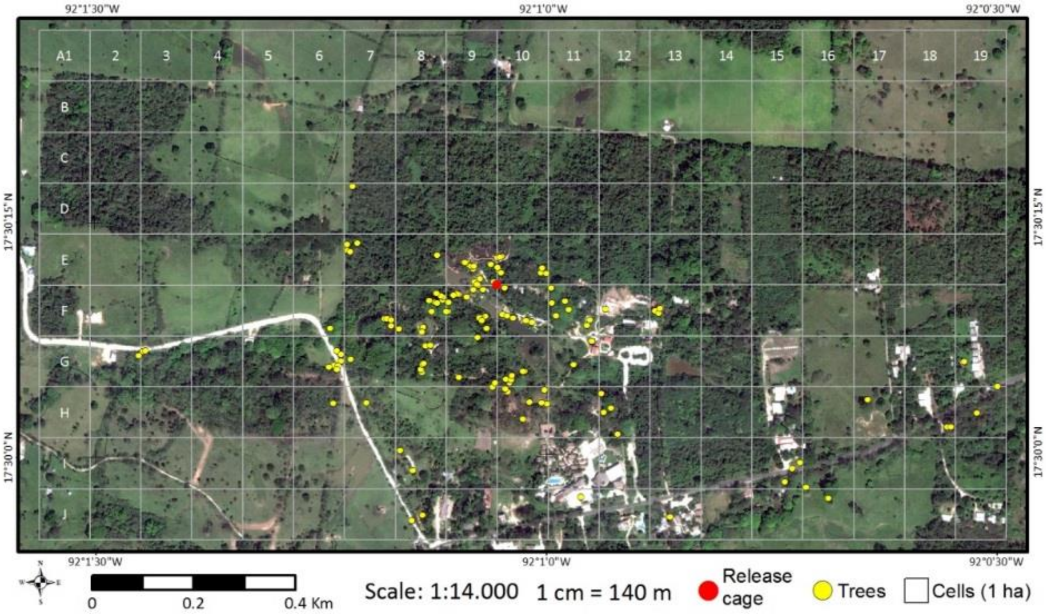


Fig. 6a. Spatial distribution of trees (n = 140) used by the scarlet macaws as a source of food at the release site during the study period (June-November 2014). Grid = 1ha cells.

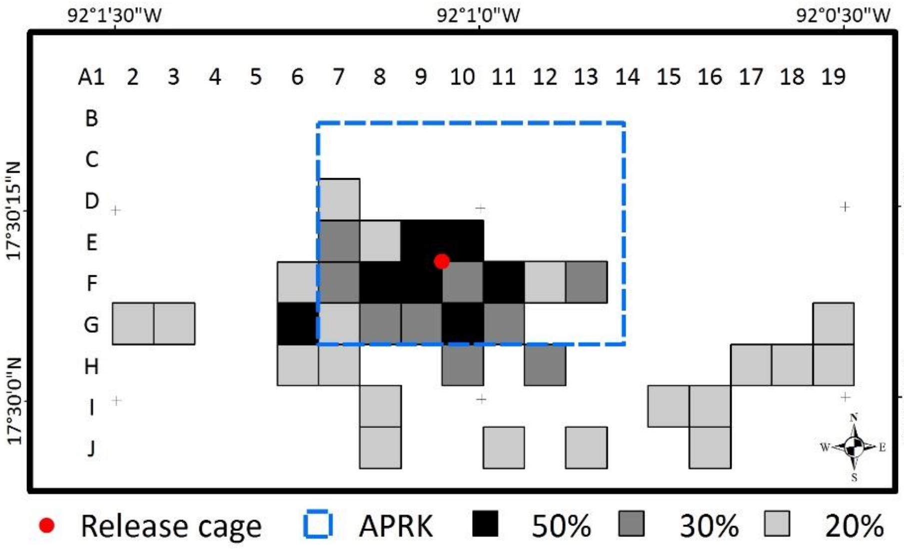


Fig. 6b. Map of 1ha cells (N = 36) harboring trees used by the scarlet macaws as a source of food from June to November 2014. Color intensity indicates levels of concentration of food trees. Square with broken line indicates the grounds of Aluxes Ecopark. Red dot shows location of release cage and feeding platforms used for post-release food provisioning. Total area shown in the map, 190ha.

Total range and foraging range estimates

Total range used (feeding and non-feeding activities) by the macaws for the study period was estimated at 59ha (Fig. 7a). The mean monthly area used by the macaws for feeding and non-feeding activities was 26.8±8.1ha and it ranged from 16ha in June to 37ha in July (Appendix 2). The Morisita's index showed that the spatial distribution of cells occupied by macaws during our study period was significantly clumped (iMor = 6.89) and that did not follow a random pattern (X^2 = 8478.617, DF = 58, p<0.001). The monthly range distribution shows that macaws also shifted areas of activity and this involved an expansion of their range outside of the grounds of the release site. Range estimated from feeding records was 36ha or 61% of all cells used by the macaws (Fig. 7b). Mean monthly area used by the macaws for feeding was 14.3±2.7ha and it ranged from 11ha in June to 19ha in August (Fig. 7b; Appendix 3). The Morisita's index indicated that the spatial distribution of cells occupied by macaws during the study period was clumped (iMor = 2.26) and that it did not follow a random pattern (X^2 = 389.2968, df = 35, p<0.001). The monthly feeding range shows that the macaws expanded their foraging range outside the grounds of the release site (Fig. 7b, Appendix 3). Intensity of use (number feeding records) of habitat cells was closely associated with the number of food trees found in each cell (r_s = 0.816 p <0.001).

Cumulative monthly range increase

Cumulative cell occupancy by macaws increased over the months of the study period (Fig. 7a). The macaws added new cells to their habitat-range at a rate of 9.3 cells per month. Addition of habitat cells over the months by the scarlet macaws was positively associated (r_s = 0.940 p <0.005) with cumulative habitat cells used for feeding, suggesting that monthly range expansion was closely associated with the addition of new food trees and species (Fig. 7b).

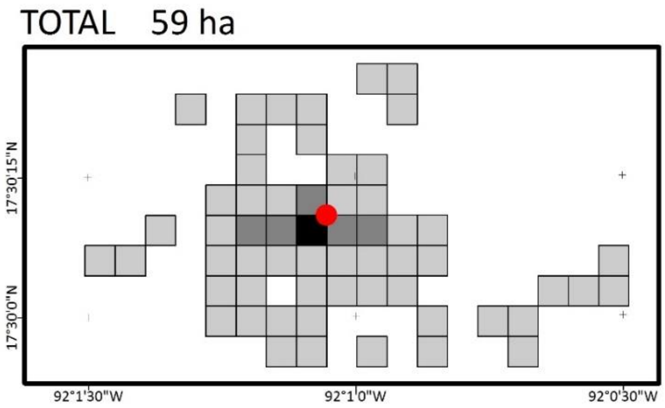


Fig. 7a. Total range used by the scarlet macaws for the study period, given by location of feeding and non-feeding activities (see methods), during the study period. Cells are 1ha. Intensity of use indicated by the black to light gray shaded pattern. Black represents heavy use (>15%), gray moderate use (5–15%) and light gray light use (<5%). Red dot indicates the location of release cage. Monthly variation shown in Appendix 2.

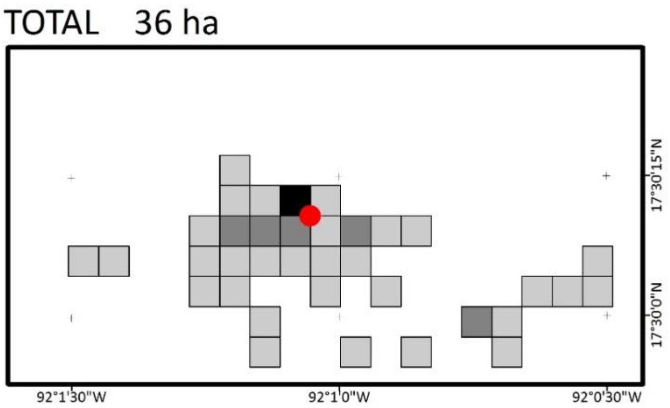


Fig. 7b. Total foraging range of scarlet macaws for the study period, given by the location of feeding records. Intensity of use indicated by the black to light gray shaded pattern. Red dot indicates the location of release cage. Monthly variation shown in Appendix 3.

Cumulative DBH of feeding trees and habitat cells

A few habitat cells contained the highest values of cumulative DBH of food trees. Eight cells accounted for 52% of the cumulative DBH. Another seven cells accounted for 27% and the remaining cells accounted for 21% (Fig. 8). Intensity of use of habitat cells for feeding was positively associated with the cumulative DBH of trees used for feeding ($r_s = 0.781$ p <0.001).

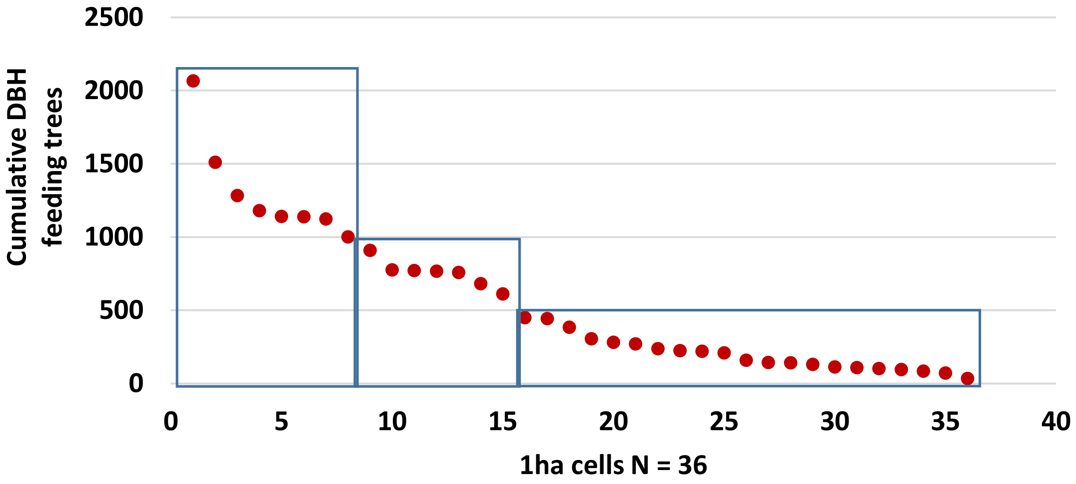


Fig. 8. The sum of DBH in cm of food trees as a function of habitat cells in which the macaws fed in the study period. Cumulative DBH values were skewed toward 15 cells. The boxes separate, for illustrative purposes, three groups of cells differing in cumulative DBH.

Recurrent use of food trees

The macaws used 59 food trees more than once as a source of food during the study period. These trees belonged to 23 species. Notably, 54% of such records were of trees of the four top-ranking species in their diet (*C. stenoclada* and *M. calabura, E. cyclocarpum* and *P. guajava*), with the first two accounting for 40% of such records (Fig. 8). Mean number of months food trees were reused by the macaws was 1.4±0.70 (range 1–4). Mean number of times individual food trees were used by the macaws more than once was 3.4±2.1 (range 2–14).

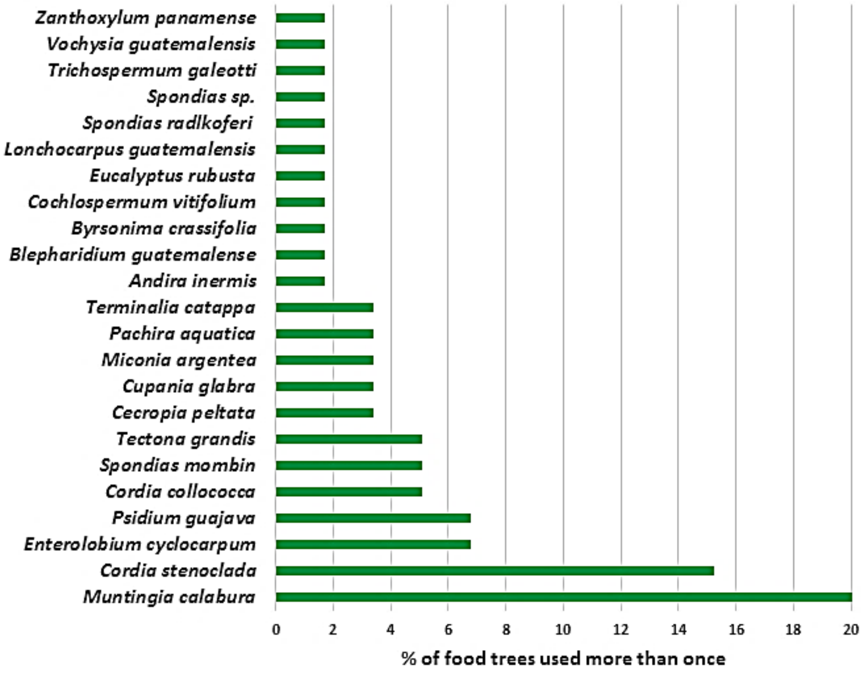


Fig. 8. Tree species used as a source of food by scarlet macaws ranked by the number of food trees used more than once during the study period

Discussion

Although our study did not encompass an annual cycle of monitoring the use of wild foods by the reintroduced macaws and thus annual cycle-related seasonal changes in dietary preferences and range are unknown, it nonetheless provided enough information suggesting an initial successful adaptation of the macaws to the wild. Field observations showed that the reintroduced scarlet macaws used 31 species of trees as a source of seeds, fruit and other food items during the study period. A subset of five tree species dominated their diet, by number of trees used, number of months used and number of feeding records. It also showed that the macaws added an average of five new tree species to their diet per month, a pattern paralleled by an overall addition of food trees. The reintroduced macaws increased range area over the months of the study period as they added tree species to their diet and also habitat areas where they carried out non-feeding activities.

The reintroduced macaws fed on five of seven tree species used for pre-release food training. Two of these, (*E. cyclopcarpum* and *S. mombin*)*,* were the third and sixth highest ranking in their diet (Appendix 1). Pre-release food training may have accelerated the process of discovery of potential food resources by the macaws in the forest of the release area, although we cannot ignore a serendipitous detection of wild foods familiar to the macaws. The most important plant families in the diet of the reintroduced macaws in Palenque were Fabaceae, Malvaceae, Anacardiaceae, Boragynaceae and Myrtaceae. Species in these families have been reported as important in the diet of wild *A. macao* in Manu National Park and Tambopata-Candamo Reserve Zone in Peru [46] and in National Wildlife Refuge Curú [35] and in Parque Nacional Piedras Blancas [36], both in Costa Rica.

Seeds and fruit pulp were the predominant items in the diet of the reintroduced scarlet macaws in Palenque. Notably, they also used other plant parts to their diet such as leaves, stems, shoots, flowers and bark and were also observed eating leaf-gall larvae. This suggests that the reintroduced macaws identified plant parts suitable as food to satisfy their metabolic and nutrient requirements. Such pattern of food use is typical of scarlet macaws in the wild and in reintroduced populations. For example, seeds were the most important food item in the diet of wild scarlet macaws in Belize, but supplemented it with consumption of fruit, young leaf, stems and leaf-gall larvae [37]. In Tambopata National Reserve in Peru, seeds and fruit pulp dominated the diet of wild scarlet macaws [22]. In a tropical forest of Costa Rica wild scarlet macaws fed on seeds, fruits, leaves, flowers and bark [38]. Seeds and fruit pulp accounted for 73% and 10% of the diet, respectively, in reintroduced scarlet macaws in the National Wildlife Refuge Curú, Costa Rica, but also complemented their diet eating bark, flowers, leaves and lichen [35]. The reintroduced scarlet macaws in Palenque had an item-based diet as diverse as that of wild scarlet macaws, with seeds and fruits dominating their diet.

A study conducted in Manu National Park and Tambopata, Peru, showed that seeds consumed by 17 species of parrots, including *A. macao*, tended to be higher than other plant materials in protein and lipid content and lower in fiber, and seem to contain important levels of toxicity [39]. The authors indicate that the ability to deal with food items rich in toxins may allow rainforest-dwelling parrots to use a high diversity of plant species as a source of food. This trait may have been advantageous in the success with which scarlet macaws reintroduced in Palenque incorporated a wide array of tree species to their diet. While post-release food provisioning helped the macaws deal with metabolic costs while adapting to a free-ranging life, notably such provisioning consisted of only sunflower seeds. Clearly, by gradually incorporating a suite of tree species to their diet and by consuming a varied set of plant parts, the scarlet macaws seem to have been able to meet the higher energy demands of a free-ranging life, while at the same time balancing their diet. The low mortality of the reintroduced population truly attests to their dietary success.

The low values of the overall dietary niche breadth index (Levin's index) for the study period for the macaws in Palenque, suggests a relatively narrow dietary niche breadth or a concentrated use of a few existing resources. Low values of the index are consistent with reported low dietary niche breadth index values for 13 parrot species, including *Ara macao*, in Tambota National Reserve, Peru. Here the index ranged from 0.24 to 0.60, with ten species having an index < 0.50 or a narrow dietary niche breadth [22]. Low values of the index are also reported for wild *A. macao cyanoptera* in Belize; dry season Levins' diet breadth index was 0.394 and 0.216 in the wet season [37]. In a reintroduced population of *A. macao* in Costa Rica, Levins' diet breadth index was 0.118 [35]. Predicted dietary species richness in the diet indicated that about 10–13 tree species could potentially be added to the macaws diet documented by our study. Clearly, reintroduced macaws should be adding new species as they become more knowledgeable about wild foods, such that the diversity of their diet is likely to increase over time. Our data showed that the reintroduced macaws added about five new tree species to their diet per month and that trees of many of these species were highly dispersed. This suggests that they were probably using and expanding a cognitive map regarding the spatial and temporal location of food resources in the release area, such as has been reported in other birds [40], and it is possible that their foraging may have also been based on random exploratory movements resulting from tree-scale foraging experiences [41]. Bearing in mind the above and the short duration of our study, it is likely that our data set is an underestimate of food species that the reintroduced macaws use as a source of food.

The vegetation surveys showed that three of the species dominant in their diet (*C. stenoclada, E. cyclocarpum* and *M. argentea*) were highly dominant in the tree community. The finding of trees of these species by the macaws could have been favored by their dominance in the landscape of the release area. However, the lower dominance of other tree species in their diet may have involved a greater effort by the macaws in finding individual trees of each. Spatial analysis showed that food trees used by the macaws during the study period were highly dispersed and that about half of them were found outside the boundaries of the release site, suggesting that the macaws were quite capable of monitoring the location of sources of food within and beyond the release site. The macaws seem to prefer to spend time in areas of the release site with concentrations of large trees, as indicated by their DBH. Such trees may not only provide them with more food, but may also be more suitable as day roosting sites, than smaller trees.

It is likely that the presence of the food-provisioning platform by the release cage may have encouraged the macaws to use areas of the forest nearby and to forage upon trees near the feeding station. This may explain the concentration of 47% of the food trees recorded in the study period within the area of the release site and around the release cage, but notably spatial analysis showed that the other 53% was found in areas beyond the release site. A similar situation accrues to areas of the habitat used for non-feeding activities (see Fig. 7). Thus, it is clear that while the presence of the food-provisioning platform was a factor influencing their presence and activities in areas nearby, the macaws also seem to have responded to changes in the availability of food by shifting habitat areas to find food trees and also selected areas where they conducted non-feeding activities, both at variable distances from the feeding platform. This supports the general notion that anchoring the macaws, via food provisioning, to the release site and its immediacy would facilitate a gradual and limited expansion of the range thus facilitating their adaptation to a free-ranging life.

While macaws were able to gather in large numbers at the food provisioning feeding platforms by the release cage and at night roosting sites (>30 individuals; A. Estrada unpublished), data showed that when harvesting wild foods, 92% of the foraging flocks consisted of $\leq$ 6 individuals. The capacity of large flocks to split up into smaller flocks when searching for and harvesting wild foods, together with their capacity to gather in large flocks in the day and night roosting sites, may diminish food competition and may also enhance social tolerance, protection from potential predators and information transmission between individuals [42,43].

Long-term supplementary feeding seems to be associated with the success of reintroduction [44], as it promotes site fidelity, improved survival and breeding success of reintroduced parrots [22]. Pre-release food training is assumed to improve recognition of food sources in the wild [e.g., 45,46], and our results seem to be consistent with these assumptions. Pre-release food training and supplementary feeding may work together to enhance the capacity of naïve macaws to discover and use wild foods to sustain themselves. This may also result in the discovery of additional food resources and safe roosting sites. In line with this concept, we assumed that the release of six flocks of macaws, spaced by 2–3 month-long intervals between April 2013 and June 2014, would create an information chain (*sensu* [47]) about food resources from flock to flock. Our observations indicated that flocks of macaws released in such sequence went through a relatively fast integration with members of flocks released earlier (A. Estrada, unpublished), an aspect probably facilitated by the design of post-release food provisioning. Such design involved positioning the feeding platform for released macaws, right outside of the pre-released cage [13].

Parrots have significantly larger brains relative to body mass than other birds and this seems to be associated with a higher learning capacity and behavioral flexibility in this group [48, 49]. Neotropical parrots are known to be highly adaptable, with single populations ranging across different types of habitats, shifting their dietary preferences according to the spatial and seasonal presence of resources, and readily adapt to the presence of new foods [39]. They are highly social and social learning is an important component of their life history traits [43,50]. Recent studies suggest that the innovation rate of avian habitat generalists is driven by their higher propensity to eat new foods and are more successful than specialists in environments modified by humans or in environments in which they have been reintroduced [50,51]. Behavioral flexibility enables animals to react to changes in the environment and it is mediated by learning [52-54]. Before release, the macaws in Palenque were naïve about the habitat and potential food resources available to them in the wild. Their success in discovering and locating wild foods was probably a combination of neophilia, neophobia, accumulated social learning, behavioral flexibility, and a high cognitive capacity [54]. Thus, ecological generalism, high sociality and behavioral innovation may have been key features facilitating the observed short-term success of the reintroduced scarlet macaws in adopting wild foods in Palenque (Fig. 9).


a b c


d

Fig. 9. Reintroduced scarlet macaws feeding on (a) seeds and pulp of *Cordia stenoclada*, (b) flowers of *Luehea speciosa*, (c) seeds and pulp of *Psidium guajava*, (d) leaves of *Pachira aquatica.* Photos by Ángela María Amaya Villarreal.

Implications for conservation

The ability of the reintroduced scarlet macaws in Palenque to successfully find and track food resources, as shown by our study, is an important aspect for consideration as an indicator of short-term reintroduction success. It is clear that without significant training or wild birds to model, these birds investigated, sampled, and clearly developed foraging skills and a dietary breadth that is rapidly approaching that of wild macaws. Reintroduction success in parrots has been proposed as first-year survival >50% and released birds breeding with conspecifics [4]. In Palenque, survival of 96 reintroduced macaws is 91% in May 2015, two years after the first release. Moreover, the observation of nine nesting events between August 2014 and March 2015 (two in artificial nests and seven in natural cavities; A. Estrada, unpublished) and a successful use of wild foods, clearly highlights the initial success of adaptation to the wild by the captive bred macaws. The short-term success reported here was probably due to the implementation of a soft-release protocol involving pre-release wild food training and daily post-release food provisioning [13]. Contributing to this may have been the release of flocks at relatively short time intervals (2–3 months) to promote social integration and diffusion-chain learning [47].

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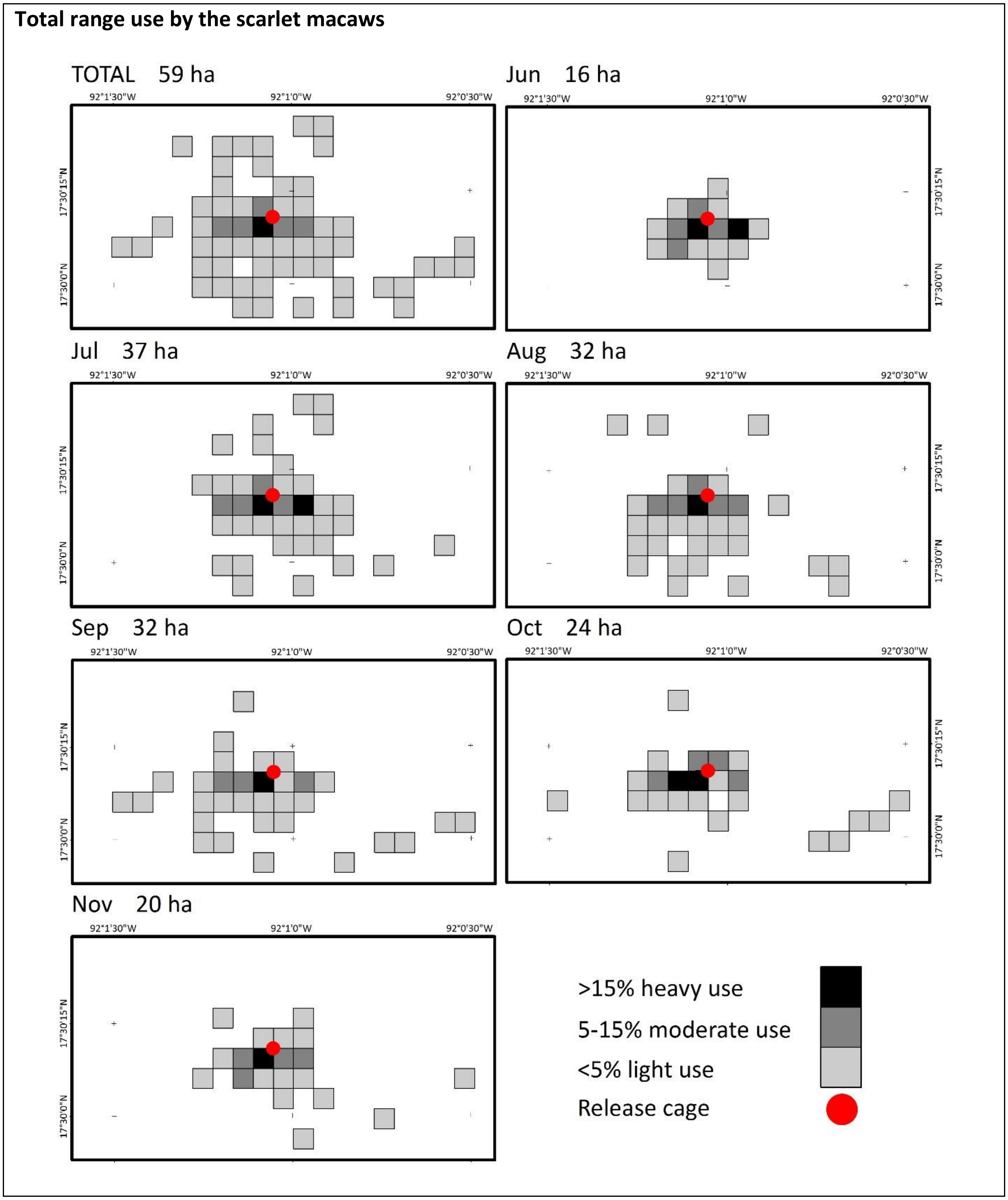
Appendix 1. List of tree species used by the scarlet macaws released in Palenque for the period June-November 2014. (Taxonomy follows Tropicos.org. Missouri Botanical Garden. 03 Apr 2015 http://www.tropicos.org). IVI: importance value index (see vegetation census in methods). Plant parts eaten codes: ripe fruit (1), unripe fruit (2), seeds (3), young leaves (4), mature leaves (5), shoots (6), stems (7), flowers (8) , tree bark (9), insect galls (10).

Tree species (plant family)	Trees used	Feeding records	Months used	IVI	Used for pre-release food training	Plant part eaten
Cordia stenoclada (Boraginaceae)	20	61	Jun/Jul/Aug/Sep/Oct	0.15		1,2,3,6,7,9
Muntingia calabura (Muntingiaceae)	16	41	Jun/Jul/Aug/Sep/Oct			1,2,3,5,7,9
Enterolobium cyclocarpum (Fabaceae)	13	25	Jun/Jul/Aug/Sep/Oct	0.31	yes	7,9,10
Psidium guajava (Myrtaceae)	11	19	Jul/Aug/Oct/Nov			1,2,3,9
Cupania glabra (Sapindaceae)	12	14	Oct/Nov			3,8
Spondias mombin (Anacardiaceae)	6	13	Aug/Sep/Oct/Nov			2,7
Pachira aquatica (Malvaceae)	3	13	Jul/Aug/Nov			3,4,56,7,8,9
Miconia argentea (Melastomataceae)	8	11	Jul/Aug/Sep/Nov	0.31		1,2,3,4,5,7,8
Tectona grandis (Lamiaceae)	6	9	Sep/Oct			3
Terminalia catappa (Combretaceae)	2	9	Jul/Aug/Oct/Nov			2,3,8,9
Cordia collococa (Boraginaceae)	5	8	Aug/Oct	0.07		3,8
Cecropia peltata (Urticaceae)	3	6	Jun/Jul/Aug/Sep	0.22	Yes	1,3,7,9
Vochysia guatemalensis (Vochysiaceae)	3	6	Jul/Aug			3,9
Blepharidium guatemalense (Rubiaceae)	4	5	Aug/Sep/Nov			3,6,8
Spondias sp. (Anacardiaceae)	4	5	Aug			2
Spondias radlkoferi (Anacardiaceae)	3	5	Jun/Aug/Sep	0.04	yes	2
Lonchocarpus guatemalensis (Fabaceae)	3	4	Jul/Aug			6,7,9
Cochlospermum vitifolium (Bixaceae)	1	4	Jun/Nov	0.07		4,5,7,9
Byrsonima crassifolia (Malpighiaceae)	1	4	Aug			1,3
Albizia tomentosa (Fabaceae)	3	3	Jul/Aug/Sep	0.09		7,9
Zanthoxylum panamense (Rutaceae)	2	3	Sep	0.08		2,3
Andira inermis (Fabaceae)	1	3	Jul			3,9
Guazuma ulmifolia (Malvaceae)	2	2	Nov	0.46	yes	2,3
Eucalyptus robusta (Myrtaceae)	1	2	Oct			1,3
Trichospermum galeotti (Malvaceae)	1	2	Aug			7,9
Andira galeottiana (Fabaceae)	1	1	Aug	0.08		2
Cedrela odorata (Meliaceae)	1	1	Nov	0.03		2,3
Ficus benjamina (Moraceae)	1	1	Jul		yes	1,3
Leucaena sp. (Fabaceae)	1	1	Jul	0.08		9
Luehea speciosa (Malvaceae)	1	1	Nov			8
Picramnia antidesma (Picramniaceae)	1	1	Nov			7
N 31	140	283				

Appendix 2. Total and monthly range of scarlet macaws, given by location of feeding and non-feeding activities (see methods), during the study period. Cells are 1ha. Intensity of use indicated by the black to light gray shaded pattern. Total area encompassed by each map 190ha.



Appendix 3. Total and monthly foraging range of scarlet macaw, given by the location of feeding records. Cells are 1ha. Intensity of use indicated by the black to light gray shaded pattern. Total area encompassed by each map 190ha.