

LILAC-CROWNED PARROT DIET AND FOOD RESOURCE AVAILABILITY: RESOURCE TRACKING BY A PARROT SEED PREDATOR¹

KATHERINE RENTON²

The Durrell Institute of Conservation and Ecology, The University of Kent at Canterbury, Kent, CT2 7NS, UK

Abstract. The pattern of food resource availability and use by Lilac-crowned Parrots (*Amazona finschi*) was evaluated in tropical dry forest of the Reserva de la Biosfera Chamela-Cuixmala, western Mexico. Monthly fruiting phenology transects were conducted throughout the year in deciduous and semi-deciduous forest to determine temporal and spatial variability in resource abundance. Resource use by parrots was evaluated through observations of diet and habitat use. There was significant temporal and spatial variability in food resource abundance, with semi-deciduous forest providing greater food resources for parrots during the dry season, whereas food resource abundance increased in deciduous forest during the rainy season. The critical period of food resource scarcity occurred during May–June at the end of the long dry season. Lilac-crowned Parrots were pre-dispersal seed predators, and exhibited high flexibility in diet, incorporating dietary switching, as well as niche-breadth contraction and expansion, which corresponded with temporal variations in food resource availability. There was low overlap in parrot diets between seasons, with parrots exhibiting a narrow food niche-breadth during the late dry season when resource availability declined. Parrots also demonstrated spatial variation in habitat use, corresponding to fluctuations in the availability of food resources in different habitats. This flexibility in foraging enables parrots to closely track and exploit seed resources which exhibit high temporal and spatial variability in abundance.

Key words: *Amazona finschi*, *deciduous forest*, *habitat use*, *niche breadth*, *plant phenology*, *seasonality*.

Resumen. En este trabajo se evaluó el patrón en la disponibilidad de recursos y su uso por el loro corona lila (*Amazona finschi*) en el bosque tropical seco de la Reserva de la Biosfera Chamela-Cuixmala, oeste de México. A lo largo de un año, se realizaron transectos mensuales para documentar la fenología de fructificación en el bosque tropical caducifolio y subcaducifolio, y para determinar la variabilidad temporal y espacial en la abundancia de recursos. El uso de los recursos por los loros fue evaluado por observaciones de la dieta y el uso del hábitat. Se encontró una variabilidad temporal y espacial significativa en la abundancia de recursos alimenticios; el bosque subcaducifolio suministró mayores recursos alimenticios para los loros durante la época seca, mientras la abundancia de recursos alimenticios aumentó en el bosque caducifolio durante la época de lluvias. El periodo crítico de escasez de recursos alimenticios ocurrió en mayo–junio, al final de la larga época seca. Los loros corona lila son depredadores de semillas, y exhibieron una alta flexibilidad de dieta, incluyendo cambios en la dieta, además de la contracción y expansión de la amplitud del nicho, lo que correspondió con las variaciones temporales en la disponibilidad de recursos alimenticios. La dieta de los loros presentó poca similitud entre estaciones; los loros exhibieron poca amplitud del nicho al final de la época seca, cuando la disponibilidad de recursos declinó. Los loros también mostraron variación espacial en uso del hábitat, correspondiendo a las fluctuaciones en la disponibilidad de recursos alimenticios entre hábitats. Esta flexibilidad en el forrajeo permite a los loros de seguir y aprovechar recursos como las semillas, las cuales exhiben una alta variabilidad temporal y espacial en su abundancia.

INTRODUCTION

Conservation of threatened species depends on preserving all habitat types required to meet

their resource needs throughout the year, as well as maintaining connectivity between resource patches (Saunders et al. 1991). With current rates of deforestation, natural habitat is increasingly reduced to forest remnants within a mosaic of agricultural land. Understanding the relationship of parrot populations to food resources enables determination of the key resources, habitats, and areas required for conservation, and may help to predict the impact of habitat frag-

¹ Received 2 March 2000. Accepted 27 September 2000.

² Present address: Estación de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México, Apto. Postal 21, San Patricio, Jalisco 48980, México, e-mail: krenton@ibiologia.unam.mx

mentation on threatened populations (Saunders 1990). Hence, basic knowledge is required on how patch dynamics are expressed in nature, and how populations and organisms respond to them (Wiens 1976).

Most studies on the relationship of bird communities to resource variability have been conducted on frugivores (Levey 1988, Loiselle and Blake 1991, Whitney and Smith 1998). However, the behavior of granivores in response to food availability is similar to that of frugivores (Poulin et al. 1994). Granivory is relatively uncommon among bird feeding guilds (Poulin et al. 1994), and may require high flexibility in diet and mobility at several spatial scales in order to exploit such ephemeral and variable resources.

Canopy bird species comprise 40–50% of tropical forest bird communities, while large-bodied frugivores and parrots dominate canopy bird communities (Terborgh et al. 1990). Canopy bird species may experience high variability in food resources due to the greater seasonality of canopy trees compared to the understory (Frankie et al. 1974). Most parrot species are primarily canopy seed-eaters (Smith and Moore 1991, Galetti 1993), although some parrot species may be frugivorous (Wermundsen 1997). Little is known about the relationship of parrots to food resources, although most parrot species rely on food types (i.e., seeds and fruits) which may demonstrate high temporal and spatial variability in abundance. It may be predicted that seed predators such as parrots will track food resources closely in order to exploit temporal and spatial abundances in plant seed production.

The Lilac-crowned Parrot (*Amazona finschi*) is a threatened species endemic to the Pacific coast of Mexico. Tropical dry deciduous forest along the Pacific coast of Central America is a highly threatened forest type (Beissinger et al. 1996) which exhibits marked seasonality in plant productivity (Janzen 1967, Frankie et al. 1974, Bullock and Solis-Magallanes 1990). This study aims to determine whether there is temporal and spatial variability in food resource abundance for Lilac-crowned Parrots in tropical dry deciduous forest, and to evaluate the relationship of parrot diet to food resources.

METHODS

STUDY SITE

The study was conducted at the 131-km² Reserva de la Biosfera Chamela-Cuixmala (19°22'N,

104°56'W to 19°35'N, 105°03'W), on the Pacific coast of Mexico. The study site has a dry tropical climate exhibiting a marked seasonality in precipitation, with 85% of the 748-mm average annual rainfall occurring from June to November, and a prolonged drought from mid-February to late May (Bullock 1986). The reserve has a hilly topography varying in elevation from 20 m to 520 m above sea level. The dominant vegetation type on the slopes is tropical dry deciduous forest, with semi-deciduous forest in the larger drainages and more humid valleys (Lott 1993).

FOOD RESOURCE AVAILABILITY

Phenology transects. A total of 45 phenology transects of 200 m × 6 m were established, with 15 transects in each of three habitat types: (1) deciduous forest, (2) semi-deciduous forest, and (3) watercourses, in order to determine habitat variation in resource availability (Chapman et al. 1994). Transects were dispersed within the study area to obtain a representative sample of resource availability, and were constructed away from road or trail systems to avoid recording edge species. Transects in deciduous forest were varied with respect to aspect, and included southeast slopes ($n = 3$), southwest slopes ($n = 2$), northeast slopes ($n = 3$), northwest slopes ($n = 2$), along ridge tops ($n = 3$), and at the bases of slopes ($n = 2$). Areas of semi-deciduous forest between the Arroyo Chamela and the Rio Cuitzmala were identified from aerial photographs of the region (scale 1:50,000) taken during the dry season. Watercourses within the study site comprised a mixture of deciduous and semi-deciduous forest species. Transects were established along four main watercourses: Caiman, Carayes, Cajones, and Limbo. Placement of transects along these watercourses was determined by dividing the main watercourses and their tributaries on the map into 500-m numbered sections, which were then randomly selected. Each 200-m transect was established within one of the 15 selected 500-m sections; the chosen point was located in the field using a Geographical Positioning System.

Transects were monitored by the same observer during the second and third weeks of each month from January 1996 to July 1997 (excluding December 1996). Fruit or seed bearing trees greater than 10-cm diameter at breast height (dbh) were recorded when detected within a 3-

m band on either side of the transect line in order to determine canopy variation in resource availability (Bullock and Solis-Magallanes 1990, Chapman et al. 1994). Where a tree occurred on the boundary of the 3-m transect width, the tree was included if the mid-point of the trunk was rooted within the transect area.

Tree species were identified by comparison with samples in the herbarium at the Estación de Biología Chamela of the Instituto de Biología, Universidad Nacional Autónoma de México. The dbh of each fruiting tree was measured as a correlate of fruit crop abundance (Chapman et al. 1992). Where the trunk branched below breast height (1.3 m), the dbh of each trunk branch was measured and summed to give a total dbh for that tree.

Data analysis. The number of fruiting trees, and their dbh were each summed over all tree species in all transects in each of the three habitat types in order to obtain habitat-wide estimates of resource abundance in each month. Only parrot food-plant species were recorded in the transects, and fruit or seed crops were included in the analysis at the stage of ripeness when consumed by parrots. For the purpose of the phenology study, June was included as a dry-season month because in 1996 the first rains did not commence until the end of June, after phenology transects for that month had been completed. Preliminary analysis using the Kolmogorov-Smirnov statistic with Lilliefors significance level (Zar 1996) determined that the data did not deviate significantly from the normal distribution required for parametric analysis ($K-S_{33} = 0.13$, $P = 0.18$). Seasonal variation in food resource abundance was analyzed by two-way ANOVA on the number of trees and sum of dbh of fruiting trees in each habitat type during the dry and rainy season. The general linear model was used to account for missing values for the month of December.

PARROT DIET AND RESOURCE USE

The diet of Lilac-crowned Parrots throughout the year was determined by observations of feeding activity. During each month of the year, trails were walked in deciduous and semi-deciduous forest, and along watercourses during the first four hours of the morning and the last three hours of the afternoon, when parrots conduct the majority of foraging activity. When feeding parrots were encountered, the date, time, location,

food species, and habitat type were noted, as well as the number of parrots observed feeding on each food resource, and the plant part eaten, i.e., fruit pulp, seed, or flower. A feeding bout was recorded as one observation of one or more parrots feeding on one food source. If the parrots changed to another food source during the period of observation, this was recorded as a second feeding bout (Galetti 1993).

NICHE BREADTH AND SIMILARITY MEASURES

Diet observations were analyzed using the number of individuals observed feeding on a particular resource, and the number of feeding bouts. Niche breadth was evaluated using the standardized Levins' and Hurlbert's niche-breadth indices, where a value close to 0 indicates dietary specialization, and a value close to 1 indicates a broad diet (Levins 1968, Colwell and Futuyma 1971, Hurlbert 1978).

Levins' (1968) standardized niche-breadth index was calculated from observations of Lilac-crowned Parrot diets during four periods of the year corresponding to the early dry season (January–March), the late dry season (April–June), the early rainy season (July–September), and the late rainy season or rainy-dry transition (October–December). Niche-breadth indices were then related to the number of food species available during each three-month period as determined by the phenology transects. Hurlbert's (1978) niche breadth incorporates a measure of the proportional abundance of resources in each season, and was calculated using both number of food trees, and sum of dbh of fruiting trees.

Similarity or overlap in parrot diets between the dry and rainy seasons was evaluated using the Morisita index of similarity for quantitative data on occurrence of food items in the diet (Krebs 1989). Chi-square contingency analysis was conducted to test for differences in the number of feeding bouts recorded in each of the three habitat types during the four periods of the year.

RESULTS

TEMPORAL AND SPATIAL VARIATION IN FOOD RESOURCES

A total of 36 food plant species of 15 families was recorded in the phenology transects. There was a sharp decline in resource abundance by both number of trees and species during the late

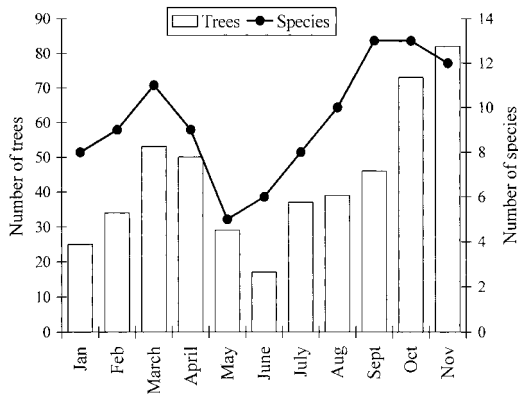


FIGURE 1. Number of Lilac-crowned Parrot food trees and species available each month over all habitat types in 1996.

dry season in May and June, rising again in July with the start of the rainy season (Fig. 1). Food resource abundance for Lilac-crowned Parrots was greater in semi-deciduous forest during the early dry-season months of January–February (Fig. 2) due to fruiting of *Brosimum alicastrum*. The peak resource abundance in deciduous forest and along watercourses during March and April resulted from fruiting of *Comocladia engleriana*, *Spondius purpurea*, *Caesalpinia erios-tachys*, and *Ficus cotinifolia*. The sharp April peak of resource abundance in semi-deciduous forest and along watercourses arose from fruiting of *Astronium graveolens*. All habitat types began to decline in resource abundance during the late dry season in May–June; however, semi-deciduous forest maintained some food resource abundance during this period with fruiting of *Astronium graveolens*, *Guarea glabra*, and *Ficus* spp.

There was a slight peak in resource abundance along watercourses during July following ripening of *Sciadodendron excelsum* fruit, and the onset of fruiting of deciduous forest species such as *Celaenodendron mexicanum*, *Crataeva tapia*, *Jatropha* spp., and *Caesalpinia* spp. These species commenced fruiting earlier along watercourses than on the slopes, possibly due to greater soil humidity. The increase in resource abundance in deciduous forest, as well as along watercourses, during the latter part of the rainy season was due to fruiting of many deciduous forest species: *Acacia* spp., *Caesalpinia* spp., *Celaenodendron mexicanum*, *Esenbeckia nesiotica*,

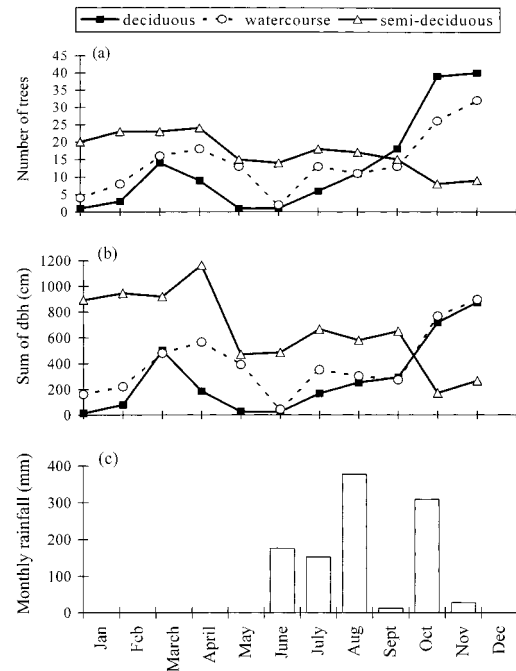


FIGURE 2. Temporal patterns of food resource availability in three habitat types and monthly rainfall during 1996. (a) Resource abundance by number of trees. (b) Sum of diameter at breast height (dbh) of fruiting trees. (c) Total monthly rainfall.

Jatropha spp., *Lysiloma microphyllum*, *Pithecellobium* spp., and *Plumeria rubra*.

Habitats differed significantly in their response to seasons (Table 1). Semi-deciduous forest had greatest resource abundance for Lilac-crowned Parrots during the dry season, which declined during the rainy season (Fig. 2). Conversely, deciduous forest had lowest resource abundance during the dry season, which increased during the rainy season (Fig. 2).

SEASONALITY IN PARROT DIETS

Lilac-crowned Parrots were observed to consume 33 food species throughout the year (Table 2). Lilac-crowned Parrots were primarily predispersal seed predators with seeds forming 81.8% of the diet, fruit 8.8%, insect larvae 6.6%, and bromeliad stems 2.9% of the diet ($n = 137$ feeding bouts).

Parrot diet also varied considerably between the dry and rainy seasons, with little overlap or similarity in food items between the seasons (Morisita index = 0.11). The main food items during the dry season were seeds of *Astronium*

TABLE 1. Results of two-way ANOVA using the general linear model on number of trees and sum of diameter at breast height (dbh) of food trees from phenology transects in three habitat types during the dry and rainy season of 1996.

Source	df	Number of trees		Sum of dbh	
		F	P	F	P
Season	1, 27	5.48	0.03	0.49	0.49
Habitat	2, 27	0.28	0.76	5.17	0.01
Season × habitat	2, 27	5.81	<0.01	5.51	0.01

graveolens (38.1%, $n = 207$ parrots), *Brosimum alicastrum* (18.8%, $n = 102$), and *Celaenodendron mexicanum* (10.3%, $n = 55$). During the rainy season, the diet comprised seeds of *Celaenodendron mexicanum* (16.8%, $n = 72$), and fruits of *Sciadodendron excelsum* (16.8%, $n = 71$), along with seeds of *Jatropha standleyi* (14.5%, $n = 62$), *Jatropha malacophylla* (14%, $n = 60$), and *Caesalpinia pulcherrima* (13.1%, $n = 56$).

RESOURCE USE AND AVAILABILITY

Levins' niche breadth, B , was narrower in the dry season ($B = 0.22$) than in the rainy season ($B = 0.55$), and declined most sharply in the late dry season of April–June ($B = 0.10$, Fig. 3). Variations in Levins' niche breadth for Lilac-crowned Parrots during each period of the year were strongly correlated with the number of food species fruiting over each three-month period ($r^2 = 0.96$, $P < 0.05$, Fig. 3). This suggests

TABLE 2. Diet observations for the Lilac-crowned Parrot at the Reserva de la Biosfera Chamela-Cuixmala between 1996–1997.

Family/Species ^a	Part eaten ^b	Parrots	Feeding bouts	Months
Anacardiaceae/ <i>Astronium graveolens</i>	unrp se	207	24	May–June
Anacardiaceae/ <i>Comocladia engleriana</i>	unrp se	41	3	March–April
Apocynaceae/ <i>Plumeria rubra</i>	unrp se	12	6	Feb, Sept, Oct
Araliaceae/ <i>Sciadodendron excelsum</i>	rp fr	71	7	July
Bombacaceae/ <i>Ceiba aesculifolia</i>	rp se	2	1	March
Bromeliaceae/ <i>Bromelia</i> sp.	phylum	10	4	July–Sept
Bursaceae/ <i>Bursera</i> sp. nov.	rp se	40	1	Nov
Capparidaceae/ <i>Crataeva tapia</i>	unrp se	2	1	April
Euphorbiaceae/ <i>Celaenodendron mexicanum</i>	unrp se	127	16	Feb, March, July
Euphorbiaceae/ <i>Jatropha malacophylla</i>	unrp se	60	1	July
Euphorbiaceae/ <i>Jatropha standleyi</i>	unrp se	62	4	July
Homoptera/Leaf gall of <i>A. graveolens</i>	larvae	18	9	April–July
Leguminosae/ <i>Acacia farnesiana</i>	unrp se	2	1	March
Leguminosae/ <i>Bauhinia unguolata</i>	unrp se	37	8	Feb–March
Leguminosae/ <i>Caesalpinia eriostachys</i>	unrp se	1	1	Feb
Leguminosae/ <i>Caesalpinia pulcherrima</i>	unrp se	56	12	Nov
Leguminosae/ <i>Erythrina lanata</i>	unrp se	2	1	May
Leguminosae/ <i>Lysiloma microphyllum</i>	unrp se	8	1	March
Leguminosae/ <i>Pithecellobium dulce</i>	se + fr	2	1	April
Leguminosae/ <i>Pithecellobium lanceolatum</i>	unrp se	8	2	Sept–Oct
Meliaceae/ <i>Guarea glabra</i>	rp se	32	2	May–June
Moraceae/ <i>Brosimum alicastrum</i>	se + fr	102	14	Jan–April
Moraceae/ <i>Ficus cotinifolia</i>	fruit	6	3	Jan–March
Moraceae/ <i>Ficus insipida</i>	fruit	10	1	May
Rutaceae/ <i>Esenbeckia nesiotica</i>	unrp se	31	7	Sept, Oct
Sapotaceae/ <i>Sideroxylon capiri</i>	unrp se	10	1	June

^a Also identified from crop samples and observations were seeds of *Spondius purpurea* (Anacardiaceae), *Sebastiania* sp. (Euphorbiaceae), four unidentified species, and fruits of *Guapira macrocarpa* (Nyctaginaceae).

^b Part eaten: unrp = unripe, rp = ripe, se = seed, fr = fruit.

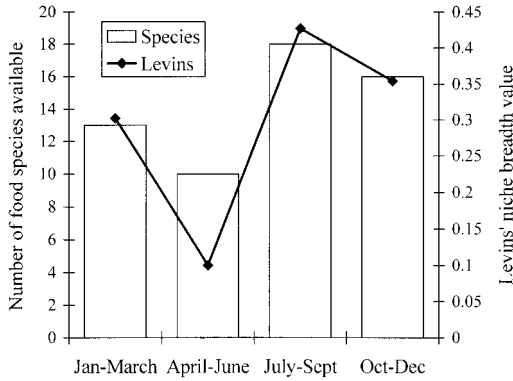


FIGURE 3. Levins' niche breadth for parrot diets compared with number of food species available during four periods of the year.

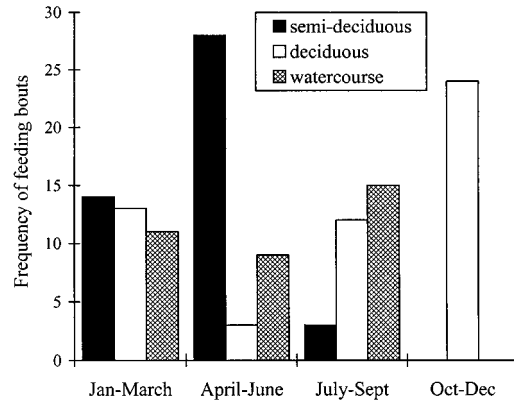


FIGURE 4. Frequency of feeding bouts by Lilac-crowned Parrots in three habitat types during four periods of the year.

that food niche-breadth of Lilac-crowned Parrots tracks resource abundance, with niche breadth being narrowest when resources are least abundant. Hurlbert's niche breadth, B' , which weights resource use by an estimate of abundance, gave a broader niche value for the dry season (by trees: $B' = 0.62$, by dbh: $B' = 0.32$) compared to the rainy season (by trees: $B' = 0.21$, by dbh: $B' = 0.14$).

Analysis of niche breadth, similarity measures, and composition of the diet indicate that Lilac-crowned Parrots may adjust food resource use in response to temporal variations in resource abundance. Chi-square contingency analysis also demonstrated a significant difference in the frequency of feeding bouts in different forest types between four periods of the year ($\chi^2_5 = 74.4, P < 0.001$). Lilac-crowned Parrots concentrated foraging activity in semi-deciduous forest at the end of the dry season, but switched to deciduous forest following the onset of the rainy season (Fig. 4). This corresponds to the pattern of food resource availability in each forest type at different times of the year, with most resources available in semi-deciduous forest at the end of the dry season, whereas resource abundance increased in deciduous forest following the onset of the rainy season (Fig. 2).

DISCUSSION

TEMPORAL AND SPATIAL PATTERNS OF RESOURCE AVAILABILITY

Food resource availability for Lilac-crowned Parrots demonstrated seasonal fluctuations in abundance and variability between forest types.

A sharp decline in resource abundance occurred in May–June at the end of the dry season, indicating that this is a critical period of food scarcity for Lilac-crowned Parrots. Semi-deciduous forest produced greater food resource abundance in the early to mid dry season than in the rainy season, and is an important source of food during the dry season, when parrots are raising young (Renton and Salinas-Melgoza 1999). In particular, semi-deciduous forest provides essential food resources during the late dry season months of May–June, and may be a key habitat type at this critical time of the year. Conversely, deciduous forest may be important in providing abundant food resources for parrots at the end of the rainy season, prior to the breeding season and egg laying.

Tropical dry forest in Mexico is being deforested at a rate almost equal to that of tropical humid rainforest (Masera et al. 1997). Current rates of deforestation along the coast of Jalisco are twice as high in semi-deciduous forest than deciduous forest, and semi-deciduous forest now comprises less than 10% of the land area in the Chamela-Cuixmala region (A. Miranda, pers. comm.). Increased fragmentation of semi-deciduous forest could result in food limitation for parrots during the breeding season. Semi-deciduous forest may also provide essential resources for other animal communities in deciduous forest during the dry season. However, little is known of the dynamics of habitat use within the animal community of tropical dry forest, and such information is essential to develop effective strategies for conservation and management of

threatened species, such as the Lilac-crowned Parrot.

PARROT DIET AND RESOURCE USE

Lilac-crowned Parrots were primarily pre-dispersal seed predators, with seeds forming 82% of the diet, whereas fruit pulp comprised less than 10% of the diet. Insect larvae did not form a major component of the diet, and has been reported only occasionally for Neotropical parrots (Martuscelli 1994, Enkerlin-Hoeflich and Hogan 1997), although insects are common in the diet of Australian parrots (Rowley and Chapman 1991, Smith and Moore 1991). Lilac-crowned Parrots were not observed consuming flowers. Most other parrot species consume flowers very infrequently (Wermundsen 1997), although flowers formed the second main food item for Scaly-headed Parrots (*Pionus maxilliani*) in Brazil (Galetti 1993).

A predominantly seed diet means that Lilac-crowned Parrots may need to adjust rapidly to changes in seed availability. Plants may have evolved high synchrony in seed production as a strategy to avoid predation by satiating potential predators (Janzen 1969, Augspurger 1981). Hence, pre-dispersal seed predators such as parrots need to be highly mobile and flexible in order to exploit each food resource as it becomes available. This flexibility in diet was demonstrated by the strong seasonality in parrot diets, incorporating dietary switching, and niche-breadth expansion and contraction. Seasonal variations in diet have been noted for Australian parrots (Rowley and Chapman 1991), and some Neotropical parrots (Galetti 1993, Wermundsen 1997). Seasonal diet switching was also recorded for seed-eating Galapagos finches, and may occur in response to environmental heterogeneity (Smith et al. 1978, Schluter 1982).

Hurlbert's index and the positive correlation between Levins' niche-breadth value and food species abundance indicate that niche breadth is determined by food availability. Lilac-crowned Parrots exhibit narrower diets in response to low food availability during the dry season, when they are restricted to exploiting a few resources. The reverse occurs in the rainy season when there is a greater variety of food resources and parrots are able to exhibit selectivity in diet.

The present study demonstrates a high flexibility in parrot diets which was closely related to temporal variations in food resource avail-

ability. Lilac-crowned Parrots also demonstrated spatial variation in habitat use corresponding to fluctuations in the availability of food resources in different habitat types throughout the year. These strategies may enable Lilac-crowned Parrots to closely track a seed resource base which exhibits high temporal and spatial variability in abundance, and they suggest an evolutionary relationship between parrot seed predators and plant seed resources.

The fact that parrots consume predominantly unripe seeds, and closely track variations in seed abundance, makes them potentially important pre-dispersal seed predators on canopy trees. The tendency for tree species in tropical dry forests to be clumped in distribution (Hubbell 1979), and the potential for seed predators such as parrots to significantly reduce seed production (Heithaus et al. 1982, Galetti and Rodrigues 1992), mean that a highly mobile seed predator may influence forest dynamics. Studies in Central American forests suggest that herbivores play a regulatory role in maintaining forest diversity (Janzen 1970, Dirzo and Miranda 1990). Parrots are among the principal canopy granivores in tropical forests. This combined with the tendency to form large feeding flocks and an ability to track resource variability, means that as pre-dispersal seed predators, parrots may play a regulatory role in maintaining diversity of canopy trees in tropical forests.

ACKNOWLEDGMENTS

I am grateful to the Fundación Ecológica de Cuixmala in Mexico, the Denver Zoological Foundation, the American Bird Conservancy, and the World Parrot Trust for logistical and financial support during the study. I thank the Secretaría del Medio Ambiente, Recursos Naturales y Pesca, Instituto Nacional de Ecología, who granted permits for the research. The Estación de Biología Chamela, of the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), provided access to their herbarium and library, and I thank Emily Lott and Steven Bullock for assistance in the identification of some plant species. I was supported by a stipend from The Durrell Institute of Conservation and Ecology, and British Airways Assisting Conservation provided international flights to Mexico. The Instituto de Biología, UNAM, provided facilities for the preparation of this manuscript, and I thank R. A. Griffiths, B. J. Miller, J. H. Vega Rivera, T. F. Wright, and two anonymous reviewers for their constructive comments.

LITERATURE CITED

AUGSPURGER, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects

- of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62:775–788.
- BEISSINGER, S. R., E. C. STEADMAN, T. WOHLGENANT, G. BLATE, AND S. ZACK. 1996. Null models for assessing ecosystem conservation priorities: threatened birds as titers of threatened ecosystems in South America. *Conserv. Biol.* 10:1343–1352.
- BULLOCK, S. H. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. *Arch. Met. Geoph. Biocl. (B)* 36:297–316.
- BULLOCK, S. H., AND J. A. SOLIS-MAGALLANES. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22:22–35.
- CHAPMAN, C. A., L. J. CHAPMAN, R. WRANGHAM, K. HUNT, D. GEBU, AND L. GARDNER. 1992. Estimators of fruit abundance of tropical trees. *Biotropica* 24:527–531.
- CHAPMAN, C. A., R. WRANGHAM, AND L. J. CHAPMAN. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26:160–171.
- COLWELL, R. K., AND D. J. FUTUYMA. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567–576.
- DIRZO, R., AND A. MIRANDA. 1990. Contemporary Neotropical defaunation and forest structure, function, and diversity—a sequel to John Terborgh. *Conserv. Biol.* 4:444–447.
- ENKERLIN-HOEFELICH, E. C., AND K. M. HOGAN. 1997. Red-crowned Parrot (*Amazona viridigenalis*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 292. The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington DC.
- FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62:881–919.
- GALETTI, M. 1993. Diet of the Scaly-headed Parrot (*Pionus maximiliani*) in a semi-deciduous forest in southeastern Brazil. *Biotropica* 25:419–425.
- GALETTI, M., AND M. RODRIGUES. 1992. Comparative seed predation on pods by parrots in Brazil. *Biotropica* 24:222–224.
- HEITHAUS, E. R., E. STASHKO, AND P. K. ANDERSON. 1982. Cumulative effects of plant-animal interactions on seed production by *Bauhinia unguolata*, a Neotropical legume. *Ecology* 63:1294–1302.
- HUBBELL, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203:1299–1309.
- HURLBERT, S. H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59:67–77.
- JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21:620–637.
- JANZEN, D. H. 1969. Seed-eaters versus seed size, number, toxicity, and dispersal. *Evolution* 23:1–27.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:501–524.
- KREBS, C. J. 1989. *Ecological methodology*. Harper and Row, New York.
- LEVINS, R. 1968. *Evolution in changing environments*. Princeton Univ. Press, Princeton, NJ.
- LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58:251–269.
- LOISELLE, B. A., AND J. G. BLAKE. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72:180–193.
- LOTT, E. J. 1993. Annotated checklist of the vascular flora of the Chamela Bay region, Jalisco, Mexico. *Occas. Pap. Calif. Acad. Sci.* 148:1–60.
- MARTUSCELLI, P. 1994. Maroon-bellied Conures feeding on gall-forming homopteran larvae. *Wilson Bull.* 106:769–770.
- MASERA, O. R., M. J. ORDÓÑEZ, AND R. DIRZO. 1997. Carbon emissions from Mexican forests: current situation and long-term scenarios. *Climatic Change* 35:265–295.
- POULIN, B., G. LEFEBVRE, AND R. MCNEIL. 1994. Characteristics of feeding guilds and variation in diets of bird species of three adjacent tropical sites. *Biotropica* 26:187–197.
- RENTON, K., AND A. SALINAS-MELGOZA. 1999. Nesting behavior of the Lilac-crowned Parrot. *Wilson Bull.* 111:488–493.
- ROWLEY, I., AND G. CHAPMAN. 1991. The breeding biology, food, social organization, demography and conservation of the Major Mitchell or Pink Cockatoo, *Cacatua leadbeateri*, on the margin of the Western Australian wheatbelt. *Aust. J. Zool.* 39:211–261.
- SAUNDERS, D. A. 1990. Problems of survival in an extensively cultivated landscape: the case of the Carnaby's Cockatoo *Calyptorhynchus funereus latirostris*. *Biol. Conserv.* 54:277–290.
- SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5:18–32.
- SCHLUTER, D. 1982. Distributions of Galapagos ground finches along an altitudinal gradient: the importance of food supply. *Ecology* 63:1504–1517.
- SMITH, G. T., AND L. A. MOORE. 1991. Foods of co-rellas *Cacatua pastinator* in Western Australia. *Emu* 91:87–92.
- SMITH, J. N. M., P. R. GRANT, B. R. GRANT, I. J. ABBOTT, AND L. K. ABBOTT. 1978. Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* 59:1137–1150.
- TERBORGH, J., S. K. ROBINSON, T. A. PARKER III, C. A. MUNN, AND N. PIERPONT. 1990. Structure and organization of an Amazonian forest bird community. *Ecol. Monogr.* 60:213–238.
- WERMUNDSEN, T. 1997. Seasonal change in the diet of the Pacific Parakeet *Aratinga strenua* in Nicaragua. *Ibis* 139:566–568.
- WHITNEY, K. D., AND T. B. SMITH. 1998. Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation. *Anim. Conserv.* 1:107–117.
- WIENS, J. A. 1976. Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* 7:81–120.
- ZAR, J. H. 1996. *Biostatistical analysis*. 3rd ed. Prentice Hall Intl., London.