

**ADULT NEST ATTENDANCE AND DIET OF NESTLING RESPLENDENT QUETZALS (*PHAROMACHRUS MOCINNO*) IN THE TALAMANCA MOUNTAINS OF SOUTHERN COSTA RICA**Scott A. Carleton^{1,2} · Kimberly G. Smith¹¹Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA.²U.S. Geological Survey, New Mexico Cooperative Fish & Wildlife Research Unit, New Mexico State University, Las Cruces, NM 88003, USA.

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Abstract · Resplendent Quetzals (*Pharomachrus mocinno*) inhabit mid to high elevation forests from southern Mexico to Panama. Lipid rich fruits from the Lauraceae family have been found to account for a large proportion of adult diet across their annual life cycle. To better understand the relationship between quetzals and Lauraceae during the breeding season, we studied food deliveries to nestlings in the Talamanca Mountains at San Gerardo de Dota, Costa Rica in the Rio Savegre watershed. Our study had four primary objectives: 1) determine parental contribution of males and females feeding nestling quetzals, 2) determine type of food delivered to nestling quetzals, 3) determine if deliveries of fruit items were related to their abundance and/or nutritional content and 4) determine if Lauraceae fruits made up a large proportion of nestling diets based on the high preference quetzals have displayed for fruits from this plant family. Hourly delivery rates were similar for the male and female (1.24 ± 0.68 and 1.44 ± 0.84). During the first 6 days, the largest proportion of the diet was animal prey; primarily lizards and beetles. After day 6, fruit rapidly became the dominant food item delivered to nestlings until fledging. The dominant number of fruits delivered to nestling quetzals were fruits from the Lauraceae family and included *Ocotea holdrigeiana*, *Necatandra cufodontisii*, and *Aiouea costaricensis*. All three had some of the highest protein and lipid content of all fruits delivered to nestlings. *O. holdrigeiana* had the highest protein and lipid content of all fruits delivered, had the lowest relative abundance, and was delivered more frequently than all other fruits. Conservation strategies for this species should take into account not just increasing available habitat, but also increasing habitat quality by focusing on species composition to provide abundant food plants for the Resplendent Quetzal to forage.

Resumen · Atención al nido y dieta de pichones del Quetzal Resplandeciente (*Pharomachrus mocinno*) en las Montañas Talamanca del sur de Costa Rica

El Quetzal Resplandeciente (*Pharomachrus mocinno*) habita bosques de media a alta elevación del sur de México a Panamá. Frutas ricas en lípidos de la familia Lauraceae han sido consideradas constituyentes importantes de su dieta a lo largo de su ciclo anual de vida. Para entender mejor la relación entre quetzales y Lauraceae durante la temporada de cría, estudiamos entregas alimenticias a pichones en las montañas Talamanca en San Gerardo de Dota, Costa Rica en la Cuenca del Rio Savegre. Nuestro estudio tuvo cuatro objetivos primarios: 1) determinar la contribución del macho y la hembra en la alimentación de crías de quetzal, 2) determinar el tipo de entregas alimenticias a crías de quetzal, 3) determinar si las entregas de artículos frutales fueron relacionadas a su abundancia y/o contenido nutricional, y 4) determinar si frutas de Lauraceae conformaron una gran proporción de la dieta de crías de quetzal basado en la alta preferencia que quetzales han demostrado por frutas de esta familia. La proporción de entregas por hora fue similar en machos y hembras (1.24 ± 0.68 y 1.44 ± 0.84). Durante los primeros 6 días, presa animales constituyeron la mayor proporción de la dieta, ante todo lagartijas y escarabajos. Después del día 6, frutos constituyeron rápidamente el artículo de dieta dominante entregado a crías hasta que estas dejaron el nido. La mayor cantidad de frutas entregadas a crías de quetzal perteneció a la familia Lauraceae incluyendo *Ocotea holdrigeiana*, *Necatandra cufodontisii*, y *Aiouea costaricensis*. Las tres tuvieron el más alto contenido lipídico y de proteína de todas las frutas entregadas a crías. Interesantemente, *O. holdrigeiana* tuvo el más alto contenido lipídico y de proteína de todas las frutas entregadas, la más baja abundancia relativa en el ambiente circundante, y fue utilizada más frecuentemente que todas las otras frutas. Estrategias de conservación para esta especie deben tomar en cuenta no solo incrementar el hábitat disponible, pero también incrementar la calidad del hábitat enfocándose en la composición de las especies vegetales, para asegurarse de proveer frutos en abundancia para la alimentación del Quetzal Resplandeciente.

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INTRODUCTION

In tropical forests, 63 to 77% of understory shrubs and trees produce fruits that are dispersed by birds, and fruit-eating birds make up a large proportion of the avifauna in these habitats (Stiles 1985, see also Loiselle & Blake 1990). In some cases, a tight association exists between these avian frugivores and their food plants (Foster 1977, Snow 1981). These species have been referred to as specialists based on the high level of selective foraging they exhibit (Snow 1981, McKey 1975, Howe & Estabrook 1977). However, the designation of many highly frugivorous birds as specialized has been questioned because seasonal diets for many tropical birds, even those that are highly frugivorous, are much more diverse than previously thought (Wheelwright et al. 1984, Solorzano et al. 2000).

Resplendent Quetzals (*Pharomachrus mocinno*), hereafter quetzal, found in the forests of Central America from Mexico to Panama, forage primarily on fruits. Once believed to be a specialist frugivore, we now know they feed on fruits from a variety of different plant species and opportunistically eat insects and lizards (Skutch 1944, Wheelwright 1983, Avila et al. 1996, Solorzano et al. 2000). Despite the breadth of their diet, many studies have documented their high preference not just for fruits, but those in the Lauraceae family, and it was originally this preference that led some to speculate about their classification as a specialist or a generalist frugivore (Wheelwright 1983, 1985, 1991; Wheelwright et al. 1984, Avila et al. 1996). Powell & Bjork (1994) found that altitudinal migration of quetzals in Costa Rica appeared to follow the fruiting phenology of trees in the Lauraceae. Subsequently, timing of the breeding season and presence of quetzals in cloud forests has also been found to correlate with peak availability of fruits and number of fruiting trees in the Lauraceae (Wheelwright 1983, Powell & Bjork 1994, Solorzano et al. 2000). In light of this, it is not surprising, that fruits from Lauraceae constitute a large proportion of the quetzal's diet (Wheelwright 1983, 1985, 1991; Wheelwright et al. 1984, Avila et al. 1996).

Quetzals inhabiting lower montane forests in the Talamanca Mountains of southern Costa Rica have never been studied. We sought to describe foraging ecology of quetzals that utilize these forests seasonally to feed young. The objectives were to 1) determine parental contribution to feeding nestlings, 2) determine timing and types of food deliveries to nestling, and 3) determine if deliveries of fruit items were related to their abundance and/or nutritional content. Furthermore, 4) we were interested in testing the hypothesis that fruits fed to young would come primarily from Lauraceae based on the high preference quetzals have displayed for foraging on these plants.

METHODS

We conducted research at the small orchard community of San Gerardo de Dota in the Talamanca Mountains of southern Costa Rica from February to June 2000 (9°33'49.86"N, 84°12'13.64"W). Our study site was surrounded by lower montane forests on the Pacific slope within the Rio Savegre watershed at an elevation of 2400 to 2800 m a.s.l.; one of the last drainages with contiguous forest from the coast to the continental divide (Holdridge 1967). The forest canopy is dominated by *Quercus* spp., heavily draped with mosses and epiphytes, with a dense understory of bamboo and lianas. The study area was approximately 11 km² and is composed of a combination of primary forest, secondary forest, orchards, and pastures. At the start of the breeding season (February) we traveled 18 km of established roads and trails until groups or pairs of birds were sighted. Once sighted, we followed quetzals to determine location of a potential nest site; quetzals excavate multiple nest sites during courtship. We identified active nests by noting the male's tail feathers protruding from the nest without movement for long periods indicating incubation or by observing a known paired male sitting outside a nest site and waiting for the pair to switch incubation duties. Once an active nest was found, we made daily visits to the nest until feeding of nestlings was observed so that we could best approximate when the nestling period began. Once active feeding was observed, we monitored different nests 6–8 hours per day, two nests per day on a rotational basis. After the failure of all but one nest, we observed the remaining nest from approximately 05:00 to 17:00 h each day, with some time spent observing foraging bouts, until fledging.

Adult nest attendance. Quetzals often perch on the same branch outside nests prior to feeding nestlings (Skutch 1944, Wheelwright 1983). A blind was set up near the nest cavity so that we could easily identify food deliveries. This is the ideal time to identify food items since it is often held openly in the bill. We identified each food item, if possible, as fruit or animal and whenever possible, fruits were further identified to genus and species and insects to family. Sample periods were from sunrise until sunset (05:00–17:00 h). After fledging, we removed nest contents, washed them through screens, and identified all seeds.

Fruit abundance and collection. We randomly chose ten vegetation transects, each 100 m in length, within a 0.5 km radius from the nest. We chose this radius based loosely on the maximum distance quetzals were observed foraging from the nest cavity. Distances traveled during foraging bouts were determined by following quetzals from the nest to foraging locations during the nestling period. We

identified shrubs and trees with fruits to species. We counted all fruits per plant when possible. When this was not possible, due to excessive fruit crops or height of the plant, we estimated relative abundance by counting number of fruits per branch visually or with binoculars and then multiplied this number times the number of branches of similar size on the plant. This likely resulted in an overestimate of fruits, but was the only method available to estimate fruits per plant. We repeated transect counts twice, once in April and once in May, during the 24-day nestling period.

Nutrient composition

Fruit collection. During and immediately following fledging, we collected fruits observed being fed to nestlings along previously sampled transects within a 0.5 km radius of the nest and from trees not associated with transects where foraging for nestlings had been observed. We stored fruits frozen at -18°C for nutritional analysis. We freeze dried fruit samples for 72 hours or until all moisture was removed. We then separated pulp from seeds and placed them in a drying oven at 60°C for 12 hours to ensure complete drying before we ground them to a homogeneous mixture for analysis using a Glen Mills ball mill (Glen Mills, Clifton, NJ, USA).

Neutral Detergent Fiber (NDF). We dried Ankom 757 filter bags (Ankom, Macedon, NY, USA) in an oven at 100°C for 15 minutes and dried fruit pulp samples for one hour to insure that all moisture was evaporated. We placed both the bag and samples, separately, in a desiccator to cool and then weighed each bag to 0.001 g. We filled each bag with 0.5 g of pulp and then heat sealed along with two empty bags as blanks. We transferred bags into an Ankom 200 fiber analyzer with 2000 ml of NDF solution and 20 g of sodium sulfite. The machine heated the samples and agitated them for 1:15 hours. We then rinsed the bags with boiling water and placed in acetone for 5 minutes. We then air-dried bags until all of the acetone was evaporated and we then placed them in a drying oven at 100°C for 12 hours to complete drying. After 12 hours, we transferred them to a desiccator to cool, and weighed to 0.001 g. We calculated the NDF for each sample using the following equation:

$$\text{Bag}_R - \text{Bag}_E - \text{Bag}_B = \text{Dry Residue Weight} \\ \text{Dry Residue Weight}/\text{Sample Weight} \times 100 = \% \text{NDF}$$

where Bag_R is weight of the bag with residue from the procedure, Bag_E is the weight of the empty bag, and Bag_B is average weight of residue picked up by the two blanks.

Minerals. We placed 11 small ceramic cups in a drying oven for 30 minutes at 60°C and then transferred them to a desiccator to cool prior to weighing. We then placed pulp samples into the drying oven for

30 minutes at 60°C and then in a desiccator to cool. We measured 1 g samples of pulp for each species into each of 11 small ceramic cups. We ashed samples in ceramic cups in an oven at 500°C for two hours, placed them in a desiccator to cool, and weighed to 0.001 g. We determined the amount of mineral content by subtracting final weight from initial weight.

C/N. We measured approximately 0.5 g of each fruit pulp sample into small tin cups and individually analyzed them on a CE Elantech NCS-2500 (CE Elantech, Lakewood, NJ, USA) elemental analyzer at the University of Wyoming Stable Isotope Laboratory. Nitrogen and carbon peaks were used to calculate percent carbon and nitrogen content of pulp samples.

Lipids. We rinsed aluminum extraction cups with petroleum ether to remove any residue, placed them in an oven with Whatman 33 x 80 mm cellulose extraction thimbles for 15 minutes, and then placed them in a desiccator to cool. We dried pulp samples in an oven for two hours, allowed them to cool in a desiccator, and weighed out 0.5–1 g of each sample in duplicate into the bottom of individual extraction thimbles. We placed the thimbles inside aluminum extraction cups and inserted into a Soxtec Avanti 2050 (Soxtec, Denmark) automated fat extraction system. We injected 80 ml of petroleum ether into each sample and allowed them to be processed on the machine for 1:30 hours. At the completion of the cycle, we transferred aluminum cups to the oven for 15 minutes, cooled them in the desiccator, and weighed them to 0.001 g. Percent fat per sample was calculated as follows:

$$\% \text{ Fat} = (W_3 - W_2)/W_1 \times 100$$

where W_1 is sample weight, W_2 is extraction cup weight, and W_3 is extraction cup weight with residue.

Protein. We determined protein content by multiplying values of nitrogen by 5.64. This method was devised by Levey et al. (2000) to overcome biases in determining plant and fruit protein from the accepted method of multiplying nitrogen content by 6.25. The latter method overestimates protein because it was developed to estimate protein in animal tissue. In plant tissue and especially fruit pulp, nitrogen is also found in free amino acids and many nitrogenous secondary metabolites as well as protein. The conversion factor, 5.64, was found by Levey et al. (2000) to be a good estimate of protein content in fruit pulp.

RESULTS

Adult nest attendance. At the start of the field season, three pairs of quetzals were monitored until they initiated nests as evidenced by incubation behavior. Two nests were presumably depredated or

Table 1. Food items brought to nestling Resplendent Quetzals (*Pharomachrus mocinno*) during the first 12 days after hatching (11–21 April 2000) and during the last 12 days (22 April–3 May 2000) at one nest located in San Gerardo de Dota, Costa Rica. Fruits made up the largest proportion of the nestlings' diet and fruits from Lauraceae were delivered more than all other fruits.

Food item	Male		Female		Total	Proportion of diet
	1–12	13–24	1–12	13–24		
LIZARDS						
Phrynosomatidae						
<i>Sceloporus malachiticus</i>	2	6	0	1	9	0.030
INSECTS						
Orthoptera						
<i>Tettigoniidae</i> sp.	0	0	1	2	3	0.010
Coleoptera						
<i>Scarabidae</i> sp.	8	7	5	1	21	0.069
<i>Cerambycidae</i> sp.	2	1	0	0	3	0.010
Lepidoptera						
Lepidoptera larvae	2	6	0	2	10	0.033
Subtotal	14	20	6	6	46	0.151
FRUITS						
Lauraceae						
<i>Ocotea holdridgeiana</i>	9	80	16	116	221	0.725
<i>Nectandra cufodontisii</i>	2	4	4	3	13	0.043
<i>Aiouea costaricensis</i>	0	3	0	0	3	0.010
Myrsinaceae						
<i>Ardisia fimbriifera</i>	0	0	1	1	2	0.007
Sabiaceae						
<i>Meliosma idiopoda</i>	0	0	1	0	1	0.003
Rosaceae						
<i>Prunus cornifolia</i>	0	2	0	0	2	0.007
<i>Rubus</i> sp.	1	0	1	3	5	0.016
Unidentified	2	0	10	0	12	0.039
Subtotal	14	89	33	123	259	0.849
Total Deliveries	30	115	39	130	314	

abandoned 5 and 7 days, respectively, after incubation was first observed, and adults presumably left the area leaving only one active nest. After considerable searching no new nests were found. Data presented here is for the only remaining nest that successfully fledged two young after 24 days. During the 24-day nestling period a total of 101.5 hours of observations were made. The male and female made food deliveries to their young roughly the same number of times ($n = 137$ and $n = 168$ respectively; Table 1). The male delivered 25% animal prey and 75% fruit, whereas the female delivered 7% animal prey and 93% fruit (Table 1). During the nestling period, deliveries per hour did not appear to differ between males and females (1.24 ± 0.68 and 1.44 ± 0.84 , respectively; mean \pm SD).

During the first six days, quetzals delivered primarily animal prey, insects and lizards, to their young (Table 1, Figure 1). They gradually increased delivery

of fruit relative to animal prey, and by day 6, fruit comprised the largest proportion of the total food deliveries (Table 1, Figure 1). A total of 314 food items were delivered to the nestlings over the 24-day nestling period with fruits comprising 84.9% of the diet (Table 1). Fruits from four plant families and one unidentified fruit family were represented and included Lauraceae, Myrsinaceae, Sabiaceae, and Rosaceae with 237 of the 259 fruits (91.5%) delivered belonging to the family Lauraceae (Table 1). Three Lauraceae species, *Ocotea holdridgeiana*, *Nectandra cufodontisii*, and *Aiouea costaricensis* were fruiting within 0.5 km from the nest cavity during the study. Of these three, 221 of 237 (93.2%) Lauraceae fruits delivered were from *O. holdridgeiana*.

A total of 312 seeds were removed from the nest cavity. In agreement with the observational data, four plant families were represented by seeds in the nest and were Lauraceae, Rosaceae, Sabiaceae, and Sym-

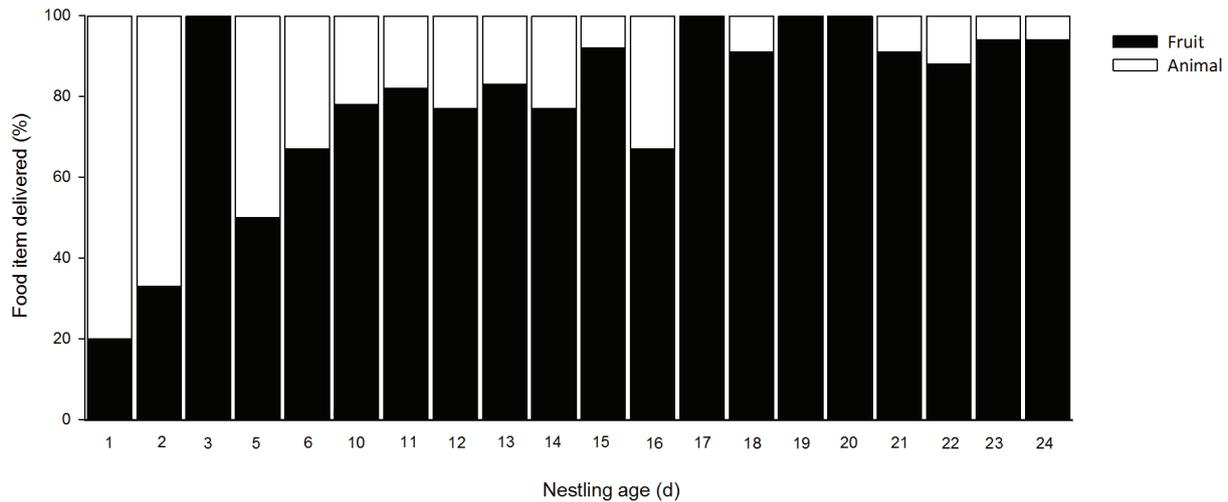


Figure 1. Daily frequencies of fruit and animal prey delivered to Resplendent Quetzal (*Pharomachrus mocinno*) nestlings in San Gerardo de Dota, Costa Rica, reveal a strong pattern of animal prey early and a shift to a predominantly fruit diet by day 6 post hatch.

plocaceae (Table 2). However, Myrsinaceae (*Ardisia fimbrilifera*) and *Rubus* (Rosaceae) species were observed being fed to nestlings, but were not represented in the nest contents (Table 2). Seeds from one additional family, Symplocaceae, were found in the nest but not recorded during observations (Table 2). No difference was found between the species and number of fruits observed being delivered to nestlings and species and number of seeds found in the nest (Student's *t*-test, $t = -0.234$, $p = 0.82$, $N = 16$).

Fruit abundance. Eleven species of fruiting plants were found within a 0.5 km radius from the nest cavity and included in order of increasing abundance *Solanum lanceifolium*, *Symplocos austin-smithii*, *O. holdridgeiana*, *N. cufodontisii*, *Gutteria costaricensis*, *Rubus* sp., *Ardisia costaricensis*, *A. fimbrilifera*, *Calyptanthes pallens*, *Meliosma idiopoda*, and *Prunus cornifolia* (Table 3). Fruits and seeds of *Solanum lanceifolium*, *Symplocos austin-smithii*, *Gutteria costaricensis*, and *Calyptanthes pallens* were not observed being fed to nestlings and were not found in the contents of the nest after fledging. Of fruits delivered to nestlings, the most abundant fruit in the environment during April and May was *P. cornifolia* with approximately 87,130 and 97,748 fruits, respectively. The least abundant fruit in April and May, and most delivered by quetzals, was *O. holdridgeiana* with 176 and 77 fruits, respectively (Table 3). *Calyptanthes pallens* was the second most abundant fruit sampled, but was not observed or found to have been delivered to nestlings.

Nutrient composition. *Ocotea holdridgeiana*, *N. cufodontisii*, and *S. lanceifolium* had the highest nitrogen, and likewise, the highest protein content of the eleven fruits (Table 4). The three Lauraceae species, *O. holdridgeiana*, *N. cufodontisii*, and *A. costaricensis* had the highest carbon content (Table 4).

Ocotea holdridgeiana and *A. costaricensis* had the highest lipid content (Table 4). *Ocotea holdridgeiana*, *M. idiopoda*, and *S. lanceifolium* had the highest mineral content (Table 4). Interestingly, *O. holdridgeiana* had the highest carbon, mineral, and lipid content and was in the top three in nitrogen, NDF, and protein content.

DISCUSSION

Nestling attendance by male and female quetzals at San Gerardo de Dota was similar to attendance reported by Wheelwright (1983) at Monteverde in northern Costa Rica with males and females generally sharing parental brooding and feeding responsibilities (Table 1). However, deliveries of fruit and animal prey differed proportionally with the male delivering more animal prey and females delivering more fruit (Table 1). Wheelwright (1983) was the first to quantify overall deliveries of food items differed for male and female quetzals and found a similar result for animal prey deliveries between the breeding pair. However, male and female delivered similar proportions of fruit (Wheelwright 1983). It is unclear what drives these individual differences, but what is clear from our study is that quetzals delivered proportionally more fruit than animal prey to their developing nestlings and that fruit deliveries were primarily from Lauraceae.

Throughout their range, quetzals are known to feed preferentially on lipid rich fruits of the Lauraceae (Wheelwright 1983, Avila et al. 1996). Because of this, it is not surprising that fruits made up the largest proportion of the nestlings' diet and as hypothesized, most fruits delivered were Lauraceae (Table 1). The dominance of fruits from the Lauraceae in diets of nestling quetzals at our study site was similar to findings by other studies (Wheelwright 1983, Avila et al. 1996). Avila et al. (1996) found that adult quetzals in

Table 2. Species of fruit observed being fed and fruit seeds found in the nest cavity after fledging of nestling Resplendent Quetzals (*Pharomachrus mocinno*) in San Gerardo de Dota, Costa Rica. Although individual species counts were different, proportion of each species represented through observation or direct count was similar.

Species	Fruits delivered	Nest contents
<i>Ocotea holdridgeana</i>	221	186
<i>Nectandra cufodontisii</i>	13	44
<i>Rubus</i> sp.	5	0
<i>Aiouea costaricensis</i>	3	29
<i>Prunus cornifolia</i>	2	27
<i>Ardisia fimbrellifera</i>	2	0
<i>Meliosma idiopoda</i>	1	20
<i>Symplocos austin-smithii</i>	0	6

southern Mexico delivered a variety of fruits to nestling and 50% of those fruits were from the Lauraceae. Wheelwright (1983) found that during the breeding season, 81% of fruit deliveries were fruits from Lauraceae, more closely matching our results.

What did differ between our study and Wheelwright (1983) was the proportion of fruit relative to animal prey delivered to nestlings. At San Gerardo de Dota, Costa Rica, and El Triunfo Biosphere Reserve, Mexico, fruits made up the bulk of the nestling diet. Wheelwright (1983), however, found that fruits constituted only 29.5% of the total diet for nestlings at Monteverde in northern Costa Rica. It is unclear why this pattern of feeding was so different across study sites. It is relatively common, even for frugivorous birds, to feed young high protein diets early during nestling development and gradually switch to an increasingly fruit dominated diet (Ricklefs 1974, Breitwisch et al. 1984). However, the pair of quetzals studied by Wheelwright (1983) continued to feed a high proportion of animal prey relative to fruits throughout the nestling period. Differences in prey abundance could be a likely explanation, but neither this nor previous studies quantified abundance of this resource.

It is interesting that such a large proportion of fruits delivered to nestlings came from only one species of Lauraceae (*O. holdridgeana*), and that *O. holdridgeana* was the only Lauraceae species in the pair's territory observed with ripe fruit; although unripe fruits from *N. cufodontisii* and *A. costaricensis* were fed nestlings. Many birds, including the quetzal, are known to key in on characteristics of fruits and fruiting displays such as ripeness when foraging (Stiles 1993 and references therein). Additionally, *O. holdridgeana* was one of the least abundant fruits (Table 3). Fruit selection by nonbreeding adults has been found to closely track fruit abundance (Loiselle & Blake 1991, Borgman et al. 2004, Blendinger et al. 2012), but we know of no studies that have directly compared fruit abundance and fruit selection for

Table 3. Total fruit abundance estimates within 0.5 km of the Resplendent Quetzal (*Pharomachrus mocinno*) nest for April and May in San Gerardo de Dota, Costa Rica. Number of fruits fed to nestlings increased with decreasing relative abundance.

Species	# delivered to nestlings	Number of fruits present	
		April	May
<i>Ocotea holdridgeana</i>	221	176	77
<i>Nectandra cufodontisii</i>	13	372	339
<i>Rubus</i> sp.	5	628	570
<i>Aiouea costaricensis</i>	3	1096	1111
<i>Ardisia fimbrellifera</i>	2	7228	7178
<i>Prunus cornifolia</i>	2	87,130	97,748
<i>Meliosma idiopoda</i>	1	16,160	16,004
<i>Solanum lanceifolium</i>	0	33	45
<i>Symplocos austin-smithii</i>	0	58	51
<i>Guatteria costaricensis</i>	0	570	510
<i>Calyptanthes pallens</i>	0	20,875	20,215

nestlings. Our results, although not directly comparable, agree with Davidar & Morton (1986), who found there was no significant correlation between bird visitation rates and fruit crop size of a tree.

The most abundant fruits in our study had the highest fruit crop sizes on a per tree basis but were fed to nestlings the least. This can possibly be explained by arguments put forth by McKey (1975) and Howe & Estabrook (1977) who believed that a fruiting strategy of a plant may influence foraging decisions for birds such as the quetzal. McKey (1975) argued that while some plants may benefit from a variety of dispersers (generalists) others profit from the services of a few more reliable dispersers (specialists). Additionally, Howe & Estabrook (1977) argue that species producing small seeds should invest little in rewards where species, such as the Lauraceae that produce large seeds, should provide rich and nutritious rewards to attract specialists like the quetzal. The argument put forth by Howe & Estabrook (1977) definitely applies to the types of fruits available to quetzals and possibly explains why the least abundant but most nutritious fruits were delivered to nestlings.

Ocotea holdridgeana had the highest lipid content of all fruits fed to nestlings (Table 4). It has been shown that birds have a high preference for lipid rich fruits annually and seasonally in response to increase fat stores for overnight survival (Blem 1976), flight (Witter & Cuthill 1993), migration (Blem 1990, Ramenofsky 1990), over wintering (Evans 1969, Houston & McNamara 1993), and during development (Brenner 1964, Brisbin 1969, Ricklefs 1967). As quetzal chicks grow, adults spend less and less time in the nest brooding, exposing the young birds to cool day and night time temperatures in the bare tree cavity that constitutes the nest (Skutch 1944). It is plausible

Table 4. Results of nutrient measurement for the 11 species of fruit found in the breeding territory of a pair of Resplendent Quetzals (*Pharomachrus mocinno*) in San Gerardo de Dota, Costa Rica. *O. holdridgeiana*, *N. cufodontisii*, and *A. costaricensis*, all in the Lauraceae family, had the some of the highest lipid and protein content of fruits fed to nestlings. Nutrient values are reported as percent dry mass.

Species	N	# delivered to nestlings	N	C	Ash	NDF	Lipid	Protein
<i>Ocotea holdridgeiana</i>	3	221	2.26	58.65	17.4	30.09	26.75	14.1
<i>Necatandra cufodontisii</i>	3	13	2.39	53.5	5.44	37.82	1.04	14.94
<i>Rubus</i> sp.	3	5	0.75	43.67	3.38	9.71	0.79	4.69
<i>Aiouea costaricensis</i>	3	3	1.60	57.86	4.48	26.83	18.76	10.00
<i>Prunus cornifolia</i>	3	2	1.51	43.22	3.19	17.72	0.22	9.47
<i>Ardisia fimbrillefera</i>	3	2	0.92	43.2	9.22	13.9	1.85	5.72
<i>Meliosma idiopoda</i>	3	1	1.05	42.75	11.96	29.01	0.36	6.57
<i>Symplocos austin-smithii</i>	3	0	0.73	43.99	5.97	28.51	0.37	4.55
<i>Solanum lanceifolium</i>	3	0	2.71	44.99	14.64	33.25	0.26	16.91
<i>Calyptanthes pallens</i>	3	0	1.03	41.89	5.38	18.3	0.31	6.42
<i>Guatteria costaricensis</i>	3	0	1.44	47.83	7.48	25.62	4.12	8.97

that high lipid Lauraceae fruits delivered to nestlings provide a high energy food source needed to not only grow, but to offset body heat lost to the surrounding environment.

Furthermore, it is interesting that quetzals in our study mainly delivered fruit species highest in lipid content to feed nestlings rather than other available fruits lower in lipid content. The results of our study disagree with those of Sorensen (1981) and Howe (1983, 1986) that birds are unable to distinguish differences in pulp composition. Other studies show that the ability of birds to distinguish among pulp composition is actually extremely high and precise (Duncan 1960, Levey 1987, Martinez del Rio 1988). Quetzals are known to congregate and preferentially forage on ripe over unripe fruits and Foster (1977) found that unripe and ripe fruits differed in nutrient composition (Table 4). Additionally, Blendinger et al. (2015) found that frugivorous birds closely tracked nutrient availability temporally when making foraging decisions. The high nutrient composition of *O. holdridgeiana*, its large mass, and presence of ripe fruits may explain its prevalence in the diet of the nestling quetzals.

Witmer & Martinez del Rio (2001) suggest that gut morphology is different between species of birds that consume diets that are either predominantly lipids or predominantly carbohydrates. Bosque & Parra (1992) found that oilbird nestlings (*Steatornis caripensis*) fed exclusively on a lipid rich fruit pulp diet, have high digestive efficiencies of lipids and proteins coupled with long digestive retention times. Digestive systems of birds that feed on carbohydrate rich fruits are typically short and digestive systems of birds that feed on lipid rich fruits are typically longer. This difference in digestive physiology is believed to be a response to the additional work and amount of time

required to digest lipids than carbohydrates. Carbohydrates can be quickly broken down into simple sugars and absorbed for immediate use. While lipids can be stored easily, breaking down lipids for absorption is a lengthy process that requires enzymes from the pancreas and bile salts from the gall bladder to reduce it to a form that can be absorbed and transported to cells. Nothing is known about the digestive physiology of the quetzal, but its preference for lipid-rich Lauraceae fruits may indicate that its gut morphology and function are designed for effectively processing lipids, similar to oilbirds, and warrants further investigation.

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REFERENCES

- Avila, HL, VH Hernandez & E Verlarde (1996) The diet of Resplendent Quetzal (*Pharomachrus mocinno mocinno*: Trogonidae) in a Mexican cloud forest. *Biotropica* 28: 720–727.
- Biebach, H, W Friederich & G Heine (1986) Interaction of body mass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* 69: 370–379.
- Blem, CR (1976) Patterns of lipid storage and utilization in birds. *American Zoologist* 16: 671–684.
- Blem, CR (1990) Avian energy storage. *Current Ornithology* 7: 59–113.

- Blendinger, PG, RA Ruggera, MG Nunez Monellano, L Macchi, PV Zelaya, ME Alvarez, E Martin, O Osinaga Acosta, R Sanchez & J Haedo (2012) Fine tuning the fruit-tracking hypothesis: spatiotemporal links between fruit availability and fruit consumption by birds in an Andean mountain forest. *Journal of Animal Ecology* 81: 1298–1310.
- Bosque, C & O de Parra (1992) Digestive efficiency and rate of food passage in oilbird nestlings. *The Condor* 94: 557–571.
- Breitwisch, R, PG Merritt, & GH Whitesides (1984) Why do mockingbirds feed fruit to their nestlings? *The Condor* 86: 281–287.
- Brenner, FJ (1964) Growth, fat deposition and development of endothermy in nestling Red-winged Blackbirds. *Journal of the Scientific Laboratories, Dennison University* 46: 81–89.
- Brisbin, IL Jr (1969) Bioenergetics of the breeding cycle of the Ring Dove. *The Auk* 86: 54–74.
- Bowes, AL & DG Allen (1969) Biology and conservation of the quetzal. *Biological Conservation* 1: 297–306.
- Borgman, KL, SF Pearson, DJ Leavy & CH Greenberg (2004) Wintering Yellow-rumped Warblers (*Dendroica coronata*) track manipulated abundance of *Myrica cerifera* fruits. *The Auk* 121: 74–87.
- Davidar, P & ES Morton (1986) The relationship between crop size and fruit removal rates by birds. *Ecology* 67: 262–265.
- Duncan, CJ (1960a) Preference tests and the sense of taste in the Feral Pigeon (*Columbia livia* var. Gmelin). *Animal Behaviour* 8: 54–60.
- Duncan, CJ (1960b) The sense of taste in birds. *Annals of Applied Biology* 48: 409–414.
- Evans, PR (1969) Winter fat deposition and overnight survival of yellow buntings (*Emberiza citrinella* L.). *Journal of Animal Ecology* 38: 415–423.
- Foster, MS (1977) Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58: 73–85.
- Foster, MS (1987) Feeding methods and efficiencies of selected frugivorous birds. *The Condor* 89: 566–580.
- Foster, MS (1990) Factors influencing bird foraging preferences among conspecific fruit trees. *The Condor* 92: 844–854.
- Griminger, P (1986) Lipid metabolism. Pp 345–358 in Sturkie, P (ed). *Avian physiology*. Springer-Verlag, New York, New York, USA.
- Holdridge, C (1967) *Life zone ecology*. Tropical Science Center, San Jose, Costa Rica.
- Houston, AI & JM McNamara (1993) A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Scandinavian Journal of Ornithology* 24: 205–219.
- Howe, HF (1980) Monkey dispersal and waste of a Neotropical fruit. *Ecology* 61: 944–959.
- Howe, HF (1983) Annual variation in a Neotropical seed-dispersal system. Pp 211–227 in SL Sutton, TC Whitmore & AC Chadwick (eds). *Tropical rain forest: ecology and management*. Special Publication of the British Ecological Society No. 2.
- Howe, HF (1986) Seed dispersal by fruit-eating birds and mammals. Pp 123–189 in Murray, DR (ed). *Seed dispersal*. Academic Press, New York, New York, USA.
- Howe, HF & GF Estabrook (1977) On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111: 817–832.
- Howe, HF & GA Vande Kerckhove (1979) Fecundity and seed dispersal of a tropical tree. *Ecology* 60: 180–189.
- Klasing, KC (1998) *Comparative Avian Nutrition*. CAB International, Oxford, UK.
- Levey, DJ (1987) Sugar-tasting ability and fruit selection in tropical fruit-eating birds. *The Auk* 104: 173–179.
- Levey, D, HA Bissell & HF O'Keefe (2000) Conversion of nitrogen to protein and amino acids in wild fruits. *Journal of Chemical Ecology* 26: 1749–1763.
- Loiselle, BA & JG Blake (1990) Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. *Studies in Avian Biology* 13: 91–103.
- Loiselle, BA & JG Blake (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72: 180–193.
- Martinez del Rio, C (1988) Physiological correlates of preference and aversion for sugars in three species of birds. *Physiological Zoology* 61: 222–229.
- McKey, D (1975) The ecology of coevolved seed dispersal systems. Pp 159–191 in Gilbert, LE & PH Raven (eds). *Coevolution of animals and plants*. Univ. of Texas Press, Austin, Texas, USA.
- Paine, RT (1971) The measurement and application of the calorie to ecological problems. *Annual Review of Ecology and Systematics* 2: 145–164.
- Powell, GVN & RD Bjork (1994) Implications of altitudinal migration for conservation strategies to protect tropical biodiversity: a case study of the resplendent Quetzal *Pharomachrus mocinno* at Monteverde, Costa Rica. *Bird Conservation International* 4: 161–174.
- Ramenofsky, M (1990) Fat storage and fat metabolism in relation to migration. Pp 214–231 in Fwinner, E (eds). *Bird migration*. Springer-Verlag, Berlin, Germany.
- Ricklefs, RE (1967) Relative growth, body constituents, and energy content of nestling Barn Swallows and Red-winged Blackbirds. *The Auk* 84: 560–570.
- Ricklefs, RE (1974) Energetics of reproduction in birds. Pp 152–297 in Paynter, RA (ed). *Avian energetics*. Publication of the Nuttall Ornithological Club No. 15.
- Skutch, AF (1944) Life history of the quetzal. *The Condor* 46: 215–235.
- Sorensen, AE (1981) Interactions between birds and fruit in a temperate woodland. *Oecologia* 50: 242–249.
- Snow, BK (1970) A field study of the Bearded Bellbird in Trinidad. *Ibis* 112: 299–329.
- Snow, DW (1962) The natural history of the Oilbird (*Steatornis caripensis*) in Trinidad, W.I. Part II. Population, breeding ecology, and food. *Zoologica* 47: 199–221.
- Snow, DW (1971) Evolutionary aspects of fruit-eating by bird. *Ibis* 113: 194–202.
- Snow, DW (1981) Tropical frugivorous birds and their food plants, a world survey. *Biotropica* 13: 1–14.
- Solorzano, S, S Castillo, T Valverde & L Avila (2000) Quetzal abundance in relation to fruit availability in a cloud forest in southeastern Mexico. *Biotropica* 32: 523–532.
- Stiles, EW (1993) The influence of pulp lipids on fruit preference by birds. *Vegetatio* 107: 227–235.
- Stiles, FG (1985) On the role of birds in the dynamics of Neotropical forests. Pp 141–168 in Diamond, W & T Lovejoy (eds). *Conservation of tropical forest birds*. International Council on Bird Preservation, Cambridge, UK.
- Wheelwright, NT (1983) Fruits and ecology of the Resplendent Quetzals. *The Auk* 100: 286–301.
- Wheelwright, NT (1985) Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66: 808–818.
- Wheelwright, NT, WA Haber, KG Murray & C Guindon (1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16: 173–192.
- Witmer, MC & C Martinez del Rio (2001) The membrane bound intestinal enzymes of waxwings and thrushes: adaptive and functional implications of patterns of enzyme activity. *Physiological and Biochemical Zoology* 74: 584–593.
- Witter, MS & IC Cuthill (1993) The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society London* 340: 73–92.