FRUITS AND THE ECOLOGY OF RESPLENDENT QUETZALS

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ABSTRACT.—Resplendent Quetzals (*Pharomachrus mocinno*) are typically termed "specialized" fruit-eating birds, although there are few data describing the breadth of their diet or the characteristics of the fruits they select. In fact, there is no general consensus about the meaning or consequences of being a fruit specialist. In the lower montane forests at Monteverde, Costa Rica, quetzals feed on a minimum of 12–18 species of fruits at most times of the year and on an annual total of at least 41 species. Although their diet includes the watery, small-seeded berries of many second-growth plants, they depend mostly on the large drupes of about 18 species in the laurel family (Lauraceae). The phenologies and habitat distributions of the Lauraceae appear to dictate the timing and direction of seasonal movements by quetzals. Mutual dependence and, possibly, general coevolution between quetzals and the lauraceous trees whose seeds they disperse are suggested by the birds' morphology, distribution, behavior, and life history.

Nestling quetzals are brought entire fruits as early as the second day after hatching. Thereafter, they consume gradually increasing amounts of fruit, but, even immediately before they fledge, most of their diet consists of insects, snails, and lizards. Brooding drops off rapidly by the time chicks are 9 days old. Considerable variation in brooding duration, parental sex roles, and nestling diet exists between nests, however, and apparently between clutches. Adults take far less time to deliver fruits to nestlings than to deliver insects or lizards, which reflects the relative ease of "capturing" ripe fruits (as opposed to animal prey) during the breeding season. The male parent delivered significantly more insects and food items in general than did the female at a first-clutch nest but not at a second-clutch nest.

Several Central American montane reserves have been established to protect populations of quetzals, the national symbol of Guatemala and an important tourist attraction throughout the Isthmus. Unfortunately, the reserves tend to be too small and to include only a limited representation of critical habitats. If other Central American quetzal populations are similar to Monteverde's, the birds must migrate to different habitats as the availability of ripe fruits fluctuates between seasons or years. Once reserves become isolated by deforestation, they will fail to prevent local extinction of quetzals.

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A SMALL group of tropical fruit-eating birds has come to be recognized as "different." The diet, behavior, and morphology of these birds, which include oilbirds, fruit-pigeons, cotingas, and toucans, seem to set them apart from other fruit-eating birds, such as flycatchers, thrushes, and finches (Snow 1971, 1981). The distinctions between the two groups prompted McKey (1975) to introduce the terms "specialized" and "generalized" frugivores. Specialists' diets are thought to be comprised mainly of the nutritious fruits of only a few plant species, for which the birds serve as major seed dispersers and with which they are believed to have coevolved (McKey 1975). There have been few long-term studies adequate to test the specialist-generalist dichotomy and the predictions of McKey's influential model, however, let alone its assumptions about differences in seed dispersal quality and behavior between specialists and generalists (Wheelwright and Orians 1982). A key question is whether, or in what ways, specialists are ecologically similar to each other. Does coevolution between fruit-eating birds and plants result in similar patterns within different habitats and taxa? Or do specialists, unified only by their distinctness from birds that are less dependent upon a fruit diet, differ from one another as well?

The difficulties of identifying specialists'

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unique traits lie partly in the shortage of natural history information. In an attempt to address the need for such information, this paper describes the ecology of Resplendent Quetzals (*Pharomachrus mocinno*), neotropical members of the Trogonidae that are typically considered specialized fruit-eating birds (McKey 1975, Snow 1981). Data on adult and nestling diets, morphology, life history, and predation in a Costa Rican population are presented in the context of current theory about avian frugivory and diet specialization.

Despite their designation as the national symbol of Guatemala and a reputation as "the most spectacular bird in the New World" (Peterson and Chalif 1973), quetzals have attracted little scientific study. Across much of their range (southern Mexico to western Panama) they are scarce, and their montane habitat is relatively inaccessible (Hanson 1982). Skutch's (1944) paper remains the most thorough descriptive account of the natural history of quetzals. Over the course of one year, Skutch documented nesting chronology, behavior, vocalizations, plumage, and nestling development at a Costa Rican site. Drawing from observations in Guatemala during the breeding season, LaBastille and others (Bowes and Allen 1969, LaBastille et al. 1972, LaBastille 1973) supplemented Skutch's work while emphasizing the conservation of quetzals.

STUDY SITE AND METHODS

Between 1979 and 1982, I studied quetzals and the reproductive biology of the plants whose fruits quetzals eat in the lower montane forests of Monteverde, Costa Rica (10°18'N, 84°48'W; Holdridge 1967). The 18-month study period (June–August 1979, June 1980–July 1981, March 1982) included one entire annual cycle and parts of breeding seasons during four different years. Monteverde lies on a plateau straddling the continental divide in the Cordillera de Tilarán. Strong northeast Trade Winds blow across the divide at all times of the year, especially during the dry season, when winds often carry sheets of mist. Westward from the divide, in the lee of the prevailing winds, habitats change rapidly along a marked moisture gradient. The forests range from epiphyte-laden "elfin" cloud forest at the crest of the cordillera (elevation 1,550 m) to the relatively dry, taller forest of the edge of the plateau 4 km to the west (1,350 m) (see Lawton and Dryer 1980 for a more complete description of forest types). The study site included the 2,700-ha Monteverde Cloud Forest Reserve. The undisturbed Arenal National Forest (ca. 33,000 ha) surrounds the Reserve on the Atlantic slope. Bordering the Reserve on the Pacific slope, the Monteverde community itself consists of scattered cattle pastures and extensive wood lots. The rainy season usually begins in early May and extends, with a brief dry spell in July, until mid-December. The abundance and diversity of fruits vary between seasons and years (G. Frankie and W. Haber pers. comm.; pers. obs.).

Two times every month from June 1980 until August 1981 (except mid-November), I censused quetzals by recording sightings and calls over a route of about 7 km from the cloud forest to the dry forest, spending about 6 h in each of four habitat types, in order to determine diets and seasonal movements. General field observations (over 2,000 h), including periodic censuses on the Atlantic slope, added information about migrations, foraging behavior, and natural history. Even during the nonbreeding season, when quetzals rarely vocalize, their noisy flight, large size, and regurgitation of bulky seeds reveal their presence. I spent more than 200 h watching at fruiting trees, especially 23 species in the Lauraceae (laurel, or avocado, family). Over 120 h were spent monitoring food deliveries to nestlings at three quetzal nests. I used a 15–60× spotting scope and binoculars to observe from a blind at a distance of about 35 m, from which I had little difficulty identifying most items brought to the nest by the parents. I made observations at a total of 11 active nests.

Quetzals habitually perch on a particular low branch when arriving at or departing from their nest. Beneath these perches I placed "seed traps" (cf. Snow 1970) of dark, fine-mesh, 1 m^2 nylon netting elevated 0.5 m above the ground. Although pocket mice (*Heteromys demerestianus*), the major vertebrate seed predators at Monteverde, can climb (Eisenberg 1963), no seeds were removed from control seed traps in which a known number of seeds had been placed. At 5-day intervals I identified and counted seeds regurgitated or defecated by perching quetzals. Most or all of the seeds in the traps were believed to have been dropped by members of the pair nesting nearby, because seed traps were positioned directly below perches that the territorial quetzals used exclusively during more than 120 h of observation. Control seed traps located a short distance away collected 0–2 seeds/week versus 20–60 seeds/week below quetzal perches. The accuracy of seed-trap sampling was confirmed by independent sightings of quetzals feeding in the field on the same fruit species in approximately the same proportions. In an attempt to identify individual birds, I banded one adult male quetzal, but its short legs and loose belly plumage completely obscured the leg bands. I could often distinguish birds, however, by differences in tail coverts (the long paired coverts that extend over the tails of males are frequently broken or lost) or bill color (females' bills vary from slate to yellow).

TABLE 1. Fruits eaten by quetzals at Monteverde, Costa Rica. Plant families are arranged according to Cronquist (1981). C = common (>10 observations); M = moderately common (2–10 obs.); R = rare (1 obs.); ? = not observed, but probable. Herbarium specimens of the Lauraceae are at the Missouri Botanical Garden under collection numbers, which follow the species name in parentheses.

	Jan–Feb	Mar–Apr	May–Jun	Jul–Aug	Sep–Oct[a]	Nov–Dec[a]
MAGNOLIIDAE[b]						
Annonaceae						
Guatteria consanguinea	C	C				
Lauraceae						
Beilschmiedia costaricensis (55)		C	C	C		
B. sp. BC (188A)	C	C				
Nectandra davidsoniana (20)				C		
N. gentlei (8)			M	M		
N. hypoglauca (75)			C	C	C	
N. salicina (79)		C	C	C		
N. sp. NC (230)		M				
Ocotea austinii (165)	M	M				
O. bernouliana (12B)						
O. klotzschiana (85)						R
O. tonduzii (133)		C	C	C		
O. wachenheimii (201)				C	C	
O. sp. FL (209)	C	C				
O. sp. K2 (169)			C	C		
O. sp. RP (176)	M					
Persea sp. RP (13C)				?		
Phoebe neurophylla (59)			C			
P. mexicana (4B)				C	C	
P. sp. SG (possibly *P. mexicana*) (27A)				C	C	
HAMAMELIDAE						
Moraceae						
Ficus tuerckheimii	C	C	C	C	C	?
F. pertusa	M	M	?	?	?	?
DILLENIIDAE						
Theaceae						
Symplocarpon sp.			M			
Malvaceae						
Hampea appendiculata	?	R				
Flacourtiaceae						
Hasseltia floribunda		C	C			
Sapotaceae						
Pouteria sp.		?				
Symplocaceae						
Symplocos sp. AS				M		
S. sp. RE				R		
Myrsinaceae						
Ardisia palmana		C				
ROSIDAE						
Rosaceae						
Rubus rosaefolia	M	?	?	?	?	?
Myrtaceae						
Eugenia sp. RF			M			
unknown sp.			R			
Melastomataceae						
Conostegia bernouliana		?	M	?		
Rutaceae						
Mappia racemosa	M	M				
M. sp. A	R					
Araliaceae						
Dendropanax arboreus				M		
ASTERIDAE						
Verbenaceae						
Citharexylum integerrimum		M	R			
C. marcradenium	C	C				

Table 1. Continued.

	Jan–Feb	Mar–Apr	May–Jun	Jul–Aug	Sep–Oct[a]	Nov–Dec[a]
Rubiaceae						
Chione costaricensis			R			
Coussarea austin-smithii	M					
Guettarda poasana		M				
unknown sp.			R			
ARECIDAE						
Araceae						
Anthurium sp.			R			
Bimonthly species total:						
Common	6	10	8	10	5	
Moderately common	5	6	5	3		
Rare	1	1	5	1	1	1
All species	12	17	18	14	5[a]	1[a]

[a] During these months, when quetzals were rarely seen, few feeding records could be gathered.

[b] Several plant species, whose precise taxonomic classification is uncertain, are distinguished by arbitrary two-letter designations.

Standard deviations are given in parentheses following all means. All statistical tests are nonparametric and are described in Siegel (1956).

Results

Adult feeding behavior.—Table 1 lists the species of fruits that quetzals have been seen to eat at Monteverde.[2] Quetzals fed on at least 41–43 species, representing 17 plant families, of the approximately 400 species of fruits known or presumed to be eaten by birds at Monteverde (judging by their size, color, and presentation; see van der Pijl 1972). In comparison, 83 species in 32 families were recorded for Emerald Toucanets (*Aulacorhynchus prasinus*), 29 species in 11 families for Three-wattled Bellbirds (*Procnias tricarunculata*) (during the 8 months of the year they spend at Monteverde), and 36 species in 22 families for Mountain Robins (*Turdus plebejus*) (Wheelwright et al. MS).

As noted by Skutch (1944), the predominant plant family in the diet of quetzals is the Lauraceae. Of the fruit species listed in Table 1, 17–19 are from that family (because of taxonomic uncertainty within the Lauraceae, some species may actually include two separate sibling species). The remaining fruit species represent 16 other families in five subclasses. Although the Lauraceae constitute only about 1/25 of the bird-dispersed species at Monteverde, they comprised almost one-half of the fruit species included in quetzals' diets. Quetzals ate most of the approximately 23 bird-dispersed species in the Lauraceae, and those made up the major portion of their diet. The Lauraceae were even more important in terms of relative frequency in the diet as estimated by field records. Because my research concentrated particularly on the Lauraceae, however, observations were probably biased towards lauraceous species. Yet, seed-trap samples from four nests, corrected for the number of seeds per fruit (cf. Snow 1970), also demonstrated the prevalence of the Lauraceae in quetzals' diets: seeds from 273 out of a total of 342 fruits (79.8%) were lauraceous (cf. data on nestling diet, below). The proportion of lauraceous fruit pulp in the diet is actually substantially higher because of the large size of lauraceous fruits.

Quetzals moved seasonally due to their dependence on, or at least preference for, the fruits of the Lauraceae. At Monteverde, the number of species with ripe fruit remains relatively constant—except within the Lauraceae—throughout the year, with slight peaks in April and October (Haber pers. comm.; I have little data on absolute fruit abundance, the more relevant measure). Yet, as the fruiting seasons of different species in the Lauraceae changed, the population of quetzals at Monteverde moved, effectively "tracking" ripe lauraceous fruits (Fig. 1). I recognized four local habitat associations

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[2] The Merck Veterinary Manual (1972) recommends a somewhat different menu for "quetzal food": "2 Tbsp Zwieback crumbs, 2 Tbsp steamed brown rice, 1 Tbsp grated carrot, 1 Tbsp grated hard-boiled egg, 1 Tbsp cottage cheese."

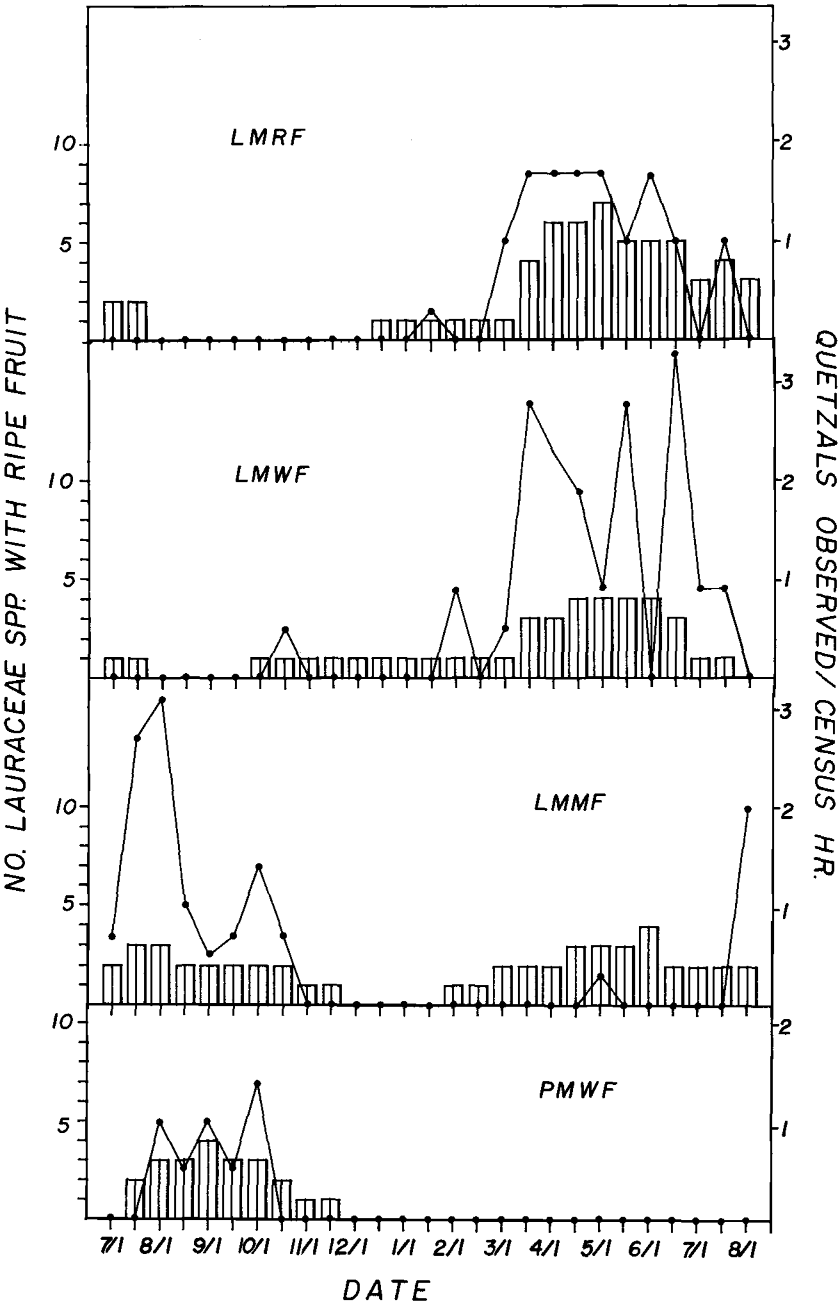

Fig. 1. Number of quetzals recorded per census hour (solid line) and number of species of Lauraceae producing ripe fruits (bars) in four habitats (PMWF, LMMF, LMWF, LMRF; see text for definitions) in different months of the year. During censuses an average of 6 h was spent traversing each habitat. No census was made in mid-November 1981.

[lower montane rain forest (LMRF), lower montane wet forest (LMWF), lower montane moist forest (LMMF), and premontane wet forest (PMWF)] that correspond to Holdridge's (1967) life zones, although they are based on differences in plant-species composition and forest structure rather than detailed climatological measurements. On the Atlantic slope, the forest (A-LMWF) resembles LMWF but has greater and more evenly produced annual precipitation. Because of the steep moisture gradient westward from the continental divide, all of the distinct habitat types occur within 6–10 km; the elevation difference between the lowest (PMWF) and highest (LMRF) is only about 200 m. Quetzals' between-habitat movements corresponded predictably to the phenology of the Lauraceae (Fig. 1), and they abandoned certain habitats despite the continuing availability of fruits (e.g. *Rubus, Ficus*) that they sometimes fed on. If tree species that are rare or only infrequently used by quetzals were excluded from Fig. 1, the relationship between quetzal densities and abundance of ripe lauraceous fruits would be even stronger. Other fruit-eating birds at Monteverde, such as Black-faced Solitaires (*Myadestes melanops*; G. Murray pers. comm.) and bellbirds, also migrate seasonally for reasons that are not yet well understood.

The peak of the breeding season (April–May) corresponded to the period of highest abundance and species richness of fruiting Lauraceae (12–15 species), especially in the habitats (LMWF, LMRF) where the birds nest. (It should be noted, however, that fruit in general is abundant then; furthermore, most birds, including insectivores, breed chiefly at the same time.) During the period when quetzals were absent from the area (October–December), only 0–3 species of Lauraceae had ripe fruit and, in 1980 at least, fruit crops of those species were low. Slud (1964) alluded to seasonal movements by quetzals, and Skutch (1944) wondered whether they migrated from the breeding area during the latter half of the rainy season or simply became much less conspicuous. Long-term observations by Monteverde residents confirm the observation of seasonal migrations by quetzals (W. Guindon pers. comm.).

Although quetzals feed almost entirely by plucking fruits on the wing, they occasionally swooped for fruits borne on ground-level shrubs (e.g. *Rubus*). When pursuing lizards and insects, or defending their nests against predators such as squirrels (*Sciurus* spp.), they sometimes landed on the ground (W. and C. Guindon, T. Blagden pers. comm.; pers. obs.). Bowes and Allen's (1969) proposal that quetzals never descend below 3.6 m during their lifetime is therefore inaccurate.

Morphology.—The morphology of quetzals seems adapted to enable them to feed on large fruits, such as those of the Lauraceae, as Snow (1973) proposed for the genus *Procnias.* I measured four quetzal museum specimens and dissected an adult female found near death with a shattered humerus. The gape width at the commissure averaged 2.1 cm. The esophagus, thin-walled, elastic, and ringed by circular muscles presumably important in regurgitating large seeds, measured 12 cm in length. Glandular tissue in a pattern of closely packed hexagons lined the 2- × 1.5-cm proventriculus. The muscular gizzard had an external diameter of 2.5 cm. Quetzals lack a crop, and the esophagus was not used to store food (cf. Walsberg 1975). The intestine was 50 cm long, and paired caecal sacs (length 4.5 cm) were packed with fruit skins, possibly indicating bacterial digestion of cellulose. Quetzals' flexible mandibles and clavicles and expansible proventriculus enable them to swallow fruits 3–4 mm wider than one would predict from gape measurements, and particularly to consume large lauraceous fruits. The median diameter of lauraceous fruits at Monteverde is 18 mm ($n = 23$ species), as opposed to a median of 9 mm for the fruits of all bird-dispersed plants of the lower montane wet forest ($n = 223$ species).

Quetzals primarily sally for fruits, as noted above. Their massive flight muscles reflect an aerial foraging mode. The pectoral muscle complex, which weighed 39 g in the dissected female, accounted for 20.6% of total body weight. Leg muscles (5 g) were a mere 2.6% of body weight. In contrast, pectoral muscles in Emerald Toucanets, which forage by hopping between branches rather than sallying, constituted only 12.8% of body weight, while leg muscles represented over 9.0% of body weight.

Nestling diets.—Table 2 presents data on the diet of quetzal chicks from the first clutch of nest 1. Nests may differ between habitats, clutches, or seasons in the relative proportions of fruits or insects delivered or in parental responsibilities, so one cannot generalize from observations at a single nest. Nonetheless, the

TABLE 2. Food items brought to nestling quetzals during the first 10 days after hatching (18–27 May 1981; $n = 44$ h observation) and during days 11–21 (28 May–7 June; $n = 27$ h). Because these observations record only items carried in the bill, they may under-represent fruit regurgitated in the nest. Proportions expressed as a fraction of identifiable items ($n = 196$). The male delivered more orthopterans ($P < 0.05$), beetles, insects in general, and items collectively ($P < 0.01$) than did the female (χ^2 one-sample test). The female delivered proportionately more *Ocotea tonduzii* fruits than did the mlae ($P < 0.01$, χ^2 two-sample test).

	Male parent		Female parent			
Item	day: 1–10	11–21	1–10	11–21	Total	Proportion of diet
INSECTS						
Odonata	1				1	0.005
Orthoptera						
Acrididae	3	3	1		7	0.036
Tettigoniidae	10	10	6	1	27	0.138
Phasmatidae	1				1	0.005
Hemiptera						
Cicadidae			1	1	2	0.010
Coleoptera						
Unidentified	23	5	9	5	42	0.214
Scarabidae	5		2	1	8	0.041
Scarabidae, larvae		2			2	0.010
Lepidoptera, larvae						
Unidentified	5	8	5	5	23	0.117
Sphingidae	1		2		3	0.015
Unidentified	1	2	2		5	0.026
Subtotal:	50	30	28	13	121	0.617
FRUITS						
Annonaceae						
Guatteria consanguinea	1				1	0.005
Lauraceae						
Ocotea tonduzii	7	8	8	14	37	0.189
Nectandra salicina	2	5		3	10	0.051
Moraceae						
Ficus tuerckheimii	1	1	1		3	0.015
Theaceae						
Symplocarpon sp.			1		1	0.005
Flacourteaceae						
Hasseltia floribunda	1				1	0.005
Myrtaceae						
Eugenia sp.		1			1	0.005
Rutaceae						
Mappea racemosa	2				2	0.010
Unidentified	1	1			2	0.010
Subtotal:	15	16	10	17	58	0.295
LIZARDS						
Iguanidae						
Norops (Anolis) sp.	1				1	0.005
Norops tropidolepus	3	1	3	1	8	0.041
SNAILS						
Unidentified	4	1	1	2	8	0.041
UNIDENTIFIED ITEMS	2	7	1	7	17	—
TOTAL	75	55	43	40	213	0.994

general patterns at this nest were similar (except for sex roles: see below) to less systematic observations at other nests. The parents brought entire fruits to the nestlings as early as the second day after hatching, gradually increasing deliveries of fruits thereafter (Fig. 2). During the first 10 days, 21.1% of the items carried to nestlings were fruits; during the final 11 days in the nest, 34.7% were fruits (Table 2). Skutch (1944), in contrast, found that nestlings ate "al-

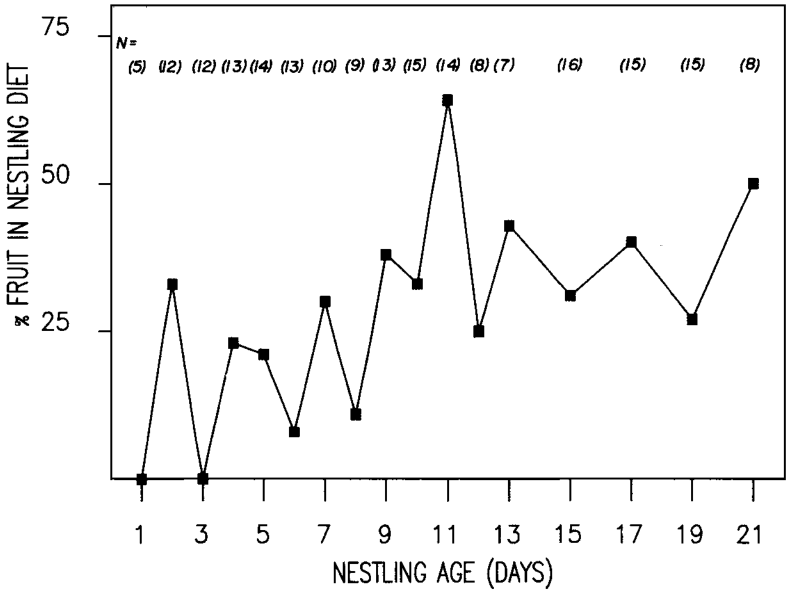

Fig. 2. Age versus proportion of fruit in the diet of nestling quetzals at nest 1. Spearman Rank Correlation: $r_s = 0.62$; $P < 0.01$. The number of food items for which frequencies were calculated is listed above each point. Each point represents 4–5 h of observation (71 h in total).

most entirely animal food" (insects, snails, lizards, and frogs) until the 10th day; fruits became important in the diet only after the 14th day. In the Monteverde population, certain insect taxa were prominent in nestling diets. Beetles (especially Scarabidae), grasshoppers (especially Tettigoniidae), and lepidopteran larvae together constituted 97.5% of all insects delivered (Table 2). Lizards and snails accounted for 8.0% of the food items delivered.

Among fruits, the Lauraceae comprised 2 of 6 species, and 47 of 58 (81.0%) individual items, delivered. The young were able to eat large drupes at an early age because of disproportionately rapid growth of the head. By age 10 days, one nestling's gape measured 2.3 cm, or slightly wider than an adult's gape, despite a body weight of only 71 g (compared to adult weights of 180–200 g). The largest items consumed by the chicks were a 25-cm walking stick (Phasmatidae), a 25-cm lizard (*Norops* sp.), and *Nectandra salicina* fruits (Lauraceae; $\bar{x}$ diameter = 1.9 cm). Adults carried animal prey in the bill and fruits in the bill and/or the stomach.

The two parents tended to bring different types of items to the nestlings. For example, the male at nest 1 (first clutch) delivered more insects, in particular beetles and grasshoppers, than did the female (Table 2; χ^2 One-sample Test: $P < 0.01$). The male also made significantly more deliveries in total ($P < 0.01$; χ^2 One-sample Test). The female brought proportionately more *Ocotea tonduzii* fruits ($P < 0.01$), and fruits in general (although differences were not significant in the latter case: $0.05 < P < 0.10$; χ^2 Two-sample Test). At a different nest (nest 2, second clutch), the total number of deliveries by each sex was equivalent (Table 3). Males and females frequently alternated bringing food to nestlings (cf. LaBastille et al. 1972), although the pattern varied considerably at all nests.

The time between successive food deliveries by the same parent ("return time") depended upon the item brought. The median return time for adults bringing fruits during the first 10 days after nestlings hatched was 15 min (n = 29), as compared to 24 min for insects (n = 63). As the growing nestlings demanded more food and the frequency of feeding trips increased (Fig. 3), return times for fruits declined. Return times for insects remained the same. During days 11–21, deliveries of fruits took a median of only 6 min (n = 32), while insect deliveries still required a median of 24 min (n = 40). For both periods, return times were significantly

Table 3. Sexual differences in reproductive behavior in quetzals during the first 12 days after nestlings hatched. Figures in parentheses are standard deviations of proportions on different observation days.

	Nest number		
	1	2	2
Clutch	first	first	second
Number of chicks	2	1	1
Hours of observation	51.1	5.0	44.9
Days of observation	12	1	9
Mean proportion of time spent brooding chicks			
Male	0.34 (0.26)	0.25	0.34 (0.07)
Female	0.13 (0.08)	0.33	0.35 (0.04)
Mean proportion of time spent perched near nest			
Male	0.10 (0.11)	—	0.18 (0.04)
Female	0.03 (0.03)	—	0.20 (0.02)
Number of food deliveries			
Male	90	8	35
Female	52	8	34

shorter for fruits than insects (Mann-Whitney U-test: $P < 0.005$). The median return time for lizards (23 min; $n = 9$) was more like that for insects than for fruits.

Reproductive biology.—Quetzals returned from the Atlantic slope in late December in 1980 and in early December in 1981. Some birds had formed pairs already. One female (recognized by her yellow bill) foraged for two months with the same male; the pair nested in the area in late March and used the same nest for their second clutch in late May. Other birds, apparently unpaired, engaged in courtship flights throughout May, during which as many as four males simultaneously chased single females. Nest excavation began by late January, although none of the early holes that I saw was completed. One pair excavated at least 5 holes in one month within 100 m of the nest that was finally selected.

During the early nesting period (through March), quetzals periodically broke from courtship and nest-building to join aggregations of up to 20 individuals feeding at a single heavily fruiting tree (typically *Ficus tuerckheimii* or *Beilschmiedia costaricensis*).

The only copulation that I observed occurred on 28 February 1981 after the pair engaged in a bout of nest excavation during which each bird perched on the side of a rotting snag and pecked at the loose wood for shifts of about 5 min while its mate called softly from a nearby branch (cf. Skutch 1944). After about 20 min of digging, the female flew to a tall tree about 100 m away; the male followed and, among dense epiphytes in the crook of a branch, briefly mounted the female.

In 1981 the first eggs were discovered in mid-March. In 1982 quetzals were just beginning to excavate nest holes by late March, but I found no active nests. Breeding was apparently delayed in 1982 because of a scarcity of fruits. Evidence of fruit shortages came from phenology censuses of 300 marked lauraceous trees (many of the Lauraceae produce heavy fruit crops only every other year), from observations of quetzals eating unripe *Beilschmiedia costaricensis* in 1982 but not in 1981, and from observations of Emerald Toucanets eating fruits they normally ignore (unripe fruits of various species, as well as *Piper* spp.). Nesting activity lasted until at least 22 July 1981, when I discovered a male still brooding young. In both 1979 and 1980 the nesting season extended through late June.

Quetzals excavated nest holes at a mean height of 8.8 m (±3.5 m) in rotting limbs or trunks of dead trees with a diameter at breast height (DBH) of 0.63 m (±0.23 m; $n = 43$ active or previously used nests). Bowes and Allen (1969) found similar nest characteristics in Guatemala, where nest heights averaged 9.5 m and DBHs were 0.51 m. Of the Monteverde nests, 74% occurred in forest, 12% on the edges

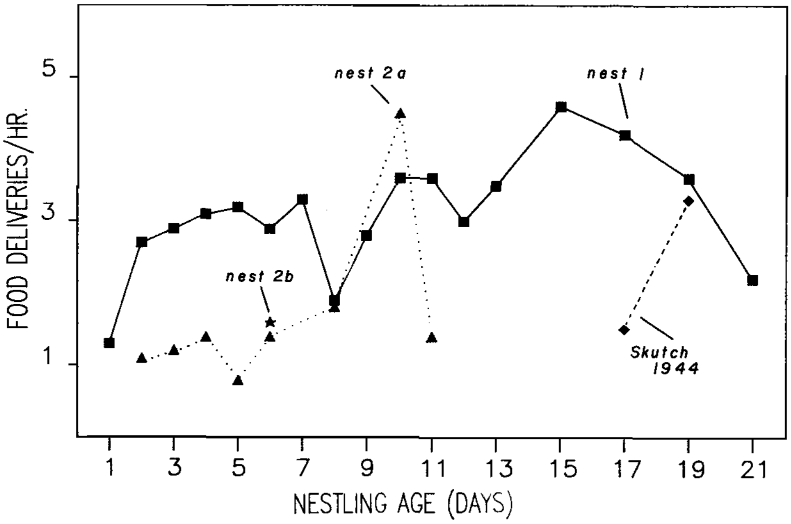

Fig. 3. Nestling age versus hourly rate of food delivery in quetzals. ■ = nest 1 (two nestlings until day 20; first clutch); ▲ = nest 2 (one nestling; first clutch); ★ = nest 2 (one nestling; second clutch); ◆ = data from Skutch (1944).

of light gaps or pastures, and 14% in snags in the open. Of 40 nests, 11 faced north-northeast, 13 east-southeast, 7 south-southwest, and 9 west-northwest. Nests were excavated in decaying *Ocotea tonduzii* and other Lauraceae (8 of the 10 decomposing snags that could be identified), *Eugenia* sp. (1/10), and *Quararibea* sp. (Bombacaceae; 1/10). If the same snag was used in different years, the cavities were dug at a lower height each year. The density of apparently suitable nesting trees far exceeded the density of nesting quetzals and seemed not to limit the population (but see Bowes and Allen 1969).

The female typically laid two sky-blue eggs, a clutch size characteristic of the Trogonidae. Although eggs were similar in size within a clutch, sizes varied widely between nests. Eggs averaged 3.72 cm in length (±0.23 cm; range 3.49–4.10 cm; $n = 6$) and 3.01 cm in width (±0.14 cm; 2.82–3.12 cm; $n = 6$). Skutch (1944) and LaBastille et al. (1972) recorded mean egg sizes of 3.89 × 3.02 cm and 3.89 × 3.24 cm, respectively. Weights averaged 17.0 g (±2.2 g; range 15.0–18.9 g; $n = 4$). Two eggs from a second clutch nest at Monteverde weighed substantially less than eggs from a first clutch nest (15.0 and 15.5 g versus 18.8 and 18.9 g).

Both sexes shared in incubation, the female sitting at night (Skutch 1944). I did not find that the male typically assumed lengthy morning and afternoon shifts, however, as Skutch (1944) did. In 16 observations at four nests, each sex incubated with equal frequency betwen 0800 and 1200; the female tended to be present during early morning and late afternoon and the male during early afternoon. Although LaBastille et al. (1972) seldom noticed eggs uncovered for more than 2–13 min, I often found that nests were unattended for 1–2 h (cf. Skutch 1944).

In two nests, chicks hatched 18–19 days after the eggs were laid. Skutch (1944) and LaBastille et al. (1972) provided excellent descriptions of the development of the nestlings, which I will not repeat, except to note that the iridescent green contours and wing coverts that appeared at about 15 days apparently were not new feathers covering black natal plumage, but rather those same black feathers developing and expanding to produce iridescence (see LaBastille et al. 1972).

One parent or the other remained in the nest 60–95% of daylight hours during the first 6–8 days after hatching (Fig. 4A and 4B). Brooding fell off rapidly after days 8–10, presumably as the still incompletely feathered chicks acquired the ability to thermoregulate. As brooding time declined, the adults increased the time spent perching near the nest, so that even late in the nestling period the nest was attended from 20–40% of the day (Fig. 4A).

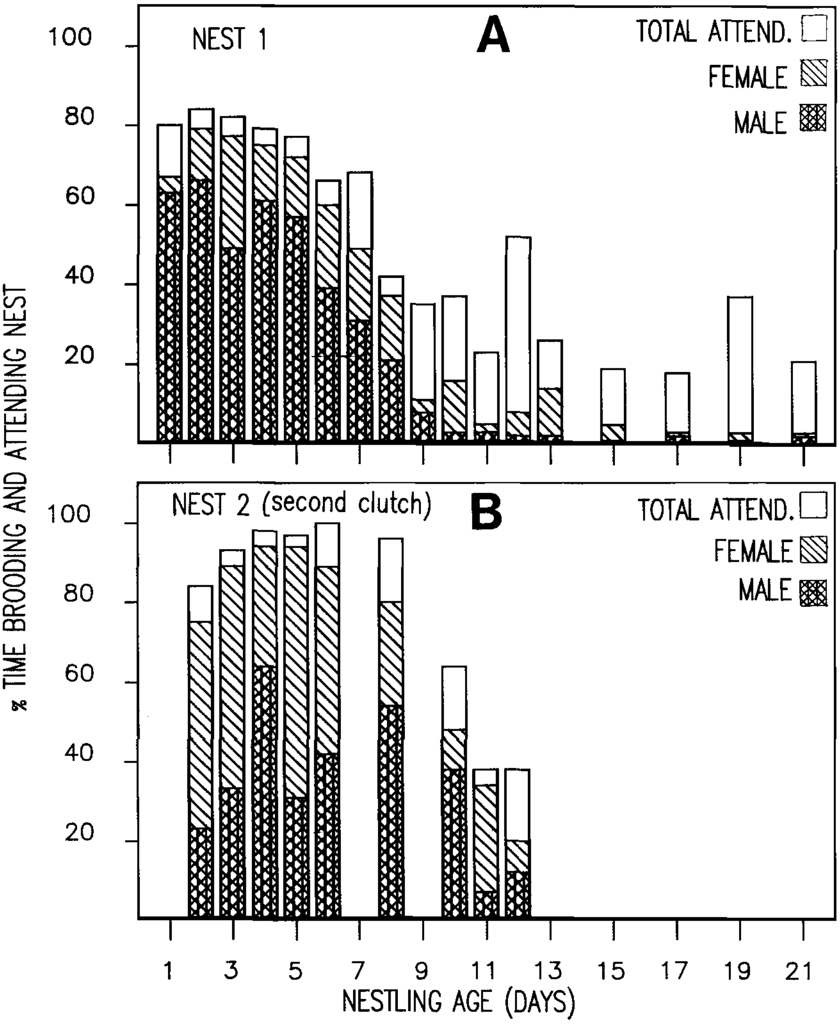

Fig. 4. (A) Nestling age versus time spent brooding and total time attending nest (brooding plus perching nearby) by both quetzal parents at nest 1 (first clutch; 71 h observation). (B) Nestling age versus time spent brooding and total time attending nest (brooding plus perching nearby) by both quetzal parents at nest 2 (second clutch; 45 h observation).

Skutch (1980) noted that, after the first clutch fledged, a second was often laid "pronto" in the same hole. In the single case that I could document this observation, the first egg of the second clutch was laid in the same nest 14 days after the chicks of the first clutch disappeared. A second egg was laid the following day. At another nest, the pair moved to a different area after fledging its first clutch, and at two other nests, where eggs were lost to predators, the pairs also chose new nest sites.

Parental duties and sex roles varied considerably at different nests (Table 3). At a first-clutch nest (nest 1) the male spent nearly three times as much time brooding and attending the nest as the female and delivered almost twice as many food items (Table 3). At a second-clutch nest (nest 2), however, the parents divided brooding, nest attendance, and feeding evenly. Skutch (1944) also described a nest (second clutch) in which the male assumed most of the feeding and nestling care after day 16.

Predation.—Nest failure was high (67–78%; $n = 9$; 1981). Probably the chief cause of egg and nestling mortality at Monteverde is the short-tailed weasel (*Mustela frenata*) (pers. obs;

J. Lowther pers. comm.). Quetzals defended their nests vigorously against squirrels (T. Blagden pers. comm.), which are known to remove the eggs of other hole-nesting birds, such as Emerald Toucanets (S. McKey pers. comm.). Snakes, botflies (Oestridae), and larger animals (other Mustelidae, Procyonidae, Felidae, Didelphidae, Cebidae) may also be important nest predators. The narrow opening of one study nest was ripped open and the eggs destroyed, apparently by a large mammal. Toucanets are widely known to eat the eggs and nestlings of other birds (Skutch 1967), and I saw intense chases and physical contact between quetzals and Emerald Toucanets several times. Both sexes defended the nest. Nests also fail commonly because of flooding of the cavity, collapse of the rotten snag, or human disturbance (Bowes and Allen 1969, pers. obs.).

As adults, quetzals probably face little predation; their conspicuous foraging behavior and tendency to spend up to several hours in or near a fruiting tree suggests that they are not "fearful frugivores" (Howe 1979). I learned of two cases of predation on adults, however, one by an unidentified hawk, and another by a margay (*Felis weidii*) that captured a brooding adult (W. Guindon pers. comm.).

DISCUSSION

Diet specialization and coevolution.—It is not surprising that the concept of "specialized frugivory" has been variously defined, for it attempts to summarize in a single term many complex attributes of behavior and life history (Wheelwright and Orians 1982). Perhaps the information presented here on the natural history of one specialized fruit-eating bird, the Resplendent Quetzal, may illustrate what the term includes and make a contribution toward answering the questions raised in the introduction. Quetzals in Costa Rica eat at least 41 species of fruits and an uncertain (though minor) amount of animal prey. They bring their offspring insects of five orders, vertebrates of two classes, gastropods, and fruits. Quetzals also eat a diversity of fruits at any one time of the year and 12–18 species over 2-month periods. Even though their diets are fairly broad, quetzals specialize in the sense that they do not take fruits in proportion to their availability. For periods of several hours or possibly days, they may feed only on 1–2 fruit species. And, while quetzals do take a diversity of low-quality fruits, their diets generally conform to McKey's (1975) model for specialists. The fruits listed in Table 1 tend to be: (1) larger than the median fruit size for the entire plant community; (2) inconspicuous (often dark green or black when ripe and presented individually amidst leaves rather than in brightly colored terminal clusters); (3) single-seeded or having a small number of large seeds; and (4) borne on trees rather than shrubs, vines, or herbs.

Much of the biology of quetzals seems tied not to one plant species but to fruiting patterns of a single family, the Lauraceae. Their selection of fruits and their movements between habitats corresponded closely to the availability of lauraceous fruits. Furthermore, major life-history events appeared timed to the fruiting phenology of the Lauraceae. Breeding occurred during the peak of fruiting in the Lauraceae, when 10–15 species had ripe fruit. Emigration from Monteverde coincided with a period of scarcity of lauraceous fruits, even though other species of fruits continued to be available. Quetzals' morphology and geographical distribution also reflect their dependence on the Lauraceae. Although the Central American Isthmus (and therefore the current range of Quetzals) is geologically recent, the Trogonidae and Lauraceae share a long fossil record and possibly have been in association since the late Cretaceous or early Tertiary (Raven and Axelrod 1974, Welty 1982). Both families are pantropical, with parallel present centers of diversity in the Neotropics and Southeast Asia (Sibley and Ahlquist 1972). The colonization of Central America by quetzals and the Lauraceae (whose fruits they depend on and whose seeds they disperse) may have occurred in tandem as the Isthmus rose during the Pliocene Epoch (Raven and Axelrod 1974).

Fruit specialists have been hypothesized to be especially effective seed dispersers, disseminating seeds unharmed to microsites appropriate for seedling establishment (McKey 1975, Howe and Estabrook 1977). Gathering data on avian seed-dispersal patterns is difficult, and it has been done only rarely and under specific conditions (Smith 1975). I did not attempt a systematic study of seed dispersal by quetzals, but my impression, based on observing their behavior and noting the location of hundreds of seed regurgitations by quetzals, is that their actual seed dissemination is poor: An estimated 60–90% of all seeds dropped by quetzals fall directly beneath the parent tree or within 100 m. Widely foraging tanagers or flycatchers probably spread seeds more effectively. Quetzals provide one aspect of high-quality seed dispersal, however, of which few bird species are capable, namely transporting bulky seeds (as in many Lauraceae) with substantial seedling reserves (McKey 1975).

Quetzals unquestionably differ from other birds for which fruit plays a less important role in their life histories. They also differ in many respects from other specialized fruit-eating birds, but at the moment we lack the data to determine which differences are merely quantitative and which justify distinguishing specialists from generalists. Thorough studies on the feeding behavior of fruit-eating birds have been done on only a handful of tropical species (see Table 6.2 in Thompson 1982; Snow 1981). Probably the most complete information on the diets of specialized fruit-eating birds comes from Frith et al. (1976) and Crome's (1975) studies on New Guinean and Australian fruit-pigeons (*Ducula* and *Ptilinopus* spp.). From analyses of crop and stomach samples from many individuals and from direct observations of feeding behavior over several years, they showed that fruit-pigeons eat fruit exclusively. The Snows' work on Oilbirds (*Steatornis caripensis*: Snow 1962a, Snow 1979) and on various cotingas (Snow 1970, 1972, 1977; Snow 1973) used the recovery of regurgitated seeds, an indirect but effective technique, to demonstrate the importance of fruits in the diets of those birds. The manakins *Manacus manacus* (Snow 1962b) and *Pipra erythrocephala* (Snow 1962c) were studied by a combination of field observations and recovery of regurgitated seeds.

Like quetzals, all of these bird species feed on many fruit species, even at any one time of the year. [Masked Tityras, *Tityra semifasciata*, which reportedly fed for 2 months almost exclusively on the fruits of a single tree species in tropical wet forest, where fruit periodically becomes extremely scarce (Howe 1977), are probably not typical of other fruit-eating birds.] They vary from obligate fruit-eaters (Oilbirds, fruit-pigeons) to birds with diverse diets (toucans, manakins). None appears highly coevolved with a single plant species (see Howe and Vande Kerchove 1979, Wheelwright and Orians 1982). Because of the brevity (relative to the life span of birds) and year-to-year irregularity in the availability of any one fruit species, birds are unlikely to evolve a strong interdependence with one or a few species (Howe 1981, Wheelwright and Orians 1982, Thompson 1982).

Crome's (1975) detailed study of fruit-pigeons in tropical Queensland suggests coevolution with, or at least dependence upon, fruiting plants at the family level, as in quetzals. *Ptilinopus* species ignore other fruits when Lauraceae are ripe, and 88% of the diet of one species consisted of fruits of the Lauraceae and Araliaceae alone. As with quetzals, fruit-pigeon population movements mirrored the changing abundance of lauraceous fruits. In the Neotropics, according to Snow (1971), three plant families (Burseraceae, Palmae, and Lauraceae) have particularly influenced the evolution of several large fruit-eating birds, such as Oilbirds and members of the genus *Procnias* (Snow 1970, 1977; Snow 1973).

Several points, however, may be relevant when considering specialization in fruit-eating birds. First, it is not only the large fruit-eating birds typically called specialists (many Phasianidae, Steatornithidae, Columbidae, Ramphastidae, Trogonidae, Cotingidae) that feed predominantly on, and appear to have coevolved with, one plant family. Many birds usually considered less specialized (Pipridae, Tyrannidae, Turdidae, Emberizidae) may be equally dependent and specialized on the small, watery fruits of the Solanaceae, Rubiaceae, and Melastomataceae (Ricklefs pers. com.; pers. obs.). Specialization in diet need not be tied absolutely to fruit quality (Wheelwright and Orians 1982); even specialized fruit-eating birds probably feed at most times on a wide variety of fruits, including fruits that may be considered "low quality" (McKey 1975). The term "specialized frugivore" has been applied to a phylogenetically disparate group of birds having different foraging modes, morphologies, social systems, favored plant species, diet breadth, life histories, and qualities of seed dispersal. Until other common attributes can be demonstrated, the term should probably be defined explicitly when used and restricted to referring to the prevalence of fruit in general in the diet.

Consequences of a fruit diet.—Because plants benefit by having their seeds dispersed, one would expect fruits to be less challenging to capture than animals (Snow 1971). Unlike animals, most ripe fruits tend not to be cryptic, scarce, toxic, evasive, or spiny. They are "easy prey" (Snow 1971). Until now, the evidence for this postulate has come from analyses of time budgets of fruit-eating birds, which demonstrated that several species may spend only 8–17% of the day acquiring fruit during the breeding season (Snow 1962b, c; Snow 1970, 1977). The significantly shorter return times for parent quetzals delivering fruits versus animal prey provide strong inferential evidence of the accessibility of fruits.

Nonetheless, even late in the nestling period, over 50% of the items brought to nestling quetzals were insects or lizards. Although fruits are generally easier to obtain than animal prey, their nutritional imbalance or paucity in the nutrients critical for nestling growth may prevent most birds from relying exclusively on fruits to feed themselves or young (Morton 1973; but see Foster 1978). It may be difficult for female quetzals to produce eggs on a diet of fruit, as suggested by the tendency for second-clutch eggs to be smaller, the observation that the female spent less time attending the nestling than the male during the first clutch but (at a different nest) not the second, and the facts that the female delivered fewer food items to nestlings and returned more often with easily acquired fruits than with insects. If these patterns are general, it may be that the female has to devote much of her time during the first clutch to storing nutrients for the second clutch, which is laid within two weeks of the fledging of the first.

Conservation of Resplendent Quetzals.—Conservation biology, incorporating concepts from island biogeography and community ecology, has identified characteristics of animals that make them particularly prone to extinction. Vulnerable species tend to occur at low population densities, feed on patchy food resources such as fruit or nectar, specialize in their diet and have restricted or inflexible ecological requirements, disperse poorly over long distances, inhabit small or isolated areas, and face severe predation (including hunting) or competition (Soulé and Wilcox 1980, Terborgh and Winter 1980). Quetzals fit the description disconcertingly well. Only about 50 pairs of quetzals breed in or adjacent to the Monteverde Cloud Forest Reserve (M. Fogden, W. Guindon pers. comm.; pers. obs.). As long as the Arenal National Forest surrounding the Reserve remains intact, the local population is in no immediate danger of the deleterious effects of inbreeding (Soulé and Wilcox 1980). Quetzals will probably be one of the first species lost, however, if the Reserve becomes isolated.

The Monteverde Cloud Forest Reserve comprises 2,700 ha, but, as currently delimited, it will fail to protect quetzal populations because it does not include habitats critical for quetzals during several months of the year (cf. Diamond 1975). It should be a high priority to expand the boundaries of the Reserve and to discover the extent of quetzals' movements during their October–December absence from the area. Guatemala's recently established Quetzal Cloud-Forest Reserve (405 ha; LaBastille 1973) and Sanctuary of the Quetzal (200 ha) represent an important start in preserving the country's national symbol—yet, again, neither can hope to sustain adequate population sizes or include a sufficient range of habitat types to prevent the local extinction of quetzals.

To protect quetzal populations, the economic as well as symbolic and historical importance (Skutch 1980) of quetzals should be stressed. Not only do they disperse the seeds and affect the regeneration of many species of valuable trees, but they attract enough foreign exchange because of tourism to justify reserve expansions. Even sedentary species with more generalized diets may require much larger reserves than expected. For example, large numbers of the typically montane Emerald Toucanet have appeared in some years at the research station La Selva, in Costa Rica's tropical wet forest, presumably because of a scarcity of fruits in their customary habitat (G. Stiles pers. comm.).

Finally, wildlife conservation laws must be enforced. A vivid illustration of this occurred as I left Costa Rica at the end of this study. One of my fellow airline passengers walked smoothly through Costa Rican customs toting a souvenir bag from which protruded the long green tail coverts of a stuffed male Resplendent Quetzal.

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CLARIFICATION: MONOPHYLY OF THE PICIFORMES

Several large changes were made by the author in the galley proofs of Olson's paper (Olson, S. L. 1983. Evidence for a polyphyletic origin of the Piciformes. Auk 100: 126–133) that had the effect of removing several passages that Raikow and Cracraft (Raikow, R. J., & J. Cracraft. 1983. Monophyly of the Piciformes: A reply to Olson. Auk 100: 134–138) had directly quoted or referred to in preparing their response from the final accepted manuscript of Olson's paper. The changes in the galleys were made without Raikow and Cracraft's knowledge, subsequent to Olson having received a copy of their response to his criticisms. The affected quotations and references to material contained in Olson's manuscript but deleted from his galleys are as follows (page numbers give the location in Raikow-Cracraft): page 134: ". . . why would such a transformation take place? Once a group of birds has become permanently zygodactyl, is it possible to become *more* zygodactyl?"; page 135: "He suggests that the Galbulae would be difficult to identify with their feet cut off but fortunately all our specimens possessed feet . . ." and ". . . in plumage pattern, the ground roller *Brachypteracias leptosomus* is quite similar to certain of the Bucconidae such as *Malacoptila*."; and page 136: the section headed "Incorrect determination of polarity" where the quote regarding *Archaeopteryx* and other "land birds" was eliminated.—J.A.W.