ON THE EVOLUTIONARY ADVANTAGES AND DISADVANTAGES OF FRUIT EATING IN TROPICAL BIRDS

Eugene S. Morton*

Chesapeake Bay Center for Environmental Studies, Smithsonian Institution,
Route 4, Box 622, Edgewater, Maryland 21037

The ecological consequences of the relationship between plants and birds that disperse their seeds are important because of their diversity and magnitude. Snow (1971) presented perhaps the first synthesis of the ecological dichotomy between fruit-eating and insect-eating birds. Predation on insects favors inconspicuousness, which, in response, promotes many different searching techniques by birds (Snow 1971; see also Ricklefs 1970). In contrast, competition in plants to attract fruit-eating birds for seed dispersal favors conspicuousness and abundance in fruit.

Fruit is often so abundant that there is little competition for it. For example, Willis (1966) observed 28 species of birds feeding on *Conostegia* berries in Colombia. Nine of these species were of one tanager genus, *Tangara* (see also Eisenmann 1961; Morton 1971a).

In these evolutionary systems, fruit eating promotes more fruit while insect eating promotes prey adaptations that oppose predation. Of course, as Snow (1971) points out, some bird species eat fruits to obtain the seeds within. However, these species do not contribute to the evolutionary development of fruit eating if they do not disperse seeds. Here the term "fruit" pertains only to those with a fleshy part eaten by birds and "fruit eaters" refers only to birds that disperse seeds.

Below, I discuss both positive and negative selective values of fruit as food for birds. Major questions examined include: Why is total frugivory so rare in birds? How has fruit and fruiting seasons influenced breeding strategies in tropical birds? In addition, I discuss a hypothesis to explain tropical and temperate zone differences in birds and plant evolution.

Over evolutionary time it might be expected that totally frugivorous diets in birds would increase and would be more common than now observed, given the mutualistic relationship between fruit and fruit eaters. The abundance of fruit, the short time needed to obtain it, and its year-long availability in the tropics (Snow 1965) seem to provide an adequate food supply for adults and young. A fruit diet for nestlings should theoretically be favored by selection, since it should provide food for larger clutches than relatively rare

* Present address: Department of Zoology, University of Maryland, College Park, Maryland 20742.

insect food. But fruit is not generally used as food for small young (Lack 1968).

Total frugivory, here defined as bird species wherein *both* adults and nestlings are sustained exclusively on fruit, is rare. Many species generally considered frugivorous, such as most manakins (Pipridae) and many cotingids (Cotingidae), are not totally frugivorous, since they feed their young partially or wholly on insects (Skutch 1969).

Nutritional reasons do not render it impossible for birds to be totally frugivorous. This is indicated by the fact that many birds are frugivorous as adults and a few also feed their young only fruit (Snow 1970). Moreover, fruit could, and doubtless has, improved nutritionally under selection caused by birds "choosing" to feed from plant species with the more nutritious fruit (Snow 1962*a*). Gardarsson and Moss (1970) have shown that the herbivorous Icelandic ptarmigan (*Lagopus mutus*) selects the most nutritious foods from a wide variety of potential food plants. The necessary ingredients are present for selection to enhance the food value of fruit.

NESTLING BIRDS AND NEST PREDATION

I believe the most plausible hypothesis to explain why fruit is infrequently used as food for small nestlings (Lack 1968, p. 172) involves the interaction between nest predation (predation on eggs or nestlings) and diet. Nest predation is the major source of selection favoring a short nestling period (Ricklefs 1969). Rapid nestling growth and development allows the shortest time possible between hatching and the stage when some capacity for actively escaping predators is achieved.

In species with relatively high nest predation, selection favors shorter nestling periods, while in species with a lower rate of nest predation, selection favors relatively longer nestling periods. A longer nestling period, if accompanied by a slower growth rate, permits more young to be raised, because slower-growing nestlings need less food per individual per unit time than do rapidly growing nestlings (Ricklefs 1968). The selective premium is on fledging the most young in *good* condition (Lack 1954).

In support of this model, hole-nesting passerines, which have low rates of nest predation, have much longer nestling periods and larger clutch sizes than passerines with more vulnerable, open cup nests (Lack 1968).

The model shows a relation between intensity of nest predation and length of nestling period. But how does this relate to diet? There are two main arguments, which are not completely unrelated, indicating that when fruit evolves as the sole food for small nestlings, one result is a longer nestling period. Therefore, relatively higher nest predation is experienced (everything else equal) than if animal food is used.

It is true that fruit has a much lower protein content than animal food (table 1). This may be an important reason for slower growth rates in frugivorous birds. It is possible, however, that feeding rates can be increased to partially compensate for the lower protein content of fruit. This is feasible

TABLE 1
NUTRITIONAL DATA FOR 100-GRAM SAMPLES OF FRUITS AND INSECTS

Species	Kilocalories	Water (%)	Protein*	Fat*	Carbo-hydrate*
Fruit:					
Oil palm	540	26.2	1.9	58.4	9.3
Fieus carica	52	85.2	0.8	0.2	11.9
Fieus platyphylla	56	83.0	1.9	0.1	10.1
Annona reticulata	92	74.2	2.1	0.5	15.7
Persea gratissima	121	80.3	1.4	11.3	8.3
Spondias mombin	42	88.0	0.8	0.2	10.1
Sapindus senegalensis	99	71.4	1.5	Trace	25.6
Passiflora incarnata ..	111	72.5	2.3	3.3	13.7
Papaya	32	90.8	0.4	0.1	7.4
Guava	64	82.2	1.1	0.4	10.4
Average	120.9	75.4	1.4	8.3	12.3
Insects:					
Flying ants (*Carebara* sp.)	. . .	60.0	10.1	1.3	. . .
Beetles (*Polycleis, Sternaocera*)	192	56.2	27.1	3.7	4.8
Caterpillars (*Gynanisa, Herse*)	86	81.1	10.6	2.7	1.4
Cricket (*Brachytrypes membranaceus*) ...	117	76.0	13.7	5.3	0
Grasshopper (*Acridium* sp.)	170	62.7	26.8	3.8	3.1
Average	141.3	67.2	17.7	3.4	2.3

SOURCE.—Leung (1968), in Jenkins (1969).
* In grams.

because fruit is much more abundant and is more easily obtained than animal food.

The first argument to support the hypothesis that total frugivory results in slower growth rates is concerned with the adaptive strategy of the *altricial* nestling condition, the most common type of nestling condition in birds. Altricial nestling birds are poikilothermic for the first several days after hatching. Still, nestling body temperature is maintained at or near the adult temperature through brooding at a relatively low energy cost to the adult. The important point is that the food energy brought to the nestling is fully used in growth rather than being spent in temperature regulation (Dawson and Evans 1957). The altricial nestling condition may be thought of as an adaptation permitting full use of food for growth and, thereby, shortening the vulnerable period in the nest.

The evolution of the altricial strategy may be tied to protein-rich animal food for nestlings. Fruit, when used for food during the poikilothermic stage of nestling life, negates the benefits of the altricial strategy by not providing sufficient protein to allow for rapid growth and is, therefore, not favored by selection as food for small nestlings. This is probably the reason why species that feed young both fruit and insects do not use fruit as food for the first few days. Perhaps fruit is fed only after the homoio-

thermic stage is reached, when weight gain slows as energy is now used for body heat maintenance as well as for growth. It is during the poikilothermic phase that protein-rich food is most needed for rapid growth.

This hypothesis is tested in figure 1. The southern house wren (*Troglodytes musculus*) and the thick-billed euphonia (*Euphonia laniirostris*) are roughly the same weight, both nest in similar situations, and both have altricial young. The house wren, in fact, sometimes usurps a euphonia nest for its own (see below). Therefore, I assume that predation rates are similar in both species. They differ chiefly in the type of food fed to nestlings, the wren being insectivorous (Skutch 1960) and the euphonia totally frugivorous (personal observation). Haverschmidt's (1952) daily weights for a brood of four wrens from Surinam are compared with two euphonia broods of five from Panama in figure 1. The wrens show the usual sigmoidal growth curve for passerine birds (Ricklefs 1968), but the euphonia growth curve is essentially linear. Adult weight is achieved by the wren in 11 days, and spontaneous fledging (i.e., leaving nest before the normal time due to a nest disturbance, an adaptation indicating that some active escape from predators is possible) can occur by day 13, although fledging normally occurs on day 17 or 18 (Haverschmidt 1952). Adult weight is achieved by the euphonia in 17 days, spontaneous fledging occurs by day 16 (but the young cannot yet fly), and normal fledging takes place on day 23 or 24 (personal observation). As a consequence, the euphonia is subjected to nest predation at least 6 days longer than the wren. These data support the hypothesis that fruit does not permit optimal growth rates under the altricial growth strategy.

The second argument suggests that total frugivory is rare in tropical birds
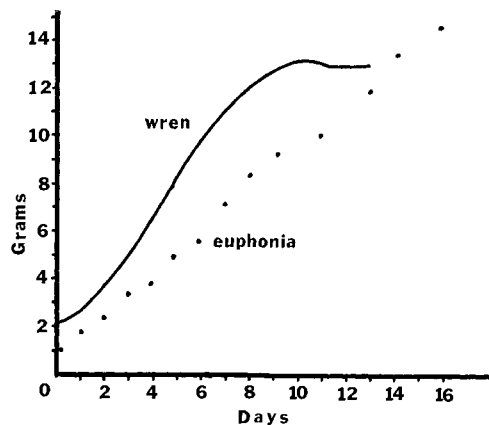

FIG. 1.— A comparison of growth in nestling southern house wrens (*Troglodytes musculus*) (data from Haverschmidt 1952) and thick-billed euphonias (*Euphonia laniirostris*) (personal observation). The insectivorous wren shows rapid early nestling growth in contrast to the almost linear growth of the totally frugivorous euphonia. Weights represent the daily average of four wren nestlings from one nest and of 10 euphonia nestlings from two nests, each of which contained five young.

because the incidence of nest predation is greater for total frugivores, since they have longer nestling periods than insectivores. Arguments for and against this idea are weakened because little is known about food fed to nestling tropical passerines. In fact, the range from totally frugivorous to totally insectivorous nestling diets is continuous, so there is no sharp dichotomy in the effects of diet on nestling periods. It is also impossible to separate from diet other factors that affect nestling periods, such as the size of the bird and safety of the nest site.

However, some support for the assumption that total frugivores do have relatively longer nestling periods is found in life-history studies of neotropical birds by Skutch (1954, 1960). His data show nestling periods in oscine passerines for 13 species of insectivores and granivores averaged 12.0 days; for 15 omnivorous species, 14.2 days; for four totally frugivorous species (all in the tanager genera *Euphonia* and *Chlorophonia*), 22.3 days. The same data for nonoscine passerines show open-nesting insectivores with an average nestling period of 11.8 days (nine species); hole-nesting insectivores, 19.5 days (10 species); and four omnivorous species with a 20.3-day average nestling period (Skutch 1969). Snow (1970) found that a comparable, totally frugivorous, nonoscine passerine, the bearded bellbird (*Procnias averano*), has a 33-day nestling period.

The hypothesis that total frugivory in nestling food leads to longer nestling periods is supported by available data. However, why do adult birds not increase feeding rates so that the rate of protein intake for frugivores is higher? Several factors might be involved in this question, but I believe predation pressure offers a parsimonious explanation. Skutch (1949) and Snow (1970) point out that brood size may be lower than feeding capacity in tropical birds to reduce predator-attracting activity around the nest. If increased feeding activity results in higher predation rates, the outcome of selection may just as likely favor safer nest sites and/or reduced clutch sizes in total frugivores as increased feeding rates (discussed below). With a predation rate of 86% (as in *Manacus manacus* [Snow 1962*b*]), a clutch size of one would be favored by selection over a clutch size of two if this reduced the predation rate by 16% (Snow 1970).

If longer incubation and nestling periods are tied to the evolution of total frugivory, predation pressure will be an increasingly strong source of selection. In many tropical passerine birds, 75% or more of nests fail to produce young due to predation (Ricklefs 1969). Observing a 75% mortality in 100 nests, we are left with 25 nests at the end of the 25-day nesting cycle. If this nesting cycle were lengthened by 9 days due to the evolution of frugivory, another 9.8 nests would be lost to predation, leaving 15.2 successful nests, a ratio of 0.61. This is calculated using a survivorship formula, $S = e^{-mt}$, where S is survivorship, e is the base of natural logarithms, m is mortality rate, and t is time in days. From this relationship, the standard measure of selection pressure, the selection coefficient (s), is easily computed. Since $1 - s$ is, by definition, 0.61, s is equal to 0.39. The longer nesting cycle is favored by selection 39% less than the 25-day nesting cycle.

Why do any species become totally frugivorous, and what are the evolutionary consequences? Hypothetically, the evolutionary sequence leading to total frugivory and its consequences may be as follows. An omnivorous species initially feeds its young approximately the same proportion of fruit to insects that adults eat. This species tends toward total frugivory should competition with other species reduce the amount of insects parents are able to find. Thus, intraspecifically, selection favors those individuals that feed an increasing amount of fruit to their young. While this is happening, or perhaps before, breeding adults become frugivorous to reduce competition with their nestlings for the same, relatively rare, insect food (discussed below). Predation pressure increases because nestling growth rate is slowed with adaptation to the fruit diet. This predation pressure may cause increased selection favoring a "safe," but consequently rarer, nesting site. I assume that selection did not favor this "new" nesting situation before the increased predation pressure, perhaps because the new site is a rarer commodity and would not have produced more offspring than the "old" nest site under the "old" predation pressure. An alternative response to increased predation pressure might be to reduce clutch size to the minimum (one egg) to reduce overall activity around the nest, thereby attracting fewer predators.

Such a rare but safe nesting-site strategy is exemplified by the South American oilbird, *Steatornis caripensis*, the only totally frugivorous caprimulgiform. It breeds in dark caves where it finds its way by echo location and is relatively safe from nest predators (Snow 1962a). If a safe nesting site is evolved, the advantages of using relatively abundant food such as fruit should result in a higher clutch size. The oilbird fits this model in having a clutch size of up to four eggs, compared with insectivorous caprimulgiform birds, which have clutches of one or two eggs.

An example of the second strategy, wherein clutch size is reduced to a minimum, is provided by the bearded bellbird (Snow 1970). Here, the nest is inconspicuous but vulnerable, and a single egg is laid. Parental visits to the chick are brief, as well as silent and otherwise inconspicuous, during the long 33-day nestling period.

The rare, safe nest site and the reduced-clutch-size adaptations to total frugivory result in relatively low population sizes which increase the probability of extinction. Additionally, if competition for insect food results in a species being "pushed" into total frugivory, it may be more difficult to return to insectivory than it was to go from insectivory to frugivory. Insectivorous species are specialized feeders relative to frugivores (Snow 1971). Fruit eaters tend to evolve wide gapes with weak bills that enable them to eat large fruits but are relatively unsuitable for probing or gleaning for insects. And, while such beaks might be useful for catching flying insects, this niche is already filled with the nocturnal goatsuckers (Caprimulgiformes) and many diurnal aerial-feeding specialists. The oilbird illustrates how similar a bill adapted to fruit eating may be to one adapted for catching large flying insects. Since fruit requires little morphological or behavioral specialization

to obtain, total frugivores tend to lack insect-finding abilities. This may also contribute to a relatively high extinction rate for total frugivores over evolutionary time.

If the above hypothetical species became totally frugivorous, and had also found a safe but not rare nesting site (or perhaps found a safe and common nesting site which then permitted the evolution of total frugivory), another situation arises. Here, an abundant food supply should result in an increased clutch size without the opposing selection pressure from predation. High populations could be maintained in this situation as long as it is not energetically worthwhile for predators to search intensively in this niche. This model may explain some of the peculiarities in the breeding biology of the genus *Euphonia*, a group of small, abundant, and (as far as we know) totally frugivorous neotropical tanagers (with the exception of *Euphonia trinitatis* [Snow and Snow 1971]). They have large clutches (four to five eggs) for tropical passerines, and they have safe nesting sites. For example, the nest of *Euphonia laniirostris* is completely concealed in the root tendrils of epiphytic plants. The entrance is usually a small natural opening in the rootlets, rather than a constructed opening, such that predators could have no visual clue to associate the entrance with a nest. The young are dark skinned to match their dark surroundings, and they make no sounds. This *Euphonia* has a nesting site that is essentially identical to any rootlet-covered branch—an abundant commodity in the tropics. The safety of the nest is indicated by the results of six nests studied, of which only one was destroyed by another small bird (southern house wren, *Troglodytes musculus*) for use as its own nest.

THE ROLE OF FRUIT FOR ADULT BIRDS

While there are few totally frugivorous bird species, the majority of neotropical species are partially frugivorous. Partial frugivory may occur to various degrees even in species generally thought to be strictly insectivorous, such as tropical vireos in the genera *Vireo* and *Hylophilus,* the tropical kingbird (*Tyrannus melancholicus*), and the barred antshrike (*Thamnophilus doliatus*) (personal observation). The common incidence of partial frugivory attests to selective advantages, some of which are obvious but others which are not so obvious. These advantages are best discussed by distinguishing between the nonbreeding period and the breeding period.

Nonbreeding period.—There is much variation in the amount of fruit eating exhibited by birds during the nonbreeding period. Many species are wholly frugivorous as adults, while many sedentary species are insectivorous but eat fruit as it becomes periodically available within their home ranges. (This does not necessarily mean that fruit is of lesser importance to these species than others, for the habitat characteristics and competitive abilities of these species may, in part, be determined by the probability of certain fruit species occurring in their home ranges. This makes the understanding of the distribution of tropical birds extremely complex and may help explain

the patchy distribution found for many sedentary tropical bird species.)

Aside from the direct benefit of abundance and the accessibility of fruit, indirect benefits or adaptive strategies may be associated with, or permitted (in an abstract sense), by fruit eating. It should be stressed that fruit is often superabundant; thus, for some time period at an individual fruiting tree or local area, fruit is so abundant that there is little competition even when many birds are feeding together. By contrast, insect food is dispersed, or, as with winged-ant and termite swarms, abundant for such a short time that avian predators cannot respond evolutionarily. (In Panama, winged ants and termites emerge during the first few heavy downpours of the rainy season.) Fruit abundance is found in a mosaic pattern in time and space, some fruit ripening as a current source is depleted in local areas (Snow 1965), although overall fruit abundance may show large seasonal variations.

This difference between fruit and insect food has resulted in striking differences in the birds that exploit them (Snow 1971). These differences are exemplified in arboreal mixed-species flocks in which many bird species are in potential competition with one another. Flocks differ in species composition, habitat, and the food habits of component species.

These flocks may be roughly divided into those composed of insectivorous species and those composed of species that take a mixed diet of fruit and insects and some nectar (termed "fruit-eating flocks" below). Insectivorous flocks occur in forest habitats, below the canopy where fruit taken by birds is not common or is absent. One such flock includes species concentrated at ant swarms where insects are routed from their normally cryptic locations (Willis 1967). Another type occurs in the lower strata of forests and is more mobile than ant-swarm flocks. These flocks are little studied, but my observations indicate that each species is quite restricted to where and how it captures its prey—an indication of competitive interaction among the species. Mobile insectivorous flocks are composed of many different species but few individuals of each.

In contrast to the very heterogeneous mixture of species in insectivorous flocks, fruit-eating flocks characteristically contain closely related congeneric species and often many individuals of the same species (Moynihan 1962). Fruit-eating mixed-species flocks overlap broadly when feeding on fruit, but are highly differentiated in their insect-searching techniques (Snow and Snow 1971). This is what one would expect when considering the basic differences between fruit and insect abundance and accessibility.

I suggest that the fruit-eating type of mixed flock is filling a distinctly tropical niche, by using what may be called the "fruit-searching" strategy. The fruit-searching strategy is effective in exploiting the spatial-temporal mosaic of fruiting patterns; moreover, it is intimately tied to the short-lived edge-habitat plants which "use" the fruit-eating mixed-species flocks as their means of seed dispersal. Because they are short-lived edge plants, seed size is often small (relatively little seed food storage is needed by edge plants as opposed to forest plants [Snow 1971]). This in turn means that their

fruit may be relatively small and abundant and that smaller birds are able
to swallow it. For this reason, the fruit-searching strategy is self-reinforcing
and related to the edge habitat. There is perhaps a good reason for small
birds to be involved in this fruit-searching strategy/edge habitat correlation
(discussed below).

What are the disadvantages of a completely frugivorous adult diet? Fruit
abundance varies seasonally in Middle America. Fruit should be equally
common throughout the year in the humid tropics as a response to competi-
tion among plant species to attract birds to their fruit (Snow 1965). How-
ever, in Middle America, bird fruit is much more abundant in the dry season,
perhaps because, as Janzen (1967) points out, vegetative competition necessi-
tates vegetative growth during the wet season. Due to these opposing selec-
tive forces, fruiting probably varies from highly seasonal, in areas with
distinctive wet and dry seasons, to relatively nonseasonal, in areas with an
even rainfall distribution (Leck 1972).

A decided decrease in fruit abundance in the late wet season (roughly
from September to December) in Panama has a great effect upon the par-
tially frugivorous birds. This effect bears upon the evolution of fruit and
insect eating generally. Competition for fruit increases in the late wet
season, and less-preferred fruit is commonly eaten when the more-preferred
fruit is no longer available (Leck 1972). Species that compose the fruit-
eating mixed-species flocks are more commonly seen alone during the late
wet season, perhaps because they are forced to rely on insects for food as
competition increases (personal observation).

In terms of fruit eating, one may divide the year (or any time period)
into periods of hard times (low fruit abundance) and good times. The
relative proportions of good times and hard times may vary enormously geo-
graphically and to a lesser extent from year to year in the same locality (see
Terborgh and Diamond 1970). There may be intense selection pressure
favoring morphological and behavioral abilities to find insects, even if the
probability of hard times is low or if hard times persist for a short time
(say 2 or 3 days). Morphology that contributes to food finding must be
adapted to hard times when limiting conditions are approached and competi-
tion is greatest.

If an omnivorous species competes well for insects during hard times, it
is much better off, evolutionarily, than if it is morphologically and behavior-
ally close to being wholly frugivorous. The small size of most of the fruit-
searching mixed-flock species may be adapted to survival during hard times.
With small body size, less insect biomass is needed to sustain the bird,
especially in warm climates where large body surface/volume ratios are not
as critical to maintaining high body temperatures. Thus, small fruit size is
permitted by the edge habitat, which also allows birds in fruit-searching
flocks to be small. During hard times, small bird size is again favored by
selection. Thus, the edge habitat, the size of fruit and birds, and hard times
may be evolutionarily related.

To summarize the hard-times aspect of frugivory, seasonal differences ap-

pear to limit fruit production in many plants to the dry, or nongrowing, season. (There may be positive selection forces at work here, too.) The effect of this on fruit-eating birds is that selection may not favor wholly frugivorous adult diets, because species must be adapted for survival during hard times. Wholly frugivorous adult diets may be favored by selection if there are no hard times or if migration to more favorable areas is possible.

Intratropical migration is rare in birds that breed in Panama. Only two passerine species, the piratic flycatcher (*Legatus leucophaius*) and the yellow-green vireo (*Vireo flavoviridis*) depart for South America during the late wet season, although partial migration may occur in other species. These species are highly frugivorous in Panama (the adult piratic flycatcher perhaps completely so), although they feed their young on insects and fruit. It seems likely that, during the late wet season, they migrate to dry-season conditions in South America where fruit is probably more plentiful (Morton, unpublished). Both species return to Panama in the dry season to breed when fruit is abundant.

Breeding period.—Hard times are not the sole source of selection against total frugivory. While fruit-eating birds are breeding, selection favors insect-finding abilities, for nest predation may impose strong selection pressure against fruit used as the sole food fed to nestlings, as discussed earlier.

What are adult birds eating when they are feeding nestlings? There are few data on this question, even though the evolutionary and ecological consequences in terms of time-energy budgets and competitive interactions are great. The predominant adult diet during breeding may be related to what predominates in the nestling diet (excluding granivory) in four major ways: (1) Adults eat fruit and feed fruit to nestlings. (2) Adults eat insects and feed insects to nestlings. (3) Adults eat fruit and feed insects (and fruit) to nestlings. (4) Adults eat insects and feed fruit to nestlings. The number of species using each of these strategies for breeding can only be expressed in qualitative terms at this time. The first strategy above is rare, the second and third are common, and the fourth is not known to be used by any species. (Possible reasons for the rarity of a totally frugivorous diet in birds were discussed above, and the first strategy is not discussed further.) Reasons for these differences and their significance are outlined below.

The second strategy is most commonly found in birds restricted to mature forest habitats, especially in the lower forest levels. Most or all of such species have specialized morphology and/or foraging behaviors. They tend to include the relatively territorial tropical species, and most breed during the wet season. Nearly all these species have a clutch of two. This is possibly a result of competition for the hard-to-get insect food and a proportionately long amount of foraging time needed for adults to nourish themselves and young, since they are "competing" for the same food. The postfledging period is a critical period, when the young improve foraging behavior needed to capture insect food. The clutch of two may be related to this need, since each parent often cares for and accompanies only one of the young (Willis 1967).

The third strategy may be a more common breeding strategy than the

second, for it has several important advantages. It is primarily a tropical strategy whose importance in avian diversity is discussed below. This strategy is favored because the advantages of frugivory (abundant and easily obtained food) are afforded the adult birds while the disadvantages of fruit as nestling food are largely avoided. Thus, the growth rates of the young permit rapid fledging and the parents are able to spend a greater amount of time looking for nestling food, since they are able to feed themselves quickly on fruit. Species using the third strategy are generally not highly territorial, but they may defend the immediate nesting area. However, most of the adult food and much of the nestling food is found in undefended areas. In Panama, most of these species begin breeding in the mid to late dry season. There may be less food for nestlings then than in the wet season, but adults are able to feed themselves easily because fruit is abundant then (Morton 1971b).

In Panama, the dry season is more pronounced and begins earlier on the Pacific slope than on the Atlantic slope of the isthmus. It would be predicted that, if fruit availability increases as dry-season conditions commence, breeding would begin later on the Atlantic slope than on the Pacific slope. Characteristically, species using the third strategy begin nesting earlier on the Pacific slope.

This is illustrated vividly by the yellow-green vireo (*Vireo flavoviridis*), because it is absent from Panama during the nonbreeding season and its vocalizations make it conspicuous when it returns to breed (Eisenmann 1962). In 1971, vireos returned to the Pacific end of the Panama Canal Zone from late December to mid-January. No birds were noted on the Atlantic end until late February. Nearly midway between the two coasts, vireos returned from mid to late January. However, at one of these midway locations (Summit Gardens), the vireos did not begin breeding until April 1, 2 months after arrival. Many other species of dry-season-breeding birds at Summit Gardens also had delayed breeding. For the thrush *Turdus grayi* and the tyrannid *Elaenia chiriquensis*, breeding began later than in the previous year here and began only when fruit became locally plentiful (largely *Miconia argentea* and *Miconia rubiginosa*).

The third strategy promotes breeding patterns adapted to rather local conditions. Species begin breeding when fruit becomes locally available, even though they may be physiologically ready to breed months beforehand. When fruit becomes abundant depends on the plant species found in the area, and this may change with distance. It is characteristic of many such bird species to show variations in the time of breeding over short distances. I have found areas 6 miles apart to differ 2 weeks to 1 month in breeding initiation in the clay-colored robin (*Turdus grayi*).

The relative amounts of fruit and insect food fed nestlings by species using the third strategy vary considerably both within and between species, and constitute another way in which these species adapt to local conditions. However, there is apparently an upper limit to the amount of fruit fed nestlings beyond which viability decreases. For example, nestling starvation was common in clay-colored robins in a local area even though fruit (*Ficus*

berries, papaya [*Carica*]), which *was* fed occasionally to the nestlings, was abundant.

There may be an immediate cause for adults not feeding young an all-fruit diet, even when the young are starving. Captive clay-colored robin nestlings (2 days old), after several hours on an all-fruit diet (*Bursera simaruba, Miconia argentea,* papaya, banana [*Musa*]*, Ficus* sp.*, Roystonea*), still gape hungrily for food but refuse to swallow more fruit. Crickets and ground meat are then readily accepted (personal observation).

The developmental pattern for each species probably proceeds innately and is nutritionally based upon the average foraging efficiency of the species. Average foraging efficiency refers to the quality and quantity of food brought over time. Perhaps the growth rate is adapted to the average rate at which the adults can provide essential amino acids, but is influenced by the probability of nestling predation.

There are few data on the relative amount of fruit and animal food fed nestlings by birds using the third strategy even though such information may be important to the study of avian competition. One can view the relative amounts of insect food to fruit brought to nestlings in terms of competition with other species for insect food. A competitively superior species is one that feeds its nestlings a greater amount of insect food than another species. A high-fruit diet for nestlings, therefore, can be looked upon as an adaptation that enables a species to co-occur with competitively superior species. I view the insect feeder as competitively superior because selection from nest predation, as discussed above, probably means that insect food is favored, since it allows young to develop faster. It is also rarer than fruit and thus functions as a limiting factor. A high insect/fruit ratio in the nestling diet indicates a species is more successfully obtaining the sought-after insect food than a species with a lower insect/fruit nestling diet ratio. A comparative study of insect/fruit ratios in nestling diets in the same general area and habitat during the same time may allow insight into competitive interactions of syntopic species. It is apparent that this complexity is characteristically a tropical phenomonon, because fruit is little used as food by birds during the breeding season in the temperate zone.

The fourth strategy, adults eating insects while feeding fruit to the young, is not found, to my knowledge, in any species. It is essentially the opposite of the third strategy. Adults would spend a relatively long time finding food for themselves and have less time for rearing nestlings. The fruit nestling diet would mean a slower growth rate and higher predation rate. That the fourth strategy does not exist in practice attests to the evolutionary attractiveness of the third strategy.

THE INFLUENCE OF FRUIT AVAILABILITY ON TEMPERATE AND TROPICAL AVIAN ECOLOGY

The use of fruit by tropical birds contrasts markedly with fruit usage in the temperate zone. The common tropical breeding strategy wherein adults

eat fruit and feed insects (and fruit) to nestlings is generally not available
to temperate-zone birds, because few plants produce fruit during the main
temperate-zone breeding season.

Karr (1971) estimates that 10% to 20% of the increased number of
tropical-zone breeding bird species over temperate-zone birds in similar
habitats is due to fruit availability. Fruit is important in that it not only
allows more species to occupy an area, but it also allows large adult popula-
tions to be maintained. Adult populations, existing on a high-fruit diet, are
not limited by food to the same extent as they are when feeding nestlings.
That is, nestling food is different and less easily obtained than adult food
and would be even harder to procure if large adult populations also fed
throughout the year on the same food. A high breeding adult population
leads to intense competition for nestling food (Ashmole 1961). This, in
addition to high nest predation (Ricklefs 1969), results in low recruitment
rates for tropical bird populations. There may be a higher "carrying
capacity" for adults than for nestlings because of the differences in food.
However, once adulthood is reached, a stable climate and an easily ob-
tained fruit diet may result in high adult populations because of increased
longevity.

The fact that temperate-zone plants do not ripen fruit during the main
spring breeding season constitutes an important difference between tropical-
zone and temperate-zone bird communities. The third breeding strategy is
not available for utilization by the majority of temperate-zone birds. A
result is that temperate-zone birds are more territorial than tropical birds
to ensure themselves an adequate food supply for nesting.

Why has selection not favored the ripening of bird-dispersed fruit in the
temperate-zone spring? Many wind-dispersed trees (e.g., red maple, *Acer
rubrum*, and the elms, *Ulmus*) do ripen seed during or before rapid vegeta-
tive growth in the spring. I believe that avian seed-dispersal agents may be
the main source of selection against spring fruit ripening.

I suggest that in the temperate-zone spring, the abundance of insects
reduces competition for this resource. Without the intense competition for
insect food (such as that which occurs in the tropics), fruit would never
be "chosen" as food for nestling birds. Moreover, breeding adult temperate-
zone birds are more sedentary due to territoriality than tropical birds and
would be rather inefficient seed dispersers. It is perhaps a result of "com-
petition" with insects as food for birds that plants have not evolved fruiting
during the avian breeding season in temperate latitudes.

Fruiting is common after the main breeding season because insects are
probably harder to find (plant defenses such as leaf tannin are in effect,
predatory insects are reducing primary consumer insects, larval stages are
over for many species, etc.) and birds choose fruit instead. Also, territorial
systems break down, allowing birds to search for and concentrate at fruiting
plants, and bird populations are highest just after the breeding season. These
factors have led to a major difference in bird and plant interaction between
the tropic and temperate zones.

SUMMARY

Positive and negative sources of selection on fruit-eating by birds are discussed. It is hypothesized that fruit is rarely favored as the complete diet for small nestling birds because it results in slower growth rates than those allowed by animal food. Nest predation pressure is greater in totally frugivorous birds and counteracts the advantages of the abundant and easily accessible food supply afforded by fruit. The evolutionary result of total frugivory is discussed, relating population size, rarity of nest sites, and clutch size to the rarity of totally frugivorous species.

Frugivory in adult birds is discussed in relation to habitat, social behavior, and interspecific competition. It is hypothesized that total frugivory in adult birds is opposed by selection from occasional periods of low fruit abundance, when the ability to obtain animal food reaches limiting conditions.

An evolutionary and ecological dichotomy between humid tropical-zone and temperate-zone birds is discussed. This dichotomy is due to the use of fruit during the breeding season by adult tropical birds, which allows them to use more time searching for animal food for nestlings. This results in a time-energy budget for breeding tropical birds that is not available for most breeding temperate-zone species. It is hypothesized that temperate-zone species would "choose," evolutionarily, animal food over fruit during the breeding season and that this has resulted in negative selection pressure on plants to produce fruit during the temperate-zone avian breeding season.

LITERATURE CITED

Ashmole, N. P. 1961. The biology of certain terns. Ph.D. Thesis. Oxford Univ. 219 p.

Dawson, W. R., and F. C. Evans. 1957. Relation of growth and development to temperature regulation in nestling field and chipping sparrows. Physiol. Zoöl. 30:315–327.

Eisenmann, E. 1961. Favorite foods of neotropical birds: flying termites and *Cecropia* catkins. Auk 78:636–638.

————. 1962. Notes on some neotropical vireos in Panama. Condor 64:505–508.

Gardarsson, A., and R. Moss. 1970. Selection of food by Icelandic ptarmigan in relation to its availability and nutritive value, p. 47–71. *In* A. Watson [ed.], Animal populations in relation to their food resources. Blackwell, Oxford.

Haverschmidt, F. 1952. Nesting behavior of the southern house wren in Surinam. Condor 54:292–295.

Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21:620–637.

Jenkins, R. 1969. Ecology of three species of Saltators with special reference to their frugivorous diet. Ph.D. Thesis. Harvard Univ. 318 p.

Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. 41:207–233.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, Oxford. 343 p.

———. 1968. Ecological adaptations for breeding in birds. Methuen, London. 409 p.

Leck, C. F. 1972. Seasonal changes in feeding pressures of fruit- and nectar-eating birds in Panama. Condor 74:54–60.

Leung, W.-T. W. 1968. Food composition tables for use in Africa. FAO-HEW, Public Health Service, Bethesda, Md.

Morton, E. S. 1971a. Food and migration habits of the eastern kingbird in Panama. Auk 88:925–926.

———. 1971b. Nest predation affecting the breeding season of the clay-colored robin, a tropical song bird. Science 181:920–921.

Moynihan, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Collections 143:1–140.

Ricklefs, R. 1968. Patterns of growth in birds. Ibis 110:419–451.

———. 1969. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. 9:1–48.

———. 1970. Clutch size in birds: outcome of opposing predator and prey adaptations. Science 168:599–600.

Skutch, A. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

———. 1954. Life histories of Central American birds. Pacific Coast Avifauna 31:1–448.

———. 1960. Life histories of Central American birds. Pacific Coast Avifauna 34:1–593.

———. 1969. Life histories of Central American birds. Pacific Coast Avifauna 35:1–580.

Snow, B. K. 1970. A field study of the bearded bellbird in Trinidad. Ibis 112:299–329.

Snow, B. K., and D. W. Snow. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. Auk 88:291–322.

Snow, D. W. 1962a. The natural history of the oil-bird Steatornis caripensis. Zoologica 47:199–221.

———. 1962b. A field study of the black and white manakin, Manacus manacus, in Trinidad. Zoologica 47:65–104.

———. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. Oikos 15:274–281.

———. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113:194–202.

Terborgh, J., and J. M. Diamond. 1970. Niche overlap in feeding assemblages of New Guinea birds. Wilson Bull. 82:29–52.

Willis, E. O. 1966. Competitive exclusion and birds at fruiting trees in western Colombia. Auk 83:479–480.

———. 1967. The behavior of bicolored antbirds. Univ. Calif. Pub. Zool. 79:1–131.