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Heterogeneity of Potential Food Abundance for Tropical Small Land Birds

There is no general all-purpose method of description of resources for small tropical terrestrial birds. To understand food resources for the birds in a habitat or for a particular species of bird, one has to determine what the bird(s) feed on and hand-tailor a census technique that collects data in a manner that correlates well with the actual resources taken by the bird. However, general statements about *potential* food may suggest detailed studies of birds and their resources that will produce informative close correlations. In this spirit, I offer a few brief stories about apparent severe heterogeneity of potential resources for birds in the tropics.

Rainy Season Insect Flush

In the lowland deciduous forest at Santa Rosa National Park (northwestern Guanacaste Province, Costa Rica), there is an abrupt and heavy production of new foliage at the beginning of the rainy season (May). Within two to four weeks of this flush of foliage, it is apparent that there is also a short-lived heavy peak in the biomass of moth and butterfly larvae feeding on this new foliage. Partly and entirely defoliated plants are common, and the ground is littered with caterpillar feces. A moment's inspection of vegetation produces numerous Lepidoptera larvae. Several months later, there is little trace of this event, other than the remnants of damaged leaves. A month earlier, there was no sign of caterpillars.

To quantify crudely this flush of caterpillars, four of us (P. DeVries, M. L. Higgins, G. Vega, D. H. Janzen) visually censused caterpillars on a 204-m trailside transect through deciduous forest. The vegetation was examined closely for 2 m on each side of the trail and up to 2 m in height, on sunny clear days with scudding clouds, and between 800 and 1200 hr. All caterpillars were collected into alcohol, and later sorted by morphospecies and measured (table 1). The

vegetation is trail-edge and understory shrubs and saplings in old secondary deciduous forest; the trail was 1–2 m in width, and the canopy was irregularly closed overhead. The trail is the Nature Trail (Sendero Natural) from the first fork, and thence across the natural bridge to the second large rock in the trail in the guapinol grove. The following species of plants made up about half of the bulk of foliage examined: *Allophyllus occidentalis*, *Casearia corymbosa*, *Hemiangium excelsum*, *Acacia collinsii*, *Maluaviscus arboreus*, *Hamelia patens*, *Psidium* spp., *Croton* spp., *Stemmadenia donnell-smithii*, *Hymenaea courbaril*, *Calycophyllum candidissimum*, *Cassia* spp., *Plumeria rubra*, *Luehea* spp., *Tabebuia neochrysantha*, *Tabebuia rosea*, *Ficus* spp., *Bursera simaruba*, *Bursera graveolens*, *Guazuma ulmifolia*, *Solanum* spp., *Myrospermum frutescens*, *Genipa caruto*, *Trichilia* spp., *Guettarda macrosperma*.

By the date of the August census, the abundance of caterpillars had fallen to the level that seems to persist through the remainder of the rainy season. There are a number of traits of the caterpillars that seem particularly relevant to their potential as bird food.

1) The average length of the caterpillars (2.0–2.5 cm) did not change over the six-month period. This suggests that a bird may be confronted with the same size distribution of caterpillars early in the season as later (and visual inspection of the caterpillars suggested that this was the case). However, with the absolute number of caterpillars much higher earlier than later in the season, the number of large caterpillars available would likewise be much greater earlier than later.

2) The caterpillars ranged from very cryptic to very aposematic, and there was no conspicuous trend in change in the proportions of these two extremes of life form over the six-month period.

3) Throughout the six-month period, birds feeding on this caterpillar peak were very inconspicuous if they

Table 1. Caterpillars encountered in a 204-m census strip in deciduous forest understory in Santa Rosa National Park, Guanacaste Province, Costa Rica.

Date	Total Length of caterpillars (m)	Average length (cm)	Number of individuals	Number of species
16 June 1977	7.5	2.5	297	87
31 June 1977	2.4	2.4	101	28
15 Aug 1977	0.7	2.5	28	16
21 Nov 1977	0.3	2.0	16	7

were there at all; this was in striking contrast to the number of foraging (foliage-gleaning) birds and birds carrying larvae (to a nest) that I see regularly in the extra-tropical spring. Perhaps tropical woodland insectivorous birds forage more cryptically than do those of extra-tropical woodlots and forests, but I have no reason to suspect this to be so. There is no hint that a wave of birds moves onto the peak of caterpillars and is responsible for its demise in August. Likewise, there was no evidence that the impermanence of the high density of caterpillars was due to a build-up of arthropod predators and parasites.

4) Studies other than the census made it clear that many of the caterpillars pupated, hatched within a few weeks, and departed as adults. In the most direct sense, this was the cause of the decline in caterpillar density as the season progressed. We are left with the mystery of why the adults do not lay a second round of eggs on the remaining and replacement foliage; the answer probably has to do with increase in secondary compound content in original foliage and increased toxicity of replacement foliage but is not the subject of this paper.

In short, there is no hint of local avian response to the large peak in caterpillar density. Furthermore, this peak occurs almost exactly at the time of breeding of insectivorous birds in northern latitude forests. Why do these birds not migrate from intermediate elevation Costa Rica to the adjacent lowland deciduous forest to breed instead of flying all the way to Pennsylvania or elsewhere? To make the question even more puzzling, I should add that Malaise trap samples from the Santa Rosa forest show that flying insects in the 1–10 mm-length class increase dramatically in density after the rains begin and then gradually decline over the next six months.

I am hesitant to suggest such a sweeping hypothesis,

but it is marginally possible that the bulk of the caterpillars taken in the census are toxic even when not glaringly aposematic. Or at least, they may be more toxic than would be an equal bulk of forest caterpillars in Wisconsin in the spring. Three natural history facts bear on this.

1) There do appear to be more aposematic caterpillars among the Santa Rosa collection than I have seen among collections of extra-tropical spring woodland caterpillars.

2) The host plants of these caterpillars are known or suspected to contain notable quantities of highly toxic secondary compounds (in addition to tannins and other digestion inhibitors). This is not the case for many of the important caterpillar host plants in extra-tropical woodlands (e.g., *Pinus, Abies, Picea, Quercus, Fagus, Betula, Salix, Acer*).

3) Each species of Santa Rosa Caterpillar appears to be almost entirely restricted to a single species of host at this site; this suggests the presence of specialists at physiologically incorporating (or sequestering) toxic secondary compounds in their tissues. Again, the tree-foliage feeding caterpillars in northern forests tend to have several or more hosts, and there is no suggestion that a major part of their feeding physiology is the sequestering of toxins from their host plants.

If the Santa Rosa caterpillars are much more toxic than would be an equal bulk of extra-tropical caterpillars, then it may explain why there does not appear to be heavy local use of the peak in caterpillar density and why the "migrants" in the Costa Rican highlands do not settle onto this peak, but rather fly on north.

Local Movements of Insects

A large number of tropical insects in seasonal habitats move from one habitat to another, as adults, apparently in response to differential disappearance of food through drying and dormancy of food (e.g., Janzen 1973a, b). One of the most conspicuous movements is from hillsides to nearby riparian vegetation as the dry season intensifies, with subsequent movement back to the hillside with its flush of new foliage when the rainy season begins. Many species therefore pass the dry season as an active adult in a riparian refugium. This results in high concentration of adult insects in riparian vegetation during the dry season and means that the density of insects on hillsides depends on the proximity of a hillside to riparian vegetation.

In the context of this volume, how important is this local heterogeneity to the insectivorous birds? I submit that there is no way to answer without careful censusing of birds at the site concurrent with analysis of bird-gut contents *and* samples of these particular insects. At the extreme case, for birds specialized on

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caterpillars, neither the hillside nor riparian vegetation has enough caterpillars to feed anything during the dry season; the movements and concentrations of insects in general are largely irrelevant for this bird. Of a less extreme nature, if a bird is a specialist on small brown beetles called Bruchidae, it should forage on the dry hillside since these beetles move the opposite direction from insects in general (Bruchidae do this because they oviposit on the fruits and seeds to be found abundantly during the dry season on dry hillside sites). On the other hand, if a bird is a specialist on small foliage-inhabiting beetles in general (e.g., Chrysomelidae), the riparian vegetation is the place to forage during the dry season.

Now, what does this have to do with migrant birds? First, migrants move all sorts of distances, from 200 m to 200 miles to 200 tens of miles. How and why they move local distances should help understand why they move long distances. Second, when migrants arrive, they settle onto a very heterogeneous resource base, a heterogeneity that shifts as the year progresses. Further, there can be enormous heterogeneity among closely adjacent "similar" vegetation types, such as young second growth with different disturbance histories (Janzen 1976a). Third, there is no possible general purpose description for this heterogeneity; the heterogeneity and how it is best described will depend on what the bird desires.

Global Heterogeneity Within the Tropics

There is, a strong temptation by ornithologists to divide the lowland terrestrial tropics into thorn forest, deciduous forest, evergreen forest, and second growth derived from each. Here I would like to emphasize that there can be major non-seasonal differences in the amounts of major kinds of bird food in what appear to be the same habitat in different parts of the tropics.

The most glaring examples that come to mind at present are those evident when West Malaysian lowland dipterocarp rainforest is compared with Costa Rican lowland rainforest (the remainder of this section is a direct quote from Janzen 1978a).

"At the lowland Pasoh rainforest, Negri Sembilan, Peninsular Malaysia, I censused the plants in flower that were less than 3 m tall in the understory of undisturbed forest along 3 km of narrow trail (early September 1976). I found 1 orchid, one 1.5 m tall Araliaceae, one 0.5 m tall Acanthaceae (*Lepidagathis longifolia*), and one 1 m tall *Ixora*-like Rubiaceae. In the lowlands of the national park, Taman Negara, 5.4 km of rainforest trail yielded 1 white-flowered ginger, 2 *Ixora*-like Rubiaceae, 1 Acanthaceae, 1 unknown family and two 10–20 cm tall Gesneriaceae with underground stems. In primary forest understory in the new

Corcovado National Park (20–160 m elevation, Osa Peninsula, southwestern Costa Rica), a trail-side survey of 4.3 km yielded 94 plants in flower of 18 species (20 November 1976). In other words, I averaged 1.3 plants in flower per kilometer in the Malayan rainforest understory and 21.9 plants in flower per kilometer of Costa Rican rainforest understory.

"These woefully small samples reflect accurately my general impression of the general abundance of flowers in the understory of rainforests of Peninsular Malaysia and Sarawak, as compared with those of Costa Rican rainforest of similar elevation. I was informed locally that 1976 was one of the heaviest years in memory for flower and fruit production in Peninsular Malaysia; November is the time of most reduced flower production in Costa Rican rainforest understory (and see Frankie et al 1974). In short, if one were to turn loose in Pasoh or Taman Negara the rainforest understory fauna of flower-visiting hummingbirds, butterflies, moths and bees found in the Corcovado, I predict that they would be dead of starvation in a few days. Furthermore they could not survive by moving out into secondary regeneration; Malaysian disturbed sites have a grossly lower flower abundance than any weedy wet season vegetation that I have seen anywhere in the African or Neotropical lowlands.

"Over the Malaysian transects mentioned above, I encountered 63 understory individuals in fruit (22 species) for an average of 7.5 per kilometer. In the Corcovado forest, there were 345 individuals in fruit (34 species) for an average of 78.4 per kilometer. Again, the fauna of understory birds that frequently eats small fruits in Neotropical rainforests would have a very rough go of it in the Malaysian forests.

"It is extremely interesting that after doing this and writing the above, I discovered Karr's (1976) statement that "about 80% of the canopy and understory tree species on Barro Colorado Island are dispersed by animals (Foster 1973), while only about 10 percent of the trees on Fogden's (1972) [Sarawak] study area were important as sources of fruits for birds". Furthermore, at the IV International Congress of Ecology, in Panama, Karr (March 1977) noted that "The most striking difference is the total lack of undergrowth frugivores in mist-net samples taken from Malaysia as compared with 25–33 percent of the individuals captured in undergrowth of African and Central American forest."

I would like to propose a rather sweeping hypothesis to account for this paucity of flowers and fruits on rainforest understory shrubs, a paucity which should have a very depressing affect on the biomass and species richness of the understory fauna. I need first, however, to belabor you with three facts about the lowland Malaysian rainforests in which the censuses were made.

1) They are dipterocarp forests, which means that between 50 and 80 percent of the tree crowns in the canopy belong to species of Dipterocarpaceae. The members of this family, in Malaysia and some other tropical Asian areas, mast fruit within (and between) habitats. Thus the bulk of the flower and fruit production by better than half of the upper canopy photosynthetic machinery is pulsed at 3- to 11- year intervals. Associated with this, the animal community is sufficiently satiated by the enormous numbers of seeds that a very large number survive to the seedling and small sapling stage (Janzen 1974a).

2) Malaysian rainforests, on the Malay peninsula or in Sarawak, are largely perched on sandy soils ranging from very old white sand deposits (such as in Bako National Park, Sarawak) to very sandy soils derived from weathering of granitic base rock that has not been inundated by the sea for an extremely long time. There is no volcanic overlay nor crust of weathering limestone on most of the terrain. There are many indirect measures of the relatively low ability of these soils to generate a vegetation with a high harvestable productivity for other organisms: when cleared, the second-growth vegetation is very slow to refill the site (Janzen 1974a, 1974b, and this is probably why plantation rubber is so successful on these soil types); the forest has largely remained uncut and unexploited by agrarian peoples despite their presence in the general area for many thousands of years (note that virtually all of nearby Java on volcanic soils is under agriculture); second growth vegetation of the sites has an amazingly low insect biomass as compared to that of comparable neotropical weedy sites (Janzen 1974a).

3) There are bees, butterflies, flower-visiting birds, and small fruit-eating birds present in the Malaysian rainforests. In other words, pollinators and dispersal agents can be drawn from these groups if the ecological and evolutionary opportunity is presented.

I hypothesize that the shortage of rainforest understory flowers and fruits is largely attributable to two forces operating simultaneously and synergistically. First, I hypothesize that the large pulse of dipterocarp seedlings and saplings takes up a large part of the resources that are available to neotropical understory shrubs; the dipterocarp offspring are apparently dying in large part through competition rather than through supporting a seed predator guild. Simultaneously, they are analogous to an enormous and very generalist herbivore in their impact on understory shrubs. Since dipterocarp seedlings never flower or fruit, they take a large portion of the understory resources without feeding part of it back into the flower-visitor and fruit-eater guild so conspicuous in a neotropical forest. Second, I hypothesize that as the soil conditions get

progressively worse, the ability to be a reproducing individual in the light-poor understory is reduced. That is to say, irrespective of the presence of the dipterocarp seedlings, if the forest canopy is held constant, and the soil fertility is depressed, the biomass (number of individuals in general) and reproductive output per hectare by understory shrubs should fall (just as it would if soil fertility were held constant and the light were decreased). In other words, the rainforests of Malaysia sit on a poorer piece of real estate than do those of lowland Costa Rica, and the flower and fruit density in the understory reflects this.

The animals are probably woven into this matrix more firmly than I have indicated so far. I have hypothesized that the habitat-wide masting behavior of these Dipterocarpaceae is driven at present, and was selected for in the past, by the seed predators in general (Janzen 1974a). Further, I have argued that the lower the overall productivity of the site, the more likely that the animals will select for masting behavior because the less food there is for them between mast crops, the more severely they are depressed in density by masting behavior. But the scarcer they are between mast crops, the fewer understory flower and fruit crops they can (will) visit; the fewer crops they visit, the less well off will be such plants and the better off will be the dipterocarp seedlings in competition with non-dipterocarps. Why does the system not progress to where there are nothing but seedlings and saplings of overstory trees in the understory? Probably because as time passes since the last mast crop, competitive and accidental deaths clear the arena for some other species of plants, and because a number of animals that visit flowers in the understory can also go elsewhere for food; many frugivores can feed on insects and other food types when understory fruits are scarce.

The focus to this point has been largely on the biomass of flowers and fruits and associated animals. However, the species richness of plants and animals should also be negatively influenced by a reduction in harvestable productivity (Janzen 1977a). My argument involves resource partitioning and specialization on the partitions. In short, as the productivity of harvestable resources in the habitat falls, more and more resource blocks become too small to sustain a specialist. They are then taken by a more generalized harvester or by another trophic level. In the context of the example under discussion, the number of species of flower-visiting species of understory birds should decline as the soil gets poorer and as the overstory becomes progressively more synchronized at supra-annual seeding. For example, in a Costa Rican rainforest there are species and morphs (often females) of hummingbirds (e.g., *Phaethornis* spp.) that specialize on

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widely scattered understory individuals in flower, and species and morphs (often males) that specialize on large clumps of flowers on forest edges (Stiles 1975). From what I have seen of Malaysian lowland rainforest, a hummingbird would have to forage at all such sites and then some to stay in the game. Simultaneously the species richness of seed predators in the habitat should also decline as soils become poorer and synchrony increases, since the progressively more pulsed nature of the seed resource makes it effectively scarcer in any but the very exceptional mast year. For example, in a Costa Rican rainforest there is a large standing crop of agoutis (*Dasyprocta punctata*) and pacas (*Cuniculus paca*) that live on the rather continuous input of fruits, seeds and young seedlings (Smythe 1970). These animals are relatively sedentary. They do not have ecological analogues in Malaysian forests, and I suspect the reason to be that in most years the seed resource is not large enough to sustain them, although in mast years it is far greater than they could ever consume before the seeds germinate.

The pulsing of productivity in a rainforest can have other interesting side effects on animals. It should select for migratory or very nomadic species, which are in turn less likely to develop local regional populations than are more sedentary species. I have argued that the wind-dispersed nature of dipterocarp seed (and that of other trees that fruit as they do, such as the legume *Koompasia*) is due to their specialization to the site on which their parent grew and not being involved in escape from seed predators through dispersal (Janzen 1977b); it may also be due to an extreme shortage of biomass of frugivorous animals owing to the fact that much of the seed production by the forest is pulsed (the frugivores would be severely satiated on seeding years just as would be the seed predators). Whatever the cause, the fact that most of the canopy-level seed production is wind-dispersed eliminates a large portion of the fruit input that is an important part of the diet of many neotropical animals. For example, I doubt very much that any Malaysian forest comes anywhere close to the figures of 0.61 to 1.93 g of fruit per m^2 calculated to fall in a Panamanian rainforest by Smythe (1970). However, in closing this paragraph, I cannot help but notice that Malaysian forests have an exceptionally high number of species of squirrels for example, 19 tree squirrels in Borneo, Davis 1962). It is possible that squirrels are particularly good at dealing with a highly pulsed food input, as compared with the other animals that eat seeds and fruits (some in fact, are specialists on insects or vegetative parts of plants). In short, as harvestable productivity becomes progressively less available, there is no reason to expect all animal life forms to be depressed

at the same rate. In fact the elimination of some could quite reasonably result in an increase in others.

The ramifications of low productivity of harvestable resources by the plant community in an average year can produce a multitude of higher-order interactions. For example, in 17 days of field work and travel between field sites by boat or small car, I saw a total of three raptorial birds in Peninsular Malaysia (and none in 11 days in Bako National Park, Sarawak). The area traversed was at least 300 miles of urban, rural and forest roads, 76 miles of large river through farmland and forest reserve (Tembeling River on the way to and from Taman Negara), and about 50 hours of hiking in forest reserves. At least 80 percent of the weather was non-rainy. I should emphasize that I was not searching for raptorial birds, but rather just watching for any kind of animal. In a similar excursion up and down the similar-sized Sanaga River in Cameroun, I took photographs of 23 birds of prey and saw at least 50 more. In Ugandan and Kenyan forest-farmland and national parks, it is hard to find a moment on a clear day when a raptor or large avian scavenger is not in view somewhere (and see Janzen 1976b). In Costa Rican lowland rainforests, forest-farmland mixes, and open pasturelands, raptors and/or scavengers are seen at least once every several hours, and much more often in many circumstances.

The ornithological literature is not designed so as to provide material relevant to comments such as those above. However, a few interesting tidbits can be extracted. For example, the black or king vulture (*Torgos calvus*) is common throughout the northern part of the Malay Peninsula but is almost never seen in the southern half (rainforested portion) of the peninsula; the same may be said of the other peninsular vulture (*Pseudogyps bengalensis*) (Robinson 1927; Medway and Wells 1976). As Wells put it (pers. comm.), there is no vulture (for all practical purposes) in West Malaysia. The standard explanation for the absence of vultures is Robinson's (1927) comment that "securing their food entirely by sight, it is obvious that a heavily forested country is quite unsuited to them and it is for this reason, probably, that they do not extend to the Malay Archipelago." This seems to me to be a quite inadequate explanation. As Peninsular Malaysia has been cleared, vultures have become rarer, not more common (Robinson 1927). Furthermore, one has to ask 1) why similarly heavily forested areas in other parts of the tropics sustain vultures; 2) why the forest was not cleared for agriculture and livestock long ago as it was in other parts of the tropics, and 3) why the contemporary invasion of agricultural peoples does not bring with it adequate food for vultures? In short, I hypothesize that rainforest Peninsular Malaysian

and Sarawak habitats never did generate enough carrion to keep vultures in the game and that the contemporary peoples occupying these habitats cannot raise enough livestock to generate enough spin-off carcasses for vultures to persist as the land is cleared. Central American rainforest and associated natural disturbance sites, when put into multi-use agriculture and livestock husbandry, sustain conspicuous populations of three species of vultures and two caracaras (hawks that act like vultures).

I doubt that the paucity of vultures or vulture-like birds in Malaysia is due to excessive hunting; however if there is less food for them, then even small amounts of hunting can do disproportionately more damage than if there is a large resource base. I doubt that the large varanid lizards, relatively common on river banks and in refuse dumps where not hunted, are competitively excluding the vulture-like birds. I saw 28 large (0.5–1-m snout-vent) *Varanus* along the bank of about 20 km of the Tembeling River at and below Taman Negara on one morning. Rather, I suspect that the absence of vultures allows the presence of these relatively slow scavengers; if the food is scarce and occurs at very long intervals, then a cold-blooded professional starver would be able to maintain a much higher biomass than birds. I was told by a Kuala Lumpur "pet" dealer that with water, a large varanid can live a year without food; I doubt a vulture could do the same.

The hypothesis that the natural habitats of West Malaysia generate a low density of food for large carnivorous birds is also supported by the species richness of falconids and accipiters. West Malaysia has 11 resident species of accipiters and 1 resident falcon (Medway and Wells 1976) and is about 132,000 km^2 in area; Costa Rica has at least 28 resident species of accipiters and 8 resident falcons and is 51,000 km^2 in area (Slud 1964). The tiny Costa Rican rainforest field station at Finca La Selva (6.1 km^2) has at least 9 resident accipiters and 4 resident falcons (Slud 1960).

Herons, bitterns and egrets are conspicuously scarce in fields, roadside ditches and empoundments, rice paddies, streams, marshes, and riverbanks in West Malaysia away from the sea. I did not see a single individual in the 17 day field period. More specifically, not a single one was seen along the 76 miles traversed of the Tembeling River, despite careful search for them. These birds are conspicuous in similar habitats in Africa and Central America. On the Sanaga river trip mentioned above, I photographed 7 species and saw at least 30 individuals. Such birds are a standard part of the scenery along large Central American rivers and in the kinds of habitats mentioned at the beginning of this paragraph. Inquiry of ornithologists in

West Malaysia produced two useful comments. First, "they are absent because they don't migrate here"; well, what is wrong with West Malaysian real estate so that migrating large piscivorous birds do not use it much as overwintering grounds? Second, "these birds are conspicuous in areas near the sea." For example, Medway and Wells (1976) noted that 6 of the 9 resident species of Malayan Ardeidae are associated with mangroves. If in fact West Malaysia is a poor habitat for these birds, then the mangroves and river deltas should be the best of the sites and appear disproportionately good compared to inland areas. Again, tiny Costa Rica has 14 species of resident Ardeidae (Slud 1964) to compare with 9 for Peninsular Malaysia (Medway and Wells 1976).

I hypothesize that herons, bitterns, egrets (and anhinga- and cormorant-type birds) are in short supply in the West Malaysian inlands simply because the waterways do not generate enough biomass of aquatic food for them. If the surrounding terrestrial habitats generate a reduced number of insects as well, which are an important part of the diet of many ardeids, the effect would be compounded.

There are two other non-intuitive major sources of global heterogeneity in small tropical terrestrial bird food: insularity and altitudinal gradients. In a sentence, the problem with Caribbean islands is that they have greatly reduced insect biomass overall and numbers of individuals of many insect groups as compared with Central American mainland vegetation of comparable elevation, seasonality, soil type, and disturbance history. Specifically, sweep samples (Janzen 1973b; Allan et al 1973) and visual inspection of secondary and primary forest understory vegetation on Puerto Rico, St. Thomas, Hicacos Island, Palominitos Island, Greater St. James, Gran Cayman, Providencia, and other small islands in the Virgin Islands show greatly reduced numbers and biomass of Hemiptera, Lepidoptera larvae, Orthoptera and herbivorous Coleoptera as compared with a great variety of mainland lowland sites in Costa Rica. Even more spectacularly, when the wet season arrives on a seasonal island, there does not appear to be the great increase in insect density so prominent on the Costa Rican mainland in very seasonal lowland sites, for example, Providencia Island (Janzen 1973b).

Not all groups of anthropods are equally reduced on small Caribbean Islands. Some Homoptera (aphids, scales, mealy bugs, leafhoppers, fulgorids, and flatids) are conspicuously over-represented in numbers and biomass on small islands; presumably this is due to some sort of release from predation and parasitization (Janzen 1973b). Ants, spiders and predaceous beetles are likewise proportionately (and in some cases, abso-

lutely) much more abundant than in comparable mainland habitats (and see Becker 1975). This is probably related to the ability of individuals of these predaceous life forms to withstand the long starvation periods associated with a highly seasonal habitat coupled with few moist refugia to pass the dry season or from which to reinvade when there is local extinction.

I have been careful not to give or dwell on data for specific islands or habitat types on the islands. I suspect that even at low levels of insect prey there is strong inter-habitat and inter-island variation in density; even the relative lack of increase in insects in the rainy season is based on only two data points and may not be absolutely generalizable. A special word of caution is needed with respect to type of insect eaten; an aphid specialist would do extremely well on the small islands between Puerto Rico and St. Thomas. However, almost any bird depending on Orthoptera or caterpillars more than 2 cm in length would starve to death on any Caribbean Island (except Trinidad). It is imperative that the insect sampling scheme be tuned to the kinds of insects eaten by the bird of concern and that the sample be taken from the relevant habitat in the appropriate season.

In closing the subject of insularity, I should note that understanding insect densities (as food) on Caribbean Islands is relevant to more than where migrants can stack themselves. John Terborgh has pointed out to me that on Caribbean (and Pacific) islands the ratio of frugivorous and granivorous bird species to insectivorous (resident) species is the inverse of the adjacent mainland. Is this because insectivores do so poorly, because frugivores do so well on islands, or because, for instance, frugivores can find the insects they need for the very short times they are rearing young (owing to the general absence of insectivores)? This may be a ridiculous hypothesis, but I suspect that when insect and other resource densities are strongly altered compared to a mainland, we may have natural experiments that help illuminate heretofore unsuspected interactions on the mainland.

Everyone expects insect biomass numbers, sizes, etc., to change going up a tropical mountain. They do, but not quite in the way expected. In short, there is a mid-elevation bulge in insect species richness and biomass (and/or individuals). Between about 800 and 1,600 m on Costa Rican and Venezuelan mountains, sweep and visual samples in primary forest and secondary vegetation tend to produce more individuals and species of arthropods than equivalent samples from the adjacent lowlands (0–200-m elevation), and very substantially more than at higher elevations (2,000–3,500 m) (Janzen 1973b; Janzen et al 1976). To me, the most plausible hypothesis for this phenomenon is a bulge in harvestable productivity at intermediate elevations. As a dependent hypothesis, the increased productivity may be due to cooler nights at intermediate elevations coupled with only slightly reduced diurnal photosynthesis; the difference, which should be related to the harvestable productivity, is thus higher at intermediate elevations. It is those hot tropical nights. A moment's reflection should show why increased harvestable productivity from plants should result in an increase in species-richness as well as biomass in the herbivorous insect life form (with subsequent changes in the insectivores of all sorts in the habitat, and see Janzen 1977a).

I will leave the relevance of the mid-elevation bulge to insectivorous birds, migrant and resident, to the other contributors to this volume. Jim Karr has pointed out to me that it is at intermediate elevations the tropics around that take the prize for the greatest mist-net catches. Intermediate elevations have been described as "migrant heaven" (Neal Smith). Paul Slud notes that these intermediate elevations may represent a giant ecotone between upper elevation bird faunas of extra-tropical origin and lowland tropical faunas. However, the generation of migrants in evolutionary time from intermediate elevations may be one way to generate an upper elevation bird of extra-tropical origin.

Acknowledgments

Literature Cited

Allan, J. D., L. W. Barnthouse, R. A. Prestbye, and D. R. Strong
1973. On foliage arthropod communities of Puerto Rican second growth vegetation. Ecol. 54:628–32.

Becker, P.
1975. Island colonization by carnivorous and herbivorous Coleoptera. J. Anim. Ecol. 44:893–906.

Davis, D. D.
1962. Mammals of the lowland rainforest of North Borneo. Bull. Nat. Mus., Singapore, 129 pp.

Fogden, M. P. L.
1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114:307–43.

Foster, R. B.
1973. Seasonality of fruit production and seed fall in a tropical forest ecosystem in Panama. Ph.D. diss., Duke University, Durham, N.C. 156 pp.

Frankie, G. W., H. G. Baker, and P. A. Opler
1974.   Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. 62:881–913.

Janzen, D. H.
1973a. Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. Ecol. 54:659–686.

1973b. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecol. 54:687–708.

1974a. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. Biotropica 6:69–103.

1974b. Epiphytic Myrmecophytes in Sarawak: mutualism through the feeding of plants by ants. Biotropica 6: 237–259.

1976a. Sweep samples of tropical deciduous forest foliage-inhabiting insects: seasonal changes and inter-field differences in adult bugs and beetles. Rev. Biol. Trop. 24:149–161.

1976b. The depression of reptile biomass by large herbivores. Amer. Nat. 110:371–400.

1977a. Why are there so many species of insects? Proc. 15 International Congress of Entomology, Washington, D.C. 1976:84–94.

1977b. Seeding patterns of tropical trees. Proc. 4th Cabot Symposium, Harvard Forest, Mass.

1978a. Promising directions of study in tropical animal-plant interactions. Ann. Missouri Bot. Garden (in press).

Janzen, D. H., M. Ataroff, M. Fariñas, S. Reyes, N. Rincon, A. Soler, P. Soriano, and M. Vera
1976.   Changes in the Arthropod community along an elevational transect in the Venezuelan Andes. Biotropica 8:193–203.

Karr, J. R.
1976.   Seasonality, resource availability, and community diversity in tropical bird communities. Amer. Nat. 110:973–94.

Medway, L., and D. R. Wells
1976.   The Birds of the Malay Peninsula. Vol. V. London: Witherby, 448 pp.

Robinson, H. C.
1927.   The Birds of the Malay Penninsula. Vol. I. London: Witherby, 329 pp.

Slud, P.
1960.   The birds of Finca La Selva, Costa Rica: a tropical wet forest locality. Bull. Amer. Mus. Nat. Hist. 121: 1–148.
1964.   The birds of Costa Rica. Bull. Amer. Mus. Nat. Hist. 128:1–430.

Smythe, N.
1970.   Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Amer. Nat. 104:25–35.

Stiles, G.
1975.   Ecology, flowering phenology, and hummingbird pollination of some Costa Rican Heliconia species. Ecol. 56:285–301.

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