Fruit-eating Birds and Bird-dispersed Plants in the Tropics and Temperate Zone

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Tropical forests have been the showcase for studies on the mutualistic relationship between plants and their avian seed dispersers. Only in the tropics can one find such a bewildering diversity of fruit types, or birds that survive on nothing but fruits. But to what degree is the typical tropical plant–bird interaction qualitatively different from interactions in the temperate zone? The emerging view from a decade of research is that plant–bird interactions everywhere are ecologically important, complex, facultative, diffuse, asymmetric and fundamentally similar.

By highlighting the unique mutualistic relationship birds have with the plants that depend on them for seed dispersal, Snow[1] and McKey[2] launched the modern study of the ecology of fruit-eating birds and bird-dispersed plants. Their gaze was towards the tropics, the fountainhead of intimate alliances between plants and animals (e.g. figs and fig wasps), and it wasn't long before a similarly specialized and obligate relationship was proposed between a tropical plant (*Calvaria major*) and its seed disperser (dodo, *Raphus cucullatus*)[3]. Following the dodo's extinction 300 years ago, *Calvaria* seeds had failed to germinate because they apparently depended upon scarification during digestion by dodos. A generation of temperate-zone field biologists, steered toward the equator by the prevailing theory[1,2], set out to explore tropical plant–bird interactions. Ever since there has been an untested assumption that birds and plants interact in qualitatively different ways in the temperate zone and the tropics, and a notion that 'the production of fleshy fruits by angiosperms and their consumption by a diverse array of vertebrates is a quintessential tropical phenomenon'[4].

The plausibility of the temperate–tropical dichotomy was supported by well-established latitudinal differences in species richness, seasonal temperature fluctuations, primary productivity, and a host of physical and biological features. More to the point, only in the tropics could one find examples of birds relying exclusively on a fruit diet. Fruit-pigeons (*Ptilinopus* spp.) in northern Queensland, for example, eat nothing but fruit; 88% of their diet may be comprised of the fruits of only two plant families[5], an example of taxonomic food specialization unheard of in the temperate zone. Every species with a predominately fruit diet – oilbirds (*Steatornis caripensis*), bellbirds (*Procnias* spp.), birds-of-paradise (Paradisaeidae) – seemed to be a tropical speciality.

As more data have emerged from temperate-zone as well as tropical research during the last decade, students of fruit-eating and seed dispersal are beginning to dispute the 'calumnious claim [that] the ecology of plant–animal interactions in the temperate zone is downright uninteresting'[6]. An international symposium held in June 1985 at the Los Tuxtlas Biological Station, Veracruz, Mexico[7], convened originally under the banner 'Tropical frugivory and seed dispersal' (until one-quarter of the papers turned out to be temperate in emphasis), proved that interesting and complex interactions between plants and their seed dispersers are not restricted to the tropics. The word 'Tropical' was expunged from the title of the proceedings. The purpose of this paper is to review the results of recent research on fruit-eating birds and fruiting plants and to ask in what respects interactions between birds and plants differ between the temperate zone and tropics.

Tropical and temperate-zone communities

Plants bearing fleshy fruits designed for dispersal by birds are more conspicuous in tropical habitats than in temperate-zone habitats in part because the tropics contain more plant species. At least 250 species of bird-dispersed plants occur within a 16 km² area in Costa Rica[8]; 90 bird-dispersed tree species co-occur within 6 ha of lower montane rainforest in New Guinea[9,10]. In contrast, mixed forests and mediterranean scrub in Spain, and various U.S. forests contain only 13–44 bird-dispersed species[6,11].

Additionally, a greater proportion of tropical plant species is disseminated by birds. The difference is most striking among trees: more than two-thirds of canopy tree species in various neotropical forests bear fleshy fruits, as compared to fewer than a third in eastern North American forests, where most trees rely on wind-dispersal[6,12]. In other parts of the world or among other plant growth forms, the regional distinction fades. Trees in tropical Africa and Asia produce fleshy fruits less commonly than neotropical trees (35–46% of species, depending upon habitat and region)[12]. Interestingly, there seems to be little difference in the proportion of understory plant species that produce fleshy fruits in the temperate zone and the tropics: 48–90% of shrubs and vines in eastern North America[6], and 44–62% in southern Spain[11], rely on birds for dispersal. Annual fruit production is generally lower in the temperate zone (0.5–7 kg/ha) than in the tropics (180–980 kg/ha)[13]. Nevertheless, if one corrects for the volume of vegetation in different habitats, mediterranean scrubland has fruit densities equivalent to tropical forests[11].

Although there are more species of fruit-eating birds in the tropics, where they generally comprise a larger fraction of the avian biomass than in temperate-zone habitats[13] (but see Ref. 11), the proportion of bird species that consume fruits is similar in various parts of the world. About one in three bird species (considering just passerines or all species combined) inhabiting a lower montane forest in Costa Rica feed on fruit[8,14]. A similar fraction of the avifauna eats fruit in other tropical forests[6] and in the temperate zone over half of the passerines of a Florida hammock forest[15] and 20–50% in Spanish habitats[11] consume fruits. Thirty-nine genera of

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eastern North American birds representing 15 families feed heavily on fruits[6].

Plant reproductive traits

Initially tropical fruits were thought to be nutritionally superior to temperate-zone fruits as a result of long periods of coevolution with their specialized seed dispersers[2]. Herrera, whose studies[11,16,17] in Spain make that region the best-known of any temperate-zone location with respect to plant–bird interactions, challenged the reigning view of temperate-zone inferiority by showing that, in terms of overall profitability (a composite measure of fruit size, seed load and nutrient content), tropical and temperate-zone fruits were indistinguishable[17]. With additional data from the tropics, it now appears that the average tropical fruit actually has a lower overall profitability than the average temperate-zone one[14]. Temperate-zone fruits compare favorably with typical tropical fruits in lipid and protein concentration[11,18]. In terms of color, most fruits eaten by birds are either black or red irrespective of region, and the relative frequency of different fruit colors among bird-dispersed plants varies little between sites, in spite of major geographical differences in floras[31].

The frequency distribution of fruit size shows a right-hand skew in all habitats, although the tail of the distribution tends to be longer in the tropics (Fig. 1). Tropical fruits, reflecting the ample gape widths of their larger avian seed dispersers (see below), may exceed 25 mm in diameter[8,9]. In contrast, temperate-zone fruits rarely exceed 18 mm in diameter[6,16,18]. Yet the median diameter of fruits of bird-dispersed plants is remarkably similar worldwide. In both the tropics and temperate zone the modal fruit is a 7–9 mm black or red berry[6,8,9,16,19]. The most thorough tropical work, notably Howe's[12,20] long-term research in Panama on two nutmeg species (*Virola*) and the limited subset of large fruit-eating birds that disperse their seeds, has tended to focus on the unusual large-fruited species[8].

An obvious difference between tropical and temperate-zone fruits is their seasonal availability. In fact, the greater species richness of tropical avifaunas has been attributed in part to the tropics' novel 'niche': birds can specialize on fruits year-round in the tropics[21]. Nevertheless, many tropical regions show distinct (though less extreme) peaks in fruit production[4,12]. A relatively monotonous tropical climate does not necessarily translate into constant fruit availability; fruit production may actually be less regular and predictable the more uniform the climate, as in southeast Asia, where even rainfall shows little seasonal variation[13]. In many tropical forests fruit-eaters are forced to rely on a small number of 'keystone plant resources' during the season of fruit scarcity[13].

While fruit production in tropical habitats proves to be less dependable than previously thought, temperate-zone fruit production can be relatively predictable seasonally and annually. Moreover, in many temperate-zone habitats ripe fruits can be found throughout the winter[22,23] and even year-round[11,15], although the density and quality of winter fruits are typically low[15,17,23,24] (but see Refs 11 and 18). Both tropical and temperate-zone birds migrate in response to fruit scarcities[6,11,13,15].

Traits of fruit-eating birds

Tropical birds, like fruits, span a greater size range than their temperate-zone counterparts[9,14]. Avian fruit-eaters the size of guans (Cracidae, which weigh up to 1700 g), hornbills (Bucerotidae), toucans (Ramphastidae), and umbrellabirds (Contingidae) are rare or absent in the temperate zone. Within the temperate zone, though, average body sizes of fruit-eating birds differ, from less than 20 g in Spain[16] to more than 40 g in North America[6,15,24,25]. In other respects, the morphology of most tropical and temperate-zone fruit-eating birds is quite similar. Traits such as wing and bill shape vary widely among fruit-eating birds, affecting fruit accessibility and influencing the types of fruits birds choose and the way they handle them, but no consistent morphological features distinguish tropical from temperate-zone species or characterize fruit-eating birds as a group distinct from insect-eaters[6,11,26]. Adaptations for fruit-eating are generally physiological and behavioral, rather than morphological[11,26]. Some temperate-zone as well as tropical species have digestive tracts highly specialized for efficiently processing fruits[2,27]. In response to seasonal changes in fruit availability and intake in the temperate zone, birds may adjust gut length and other features of their digestive systems[28].

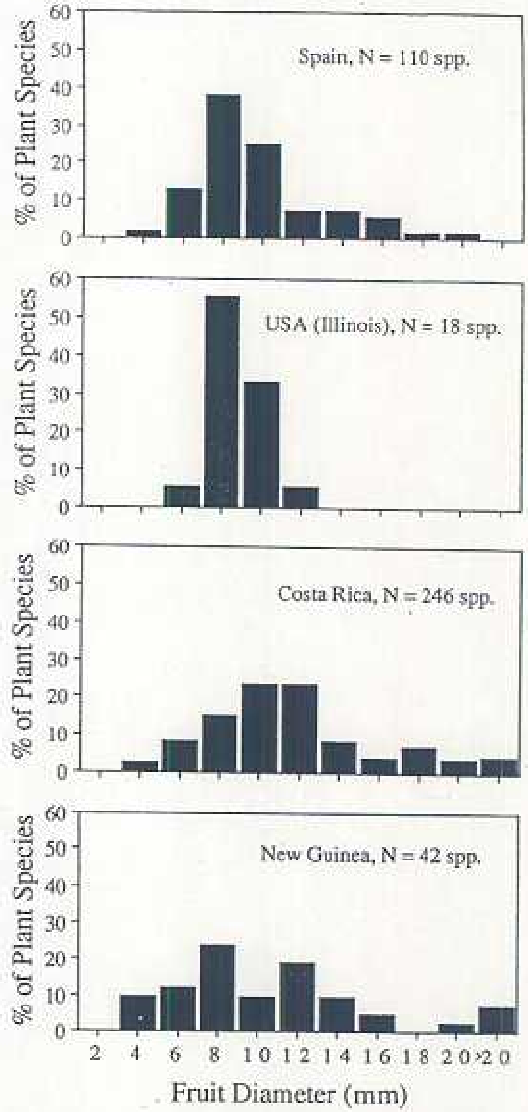

Fig. 1. Frequency distributions of fruit diameters from Spanish mediterranean scrub[16], U.S. mixed forest[18], Costa Rican lower montane wet forest[8], and New Guinean lower montane rainforest[9]. Tropical forests include considerably larger fruits than temperate-zone forests and greater variance in fruit diameters, but most habitats have similar median fruit sizes (Spain: 7.9 mm; U.S.: 7.7 mm; Costa Rica: 9.0 mm; New Guinea: 9.0 mm).

Although the temperate zone lacks any species like the exclusively frugivorous fruit-pigeons, several temperate-zone birds eat little else but fruits during the fall and winter. American robins (*Turdus migratorius*), for example, turn from an invertebrate diet to one dominated almost entirely by fruits[29]. The shift is sudden and extreme (Fig. 2). Some British thrushes (Muscicapidae) are also exclusive fruit specialists during the winter and defend

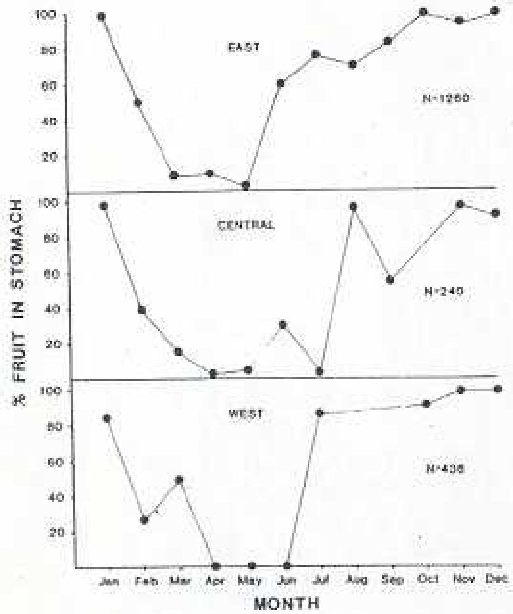

Fig. 2. The proportion of fruit (by volume) in stomach samples of American robins collected in different months in three broad geographical regions of North America. Each point represents the median value for a sample size of at least five individual birds. Total sample sizes (N) represent the number of individuals collected within each region over all months of the year. The changeover from an insect diet to a nearly exclusive fruit diet in this temperate-zone bird occurs within one to two months[29]. *Reproduced with permission from Ref. 29.*

fruiting trees from competitors[22]; in Spain a number of bird species feed on fruits continuously throughout the winter[11].

David and Barbara Snow[22], drawing on nearly four decades of research on fruit-eating birds around the world, have looked for differences in the behavior of tropical and temperate-zone species. Two main distinctions emerge. First, temperate-zone birds seem to face much greater risks of predation. Hawks threatened fruit-eating birds at a rate of 3.4 hawks per observation hour in English woodland, a much higher rate than reported from the tropics and one that doubtless affects their foraging behavior. Second, temperate-zone thrushes may defend fruiting plants from competitors from late winter until spring[22]. It remains to be seen whether tropical birds do the same during fruit shortages[13]. There is some evidence that tropical mistletoes are defended by fruit-eating birds[22].

Plant–bird interactions and seed dispersal

Both tropical and temperate-zone habitats contain plant–bird interactions of extreme generality as well as remarkable specificity. Researchers in a tropical forest in Gabon were impressed with an 'outstanding lack of specificity' in most plant–vertebrate interactions[30]. Forty or more bird species consume the small watery fruits of *Acnistus arborescens* in Costa Rica[14] or figs in Peru[13]; 15 bird species feed on *Viburnum dentatum* fruits 4000 km north of the equator[25]. Most of these birds feed on many other fruits in addition. In the same habitats but at the other end of the specialization spectrum are a few strong interactions between plants and birds[11,14,20]. The temperate-zone Sardinian warbler *Sylvia melanocephala*, for instance, is rarely found except where fruiting *Pistacia lentiscus* occur[11]. For the warbler, *Pistacia* is as much a keystone plant resource as a neotropical fig is for Peruvian rainforest birds[13]. A full explanation for why birds prefer some fruits over others remains elusive, but their choices are clearly influenced by fruit size[8,9,11], nutritional composition[18,23], color and presentation[6,26,31] and other traits.

Perhaps the most extreme examples of a specialized interaction between a fruiting plant and its avian seed dispersers involve the mistletoes (chiefly the Loranthaceae and Viscaceae) and flowerpeckers (Dicaeidae) and honeyeaters (Meliphagidae) in the Old World, or tanagers (Emberizidae) and flycatchers (Tyrannidae) in the New World[2]. Of these, the best-documented case comes not from a steamy tropical rainforest but from the arid acacia woodland of temperate Australia[37]. There the mistletoe *Amyema quandang*, a host-specific stem parasite of *Acacia papyrocarpa*, depends entirely on two bird species (mistletoebird, *Dicaeum hirundinaceum*, and spiny-cheeked honeyeater, *Acanthagenys rufogularis*) for dissemination of its seeds. Reid could find where each bird species deposited seeds, monitor the subsequent fate of dispersed seeds, and assess each bird's influence on the fitness of the mistletoe. As is likely to be the case in most seed dispersal systems worldwide, once we know more about them[7,11,12,20], neither bird species was terribly efficient at delivering seeds to sites where they stood a chance of becoming established. Only 1% of all seeds dispersed by the birds ended up on acacia stems of appropriate size. Despite the mistletoebird's more specialized diet and greater dependence on mistletoe fruits, it proved to be a less effective seed disperser than the honeyeater, just as euphonias (*Euphonia* spp.), neotropical equivalents of the mistletoebird, turned out to be poorer dispersers of mistletoe seeds than several generalized flycatchers[32].

Levey's[33] experiments on fruit handling by birds demonstrate that sloppy seed dispersal may be a fact of life for many large-seeded tropical plants. Tanagers and finches, abundant and diverse fruit-eaters in neotropical forests, crush fruits during mandibulation to avoid swallowing the seeds; as non-digestible 'ballast' from a bird's perspective, seeds occupy gut space that could be filled more profitably with fruit pulp. Almost all seeds above a certain size (relative to a bird's body size) eaten by these birds are discarded, presumably to perish in the shade of the parent plant[33].

A recent comparative study of plant–animal mutualisms sheds light on the nature of plant–bird interactions at the community level and the potential for coevolution between species pairs in a variety of habitats[34]. Unexpectedly, tropical and temperate-zone assemblages of plants and avian seed dispersers exhibit similar food web structure and patterns of interaction. Although the total number of interactions between species increases as the number of species in a mutualistic system increases, as in the tropics, the proportion of possible interactions (the connectance) actually declines. Consequently, the number of interactions per species is independent of species richness. Very few pairs of plants and birds anywhere strongly depend on each other; if anything, tropical systems show a higher proportion of weak interactions[34]. When strong interactions occur, they tend to be asymmetric, that is, a bird species may depend heavily on a plant species that benefits from dispersal by many other birds, or almost all of a plant's seeds may be dispersed by a bird species for which that plant's fruits are an insignificant part of the diet[11].

Conclusion

Interactions between fruit-eating birds and bird-dispersed plants are an important, widespread feature of temperate-zone habitats. It would be erroneous, though, to conclude from this review that the relationship between plants and their avian seed dispersers is identical in the tropics and the temperate zone. For that matter, it would be equally indefensible to maintain that interactions are uniform across the tropics. As a result of geographical differences in climate and taxonomic composition of floras and faunas, the American, African and Southeast Asian tropics differ in fruiting phenologies, species richness and density of birds and fruits, dietary overlap among fruit-eating birds, average body size of birds, and many other features[4,12]. On a smaller spatial scale interactions between tropical plants and birds are heterogeneous, too. On different sides of the mountain range dividing Costa Rica, the tree *Casearia corymbosa* is dispersed by ecologically distinct assemblages of birds[12,20]. Even at one tropical locality interactions differ. Neotropical fruit-eating birds (especially migrants) congregate in second-growth forest, where fruit abundance is higher and fruit size is smaller than in primary forest[19]. Martin's[19] and Howe's[20] studies drive home another important point, that migrants from the temperate zone play a key role as seed dispersers in the tropics, thus further blurring the concept of a single, geographically distinct type of plant–bird interaction.

Tropical regions can still claim certain distinctions. Compared to the temperate zone they are richer in species of fruit-eating birds and fruits, some of which reach considerable sizes. The tropics include oddities such as ostentatious, aril-covered capsulate fruits, and birds that can survive on an exclusive diet of fruits. One wonders, however, if we have been distracted by the garish plumages and unconventional breeding systems of some tropical birds (which, let's face it, make Sardinian warblers and American robins seem 'downright uninteresting'; Fig. 3) and led to conclude that they also differ qualitatively as seed dispersers. Do calfbirds (*Perissocephalus tricolor*) or resplendent quetzals (*Pharomachrus mocinno*) disperse seeds any more effectively than warblers or robins?

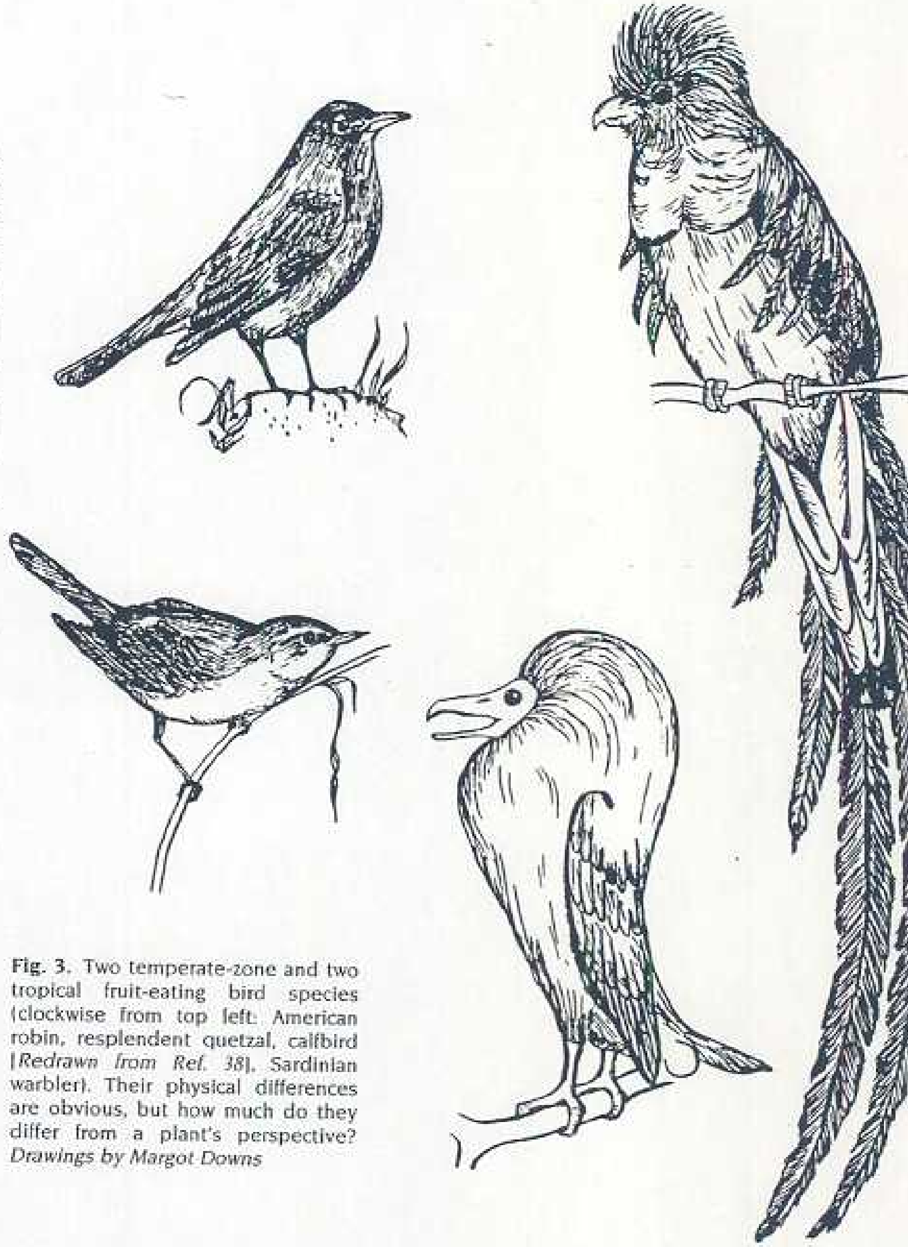

Fig. 3. Two temperate-zone and two tropical fruit-eating bird species (clockwise from top left: American robin, resplendent quetzal, calfbird [*Redrawn from Ref. 38*], Sardinian warbler). Their physical differences are obvious, but how much do they differ from a plant's perspective? *Drawings by Margot Downs*

The emerging view is that most interactions between fruiting plants and their avian seed dispersers – whether in the tropics or the temperate zone – are loose, asymmetric, variable in time and space, inefficient and non-obligate. The average fruit everywhere is small, often dull-colored, not particularly nutritious, and likely to have its seeds land in the wrong place. Birds are opportunistic foragers, concerned more with their own reproductive interests than those of the plants that provide them food. The reason for the lack of finely tuned specificity originally envisioned[2] is that coevolution between plants and their seed dispersers is diffuse and constrained for a variety of reasons, such as weak selection, spatially and temporally inconsistent selection, opposing selection, lack of genetic variability, and asymmetry in interdependence and longevity of plants versus birds[20,35,36]. The questions have been refocused with the growing awareness that temperate-zone systems hold promise in explaining the dynamics and evolution of interactions between plants and their avian seed dispersers[6].

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