

**Avian Methods of Feeding on *Bursera simaruba*  
(Burseraceae) Fruits in Panama**

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We observed 26 species of birds and noted the feeding method used by each when taking fruits of a single *Bursera simaruba* tree in Panama (Table 1). The Icterinae, represented by five species, showed the greatest diversity in feeding methods and differed from one another in feeding rate, in handling time (Table 2), and probably in dispersal consequences for *B. simaruba*. The two oriole species, which depend least on fruit in the diet (Bent 1958), also fed least efficiently and probably provided the poorest seed dispersal.

*Bursera simaruba*, or gumbo-limbo tree, is a wide-spread tropical species common in advanced secondary growth. It flowers in Panama from mid-March to mid-June; fruits are present throughout the year, but mature fruits are most abundant in the early dry season around January (Croat 1978: 943). We made observations between 0645 and 0830 on 4-8 February 1982 near Kobbe Beach, Panama (60 m elevation).

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The 12-m-tall tree grew in a cleared field 10 m from dry deciduous forest. The fruits, fleshy egg-shaped capsules about 1 cm in length, had a leathery green skin (pericarp) over a thin layer of bright pink aril covering one or two one-seeded nutlets. The abundant fruits were conspicuous because the tree we observed had lost most of its leaves.

Birds handled fruits in three ways, each having different consequences for feeding efficiency and seed dispersal: (1) fruit skin removed, nutlet with aril swallowed, and nutlet defecated or regurgitated later; (2) fruit skin removed, fruit picked and manipulated in the mouth to remove the aril, and nutlet dropped beneath the tree; and (3) fruit skin removed, aril eaten, and nutlet left on the tree.

Most visitors swallowed the fruits, but some species consistently dropped the nutlets under the tree or left them on the tree. During this study five bird species appeared to be the most effective seed dispersers on the basis of feeding method, number of individuals visiting the tree, number of days seen at the tree, and foraging rate: *Zarhynchus wagleri*, *Cacicus*

TABLE 1. Bird species and methods of feeding on fruits of *Bursera simaruba* in Panama.

Species	Feeding method (see text)		
	1	2	3
<i>Crotophaga ani</i> (Smooth-billed Ani)	X		
<i>Pteroglossus torquatus</i> (Collared Aracari)	X		
<i>Melanerpes rubricapillus</i> (Red-crowned Woodpecker)	X		
<i>Myiarchus panamensis</i> (Panama Flycatcher)	X		
<i>Megarhynchus pitangua</i> (Boat-billed Flycatcher)	X		
<i>Myiozetetes similis</i> (Social Flycatcher)	X		
<i>Myiodynastes maculatus</i> (Streaked Flycatcher)	X		
<i>Tyrannus melancholicus</i> (Tropical Kingbird)	X		
<i>Tityra semifasciata</i> (Masked Tityra)	X		
<i>Chiroxiphia lanceolata</i> (Lance-tailed Manakin)	X		
<i>Turdus grayi</i> (Clay-colored Robin)	X		
<i>Vireo flavifrons</i> (Yellow-throated Vireo)	X		
<i>Vireo olivaceus</i> (Red-eyed Vireo)	X		
<i>Vermivora peregrina</i> (Tennessee Warbler)	X		
<i>Dendroica castanea</i> (Bay-breasted Warbler)			X
<i>Protonotaria citrea</i> (Prothonotary Warbler)			X
<i>Thraupis episcopus</i> (Blue-gray Tanager)	X		
<i>Tangara inornata</i> (Plain-colored Tanager)			X
<i>Dacnis cayana</i> (Blue Dacnis)	X		
<i>Cyanerpes cyaneus</i> (Red-legged Honeycreeper)	X		
<i>Phaeucticus ludovicianus</i> (Rose-breasted Grosbeak)	X	X	
<i>Zarhynchus wagleri</i> (Chestnut-headed Oropendola)	X		
<i>Cacicus cela</i> (Yellow-rumped Cacique)	X		
<i>Icterus chrysater</i> (Yellow-backed Oriole)		X	X
<i>Icterus galbula</i> (Northern Oriole)		X	X
<i>Scaphidura oryzivora</i> (Giant Cowbird)		X	X

TABLE 2. Handling times and feeding rates for five icterine species feeding on *Bursera simaruba* fruits in Panama.

Species	$\bar{x}$ handling time (s)	$\bar{x}$ feeding rate (fruits/min)	$\bar{x}$ body weight (g)	
			Male	Female
<i>Zarhynchus wagleri</i>	1.5	5.7	211.4	115.3
<i>Cacicus cela</i>	1.4	5.6	75.9	65.5
<i>Scaphidura oryzivora</i>	9.4	2.4	204.5	171.5
<i>Icterus galbula</i>	16.6	1.3	35.2	33.9
<i>Icterus chrysater</i>	18.2	1.4	53.5	48.3

*cela*, *Megarhynchus pitangua*, *Vireo olivaceus*, and *Myiodynastes maculatus*. A squirrel, *Sciurus variegatoides*, also took fruits but may have eaten the seeds.

The five icterine species differed from one another in feeding method, feeding rate, handling time (Table 2), and probably in quality of dispersal provided. Oropendolas and caciques (*Z. wagleri* and *C. cela*) swallowed the fruits and had the shortest handling times and the highest feeding rates. At least some of the intact nutlets pass freely through the guts of *Z. wagleri* and *C. cela*, which defecate the nutlets when caught in mist nets. *Icterus galbula* removed the pulp from the nutlet and usually dropped the nutlets under the tree, while *Icterus chrysater* usually left them on the tree. These orioles had the longest handling times. Their feeding rates were the lowest, partly because they were subordinate to the other icterines and were often supplanted before getting a chance to eat the fruit. Although the two orioles probably provided little dispersal of seeds, their exploitation of fruit had relatively little impact on the tree due to their low feeding rates and subordinate status. *Scaphidura oryzivora* usually dropped the nutlets under the tree and had intermediate handling times and feeding rates. Swallowing fruits whole rather than removing the pulp from the nutlet allowed birds to forage more efficiently on *B. simaruba* fruit and may incidentally have increased the dispersal quality provided.

Feeding method, handling time, and feeding rate in the Icterinae were related to body size; the largest birds swallowed fruits and had the lowest handling times and the highest feeding rates. The failure of the smaller *Icterus* species to swallow fruits, however, was probably not because the fruits were too big, as many even smaller birds swallowed the fruits (e.g. *Vireo olivaceus*). The different methods used by icterines to handle *Bursera simaruba* are probably not determined by body size, but instead reflect differences among the species in how food is handled in general. Members of the Icterinae exhibit particularly high diversity in feeding adaptations and diet (Beecher 1951).

Within the Icterinae the largest difference in feeding efficiency and dispersal quality occurred between the oropendolas/caciques and the orioles. All of these species are often considered opportunistic frugi-

vores, because adults eat some insects and feed insects to their young. Obligate frugivores are believed to differ from opportunistic frugivores in depending more completely on fruit in the diet and, as a result of coevolution, in providing more reliable dispersal of seeds (McKey 1975, Howe 1977). When applied to oropendolas and caciques, the term "opportunistic frugivore" is somewhat misleading, because these species require and actively seek large quantities of fruit in their diet. This dependence on fruit, even though not complete, has probably influenced the foraging adaptations and dispersion patterns of adults. They meet their dietary requirements by efficient handling of fruit such as *B. simaruba*. The orioles, however, do not seem to depend on large quantities of fruit (Bent 1958). It may be that they meet their requirements by opportunistically eating small quantities of fruit as encountered. The low feeding rates on *B. simaruba*, if they also reflect how other types of fruit are handled, suggest that efficient handling of fruit has not been important for orioles.

The difference between "opportunistic" and "obligate" frugivores in the degree to which they are specialists on fruit and the quality of seed dispersal they provide may not be as great as once believed (Wheelwright and Orians 1982). Oropendolas and caciques may differ less in these respects from "obligate" frugivores than they do from the orioles.

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### Evidence of Aggressive Behavior in Female Blue Grouse

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Historically, studies of territoriality and other forms of spacing behavior have emphasized interactions between males, with little attention being given to the study of similar behaviors in females. Recently, however, work with some tetraonids has demonstrated that females do respond aggressively towards one another and that these behaviors may relate to the spacing of individuals (Stirling 1968, Herzog and Boag 1977) and/or the regulation of breeding densities and production (Robel 1970).

Results from laboratory experiments with Blue Grouse (*Dendragapus obscurus*) indicate that females will attack their mirror images (Stirling 1968). In addition, indirect evidence from field studies suggests that females may space themselves on the breeding range (Hannon et al. 1982), and Hannon (1980) hypothesized that the "cackle" call is an aggressive vocalization that mediates this spacing. Some females have cackled at, and in a few instances have approached, tape recordings of cackles (Hannon 1978); at present, however, no documented cases of females chasing or attacking other females are available. In this note I describe the details of an aggressive interaction between two females, which I observed while conducting studies of Blue Grouse on Hardwicke Island, British Columbia in 1982.

On 30 April I flushed an unidentified female at 1705 and she flew to an area of tall trees approximately 75 m away. Twenty minutes later two females began uttering "whinny" calls (Stirling and Bendell 1970) in the area where the female landed. The females continued calling vigorously, with most of the calls being whinnies; a few cackle calls also were given. As I approached, one flew in my direction and landed in a tree a few meters away. Within seconds the other female flew toward the first hen and landed in a tree 10 m from her. The second female was banded, but the first was not. Both began cackling at each other, with the banded one appearing to be the aggressor. The unmarked hen cackled softly and infrequently and walked slowly along a branch. The banded female cackled, flew to within 5 m of the other female, and walked toward her. When the banded female was 3-4 m away the unmarked hen flew 40 m to the northwest and landed in another tall tree. Again the banded female flew after her and

landed in the same area. One cackled, but as I approached the calling stopped, and the unbanded female flushed far down a hill when I disturbed her. I could not relocate the marked female.

The banded female was a known adult and had been seen in the area where the interaction occurred three times before 30 April; she had nested nearby as a yearling in 1981. Later in 1982 she was seen in the same area with a brood, and the age of the chicks indicated that her nest hatched on 13 June. The interaction I observed, therefore, occurred about 13 days before she began laying, that is, at a time when she would have been establishing a home range and preparing to breed (Hannon et al. 1979, Hannon 1980).

An unbanded female in this area began cackling immediately when I played taped cackles to a nearby territorial male on 25 April. Most females (over 85%) on my study area were marked and therefore the unbanded females seen on 25 and 30 April were probably the same individual. The interaction I observed on the latter date was possibly in an area where the home ranges of these two females overlapped, or, alternatively, the unbanded female could have been trying to establish a prenesting home range (Hannon et al. 1982). No unbanded brood females were later seen in this immediate area.

Hens did not attack female models when Hannon (1980) conducted playback experiments in the field. Therefore, she postulated that the mechanism for spacing of females is a combination of warning calls and mutual avoidance rather than one of overt aggression. Although the encounter I observed did not involve direct contact, it does demonstrate that females do interact aggressively and that both the whinny and cackle call are used in such interactions. Presently, the relative importance of mutual avoidance and overt aggression in spacing females cannot be evaluated, however, because female spacing behavior has been implicated only recently as being important in regulating breeding densities of Blue Grouse (Hannon 1980, Hannon et al. 1982), and as yet research on this problem has been limited.

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