Selection of second-growth woodlands by frugivorous migrating birds in Panama: an effect of fruit size and plant density?

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ABSTRACT. I provide evidence that migrating birds concentrate in tropical second-growth woodlands due, in part, to a greater abundance of small fruits. Migrant birds markedly increased in abundance during spring migration in late March in a young (approximately 25 years old) second-growth woodland in Panama. Migrant abundance and diversity was greater at mist-net level on the second-growth site than in nearby old forest. Diversity of canopy migrants also was greater in the young woodland than in an old second-growth forest. Thus, many migrant species appear to select young second-growth during spring migration in central Panama. Degree of frugivory by many migrant species was greater during migration than earlier in the dry season. Most migrants selecting the second-growth site were highly frugivorous and migrants accounted for most of the visits to common fruit species, but use of fruit trees appeared to be influenced by fruit size relative to gape width. Most migrants have mouths that are better suited to eating the small fruits predominating in young forest than the larger fruits charac-teristic of old forest. Abundances of bird-dispersed fruit plants and, particularly, those fruit species known to be eaten by migrants were greater in young than in old forest. The high food demands of migrating birds added to the high degree of frugivory of most migrants selecting second-growth forest suggests that the abundance of small fruits in second-growth may be a strong cause for habitat selection during migration.

KEY WORDS: frugivory, habitat selection, migrant birds, Panama, spring migration.

CONTENTS

INTRODUCTION

Patterns and underlying causes of habitat selection by birds that migrate long distances (migrants hereafter) to winter in the neotropics have received increased attention (see Keast & Morton 1980) but are still poorly understood. Migrant densities often are higher in tropical second-growth forest than in moist, low-land forest (Chipley 1977, Hutto 1980, Karr 1976, Willis 1966), although this

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pattern is not consistent throughout the neotropics; migrants are more abundant and occupy more habitat types in northern tropical regions (i.e. Mexico) (Hutto, 1980, Tramer 1974, Waide 1980, Waide *et al.* 1980). Furthermore, habitat use varies among migrant species, but few seem actually to prefer undisturbed forest (Terborgh 1980).

The conventional explanation for the greater concentration of migrants in second-growth habitats is that migrants are unable to invade the complex avian community supported by relatively stable areas of wet lowland forest. Instead, they are restricted to patchy and ephemeral habitats that putatively cannot support a complex resident avifauna (Chipley 1977, Leck 1972a, Willis 1966). Second-growth areas often are patchy in distribution and small habitat patches support fewer species than larger areas (Blake 1983; Galli *et al.* 1976; Martin 1980, 1981; Willis 1979). However, direct evidence for the influence of avifaunal complexity on habitat selection is lacking. In fact, recent evidence shows that abundance and diversity of migrants increase with abundance and diversity of residents among habitat types (Hutto 1980, F. Stiles 1980, Waide 1980, Willis 1980). Thus, avifaunal complexity seems an unsatisfactory explanation for selection of second-growth habitats by migrants.

Migrants do not breed during winter, so fitness is enhanced by surviving in the best possible condition to maximize the probability of successful migration back to breeding sites. Avoidance of predation clearly is critical for survival, so habitat selection may be influenced by predation risk (see Martin 1985). However, food also is important. Food demands are probably greatest when migrants need to build fat stores for migration (Berthold 1975), so food consumption may attain a higher priority relative to predator avoidance during migration (Metcalf & Furness 1984). Thus, food may be particularly important to habitat selection during migration, but habitat selection during spring migration in the neotropics has not been explored in detail.

Many migrants switch from insects to fruits prior to and during spring migration in the tropics (Fry *et al.* 1970; Hilty 1980; Howe & DeSteven 1979; Leck 1972a, b; Mead 1966; Morton 1971), but degree of frugivory varies among species (Greenberg 1981a, b; Morton 1980). Those species that are highly frugivorous during migration may select and concentrate in habitats with an abundance of profitable fruits, where profitability is determined by fruit size, abundance, nutritive content, and interactions among species (Martin 1985). In this paper, I examine use of second-growth habitats, degree of frugivory, and use of fruit sources by migrant species. I combine these data with published data on abundance and size of tropical bird-dispersed fruit species to provide an explanation for selection of second-growth habitats by migrants during spring migration.

STUDY AREA AND METHODS

The second-growth study site was approximately 25 years old and located along Pipeline Road in Parque Nacional Soberania in Panama. The 4.5 ha site

was located on top of a small hill between Rio Frijoles and Rio Frijolito. Most vegetation was less than 10 m high with a few emergent *Didymopanax morototoni* reaching 12–15 m. Surrounding areas were moist forest.

Mist-nets were used to sample bird communities. The community was sampled during early (January) and late (March) dry seasons of 1980 and 1981 for a total of 5994 mist-net hours. Thirteen mist-nets (12 m long, 4 shelves, 30 mm mesh) were operated in mid-January (7–23) and late March (16–27) in 1980 and mid-January (9–22) and late March (18–28) 1981. An additional 17 nets were operated in late January (23 Jan.–3 Feb.) and early March (6–12) 1981. Nets usually were operated from 06.15 to 17.30 h, when weather permitted, and were checked hourly. Netting mortality was less than 0.5%. Gape widths of captured birds were measured using calipers.

Degree of frugivory of migrant warblers (Parulidae) was quantified by recording the type of the first foraging manoeuvre (insectivorous versus frugivorous) used each time an individual was observed while walking between nets. Foraging data do not include observations made while watching fruit trees.

Bird visitation to three fruit species was quantified by noting species of bird and time of arrival and departure of each visitor that stopped to eat fruit during daily watches lasting 4–6 hours. Trees of *Didymopanax morototoni* were observed from 10 January to 3 February and from 9–21 March (169.5 hours), *Xylopia frutescens* from 11–20 March (20.1 hours) and *Miconia argentea* from 21 to 27 March (28.8 hours).

Description of trees

Didymopanax morototoni is a light-demanding pioneer species, typically found in large light gaps and disturbed areas and is distributed throughout most of the humid neotropics (Croat 1978, Crow 1980, Denslow 1980). *D. morototoni* was an emergent canopy tree on my study area, 12–15 m in height and fruited from January to late March. Inflorescences are racemose umbels in compound panicles. Fruits are approximately 8–9 mm long and 5 mm wide and include two seeds (Croat 1978).

Miconia argentea is more common in young than old forests and grows to 15 m in height (Croat 1978), although it averaged 6–8 m on my study site. It flowers from December to May and fruits from January to May. Fruiting on my study area did not begin until early to mid-March in each of the 3 years that I visited the site. Greenberg (1981a) also found that *M. argentea* fruits around early March on Barro Colorado Island. Fruits are borne in dense panicles with globose berries about 5 mm in diameter and they include many minute seeds (Croat 1978).

Xylopia frutescens is typical of young forests and can grow to 20 m in height (Croat 1978), although individuals on my site averaged 8–10 m. It flowers from April to June and fruits from January to April. Fruits are about 7 by 12 mm and include 1–3 seeds that are approximately 6 mm long (Croat 1978).

MIGRANT ABUNDANCE AND FRUGIVORY ON THE SECOND-GROWTH SITE

Migrant abundance and diversity

Twenty-six migrant species were observed or netted on this study area (Table 1). Most species were more abundant during spring migration in late March than earlier in the dry season. In fact, many species were present only as tran-

Table 1. Migrant bird species that were observed (number netted) on the study site. +++ = abundant, observed daily; ++ = common, observed most days; += uncommon, observed only a few times.

| | 1980 | | 1981 | | | |
| | | | Jan. | | Mar. | |
	Jan.	Mar.	Early	Late	Early	Late
Eastern Kingbird (*Tyrannus tyrannus*)	—	+++(1)	—	+	++	+++
Great-crested Flycatcher (*Myiarchus crinitus*)	—	+++(1)	++	++	+++(1)	+++(1)
Acadian Flycatcher (*Empidonax virescens*)	++(1)	++(2)	++(1)	++(2)	—	++(1)
Traill's Flycatcher) (*Empidonax traillii*)	—	+(2)	—	—	—	—
Grey Catbird (*Dumetella carolinensis*)	++(3)	+++(9)	—	—	—	++
Wood Thrush (*Hylocichla mustelina*)	++(7)	+++(9)	—	+(1)	++(1)	+++(4)
Swainson's Thrush (*Catharus ustulatus*)	+(1)	+++(20)	++(3)	—	++(1)	+++(18)
Yellow-throated Vireo (*Vireo flavifrons*)	—	+(1)	—	—	—	—
Red-eyed Vireo (*Vireo olivaceus*)	—	++	—	—	—	++
Black-and-White Warbler (*Mnioltilta varia*)	—	+(2)	—	—	—	—
Prothonotary Warbler (*Protonotaria citrea*)	—	+	—	—	—	+(1)
Golden-winged Warbler (*Vermivora chrysoptera*)	—	+	—	—	—	—
Blue-winged Warbler (*Vermivora pinus*)	—	+	—	—	—	+(1)
Tennessee Warbler (*Vermivora peregrina*)	++	+++(32)	—	—	—	+++(24)
Magnolia Warbler (*Dendroica magnolia*)	+++(3)	+++(1)	+++(2)	+++(1)	+++(1)	+++(2)
Chestnut-sided Warbler (*Dendroica pennsylvanica*)	+++(1)	+++(3)	+++(3)	+++(2)	+++(1)	+++(2)

Table 1 – *continued*

| | 1980 | | 1981 | | | |
| | | | Jan. | | Mar. | |
	Jan.	Mar.	Early	Late	Early	Late
Bay-breasted Warbler (*Dendroica castanea*)	+++(3)	+++(7)	–	–	++	+++(1)
Yellow-rumped Warbler (*Dendroica coronata*)	++	+	–	–	–	–
Ovenbird (*Seiurus aurocapillus*)	+++(6)	+++(5)	++(2)	+(1)	–	++(2)
Northern Waterthrush (*Seiurus noveboracensis*)	–	–	–	+(1)	–	–
Kentucky Warbler (*Oporornis formosus*)	+++(11)	+++(6)	+++(6)	+++(9)	+++(4)	+++(6)
Mourning Warbler (*Oporornis philadelphia*)	–	+(1)	+(1)	–	–	–
Northern Oriole (*Icterus galbula*)	+++	+++	–	++	–	+++
Summer Tanager (*Piranga rubra*)	–	+++(4)	–	–	++(1)	+++(1)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	–	+++(1)	–	–	–	+++(3)
Indigo Bunting (*Passerina cyanea*)	+(3)	–	–	–	–	–

sients during migration. As a result, capture rates of migrants were greater (P < 0.01, χ^2 test) in late March than earlier in the dry season in both years (Figure 1). Furthermore, capture rates of migrants were greater (P < 0.01, χ^2 test) in second-growth than nearby forest in both months of both years. The higher capture rates of migrants in second-growth do not reflect a simple trend of all birds (migrants and non-migrants) being captured faster in second-growth than in forest. Migrants were captured proportionally faster than non-migrants in second-growth than in forest (P < 0.01, χ^2 test; Figure 2).

Some migrant species may be more susceptible to netting in second-growth than in forest because they forage in the canopy above nets in forest (Greenberg 1981b). However, the greater abundance of migrants in second-growth is not simply a sampling artifact. Ground level foragers (i.e. Grey Catbird, Swainson's Thrush, Wood Thrush, Ovenbird, Kentucky Warbler) rarely use forest canopies (see Greenberg 1981b) and, thus, are equally susceptible to nets in both forest and second-growth. Yet, capture rates for these migrant species (5.1 birds/100 net-hours in 1980, 3.4 in 1981) in second-growth in March were greater (P < 0.01, χ^2 test) than capture rates (1.6 in 1980, 0.5 in 1981) of all migrant species in nearby forest during the same period (Table 1, Figures 1, 2).
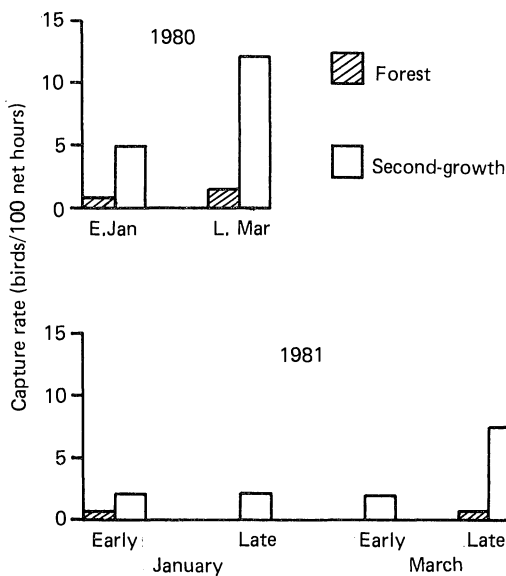
Figure 1. Capture rates (birds/100 net-hours) of migrants during early January and late March 1980 and early January, late January, early March, and late March 1981 on my young second-growth site and for January and late March on Karr's (1971) old forest site. Data for the forest site in January were only available from 1969 (Karr 1971), but the March samples are from exactly the same time periods that I sampled my second-growth site (from Karr & Freemark 1983).

Moreover, many migrant species foraged above net level on my second-growth site and some of these species were quite abundant. For instance, Eastern Kingbirds occurred in flocks of 100 (Morton 1971, personal observation), but I captured only one individual. Tennessee Warblers also occurred in large flocks in the canopy, but they were the most abundant migrants in net samples because they foraged lower as well (Table 1). Bay-breasted Warblers, Chestnut-sided Warblers, Summer Tanagers, Northern Orioles and Rose-breasted Grosbeaks also were very common in the canopy during migration and rarely captured in nets. The abundance of migrants in the canopy is further illustrated by their presence at fruit trees.

Migrant abundance at canopy fruit trees

Migrants were virtually absent at *Didymopanax morototoni* during January but they were common in March, even though March was the end of the fruiting season for *Didymopanax* (Martin 1982). Migrants also were abundant and numerically dominated visitation to *Xylopia* and *Miconia* during March (Figure 3).

Migrant frugivory and abundance

Abundance of migrants at canopy fruit trees in March was due, in part, to increased frugivory (Table 2). Migrant warblers varied in their degree of frugivory among species and over the dry season, degree of frugivory increasing in
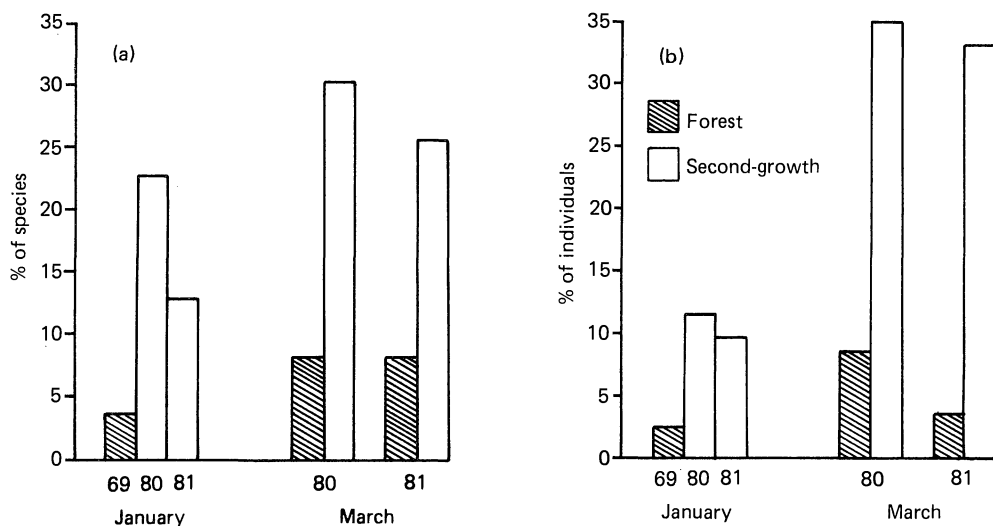
Figure 2. Percent of (a) species and (b) individuals of birds in 200-bird samples in January and late March that were migrants in my second-growth site and Karr's (1971) old forest site. Data for the forest site in January were only available from 1969 (Karr 1971), but the March samples are from exactly the same time periods that I sampled my second-growth site (from Karr & Freemark 1983).
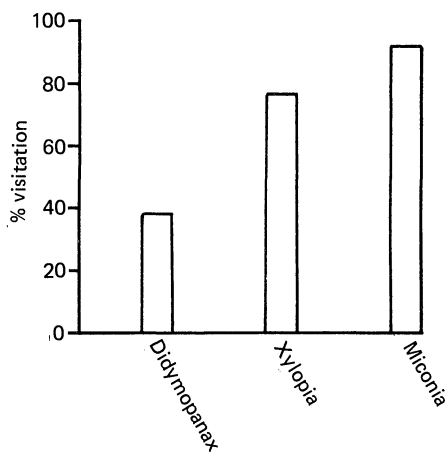

Figure 3. Percent of total time that all birds spent visiting *Didymopanax morototoni, Xylopia frutescens,* and *Miconia argentea* that was due to migrant visitation.

the order: Magnolia < Chestnut-sided < Bay-breasted < Tennessee Warblers (Table 2). These observations support and extend those of Morton (1980) and Greenberg (1981a).

The highly frugivorous Tennessee Warbler was the most common migrant on the area in March (Table 1, personal observation). Eastern Kingbirds also are highly frugivorous (Morton 1971, Martin, personal observation) and were extremely abundant (see above). Swainson's Thrush, Wood Thrush, and Grey Catbird are frugivorous during fall migration in the temperate zones (E. Stiles

Table 2. Percentage of observed foraging manoeuvres that were on fruit (N) for January and March of 1980 and 1981

	1980		1981	
	Jan.	Mar.	Jan.	Mar.
Magnolia Warbler	0(22)	0(11)	0(61)	0(29)
Chestnut-sided Warbler	8.3(168)	18.6(129)	0(103)	28.0(100)
Bay-breasted Warbler	16.1(236)	59.9(137)	7.0(57)	59.5(163)
Tennessee Warbler	25.6(39)	62.6(121)	—	81.6(98)

1980; Thompson & Willson 1978, 1979) and during winter in the tropics (Hilty 1980; Howe & DeSteven 1979; Leck 1972a, b) and all were common and more abundant in March than in January. Finally, Bay-breasted Warblers, Summer Tanagers, Great Crested Flycatchers, Northern Orioles, and Rose-breasted Grosbeaks were abundant during spring migration and were highly frugivorous. Thus, most migrants selecting my young second-growth site were highly frugivorous.

MIGRANT CONCENTRATION IN SECOND-GROWTH

Greenberg (1981b) showed that migrants use forest canopies. His study site was 70–100 years old and may have contained some vegetation components that were attractive to migrants but that are less abundant in older forest. Old forests contain pioneer and young forest elements due to creation of light-gaps (Brokaw 1982) but such elements are more abundant in younger forests. Thus, migrants may be more abundant in the canopy of Greenberg's (1981b) site than in older forest. More work similar to that of Greenberg (1981b) is needed in older forests to determine the importance of such habitats to migrants.

The results of my study clearly show that spring migrants were more concentrated in the understory (mist-net level) of my young second-growth than nearby old forest (Figures 1, 2). Furthermore, canopy migrants were at least as concentrated on my site as in the older second-growth canopy censused by Greenberg. I observed more canopy species than Greenberg (19 versus 10, respectively) and many were extremely abundant. The abundance of canopy migrants is documented by their abundance at canopy fruit trees (Figure 3).

FRUGIVORY AND SELECTION OF SECOND-GROWTH

The high degree of frugivory during migration may be a function of two factors. First, insect densities are minimal during the dry season (Buskirk & Buskirk 1976; Janzen 1973; Smythe 1974; Wolda 1977, 1978) and frugivory may be inversely related to insect abundance (Morton 1973, Stapanian 1982). Second, fruits are an efficient source for building energy reserves for migration (Fry *et al.* 1970, Mead 1966). Thus, frugivorous migrants should select sites

and habitats that provide profitable fruits, where profitability is a function of energy content of fruits, handling time (fruit to gape size), search time (food abundance), and behavioural considerations (i.e. predator avoidance, behavioural interference) (see Martin 1985).

Fruit size

Size of fruits may be a major factor affecting fruit and habitat selection (Martin 1985, Wheelwright 1985). Since migrants are small-gaped, then migrants should prefer areas with an abundance of small fruits. Seed size is generally smaller and seed crop size is generally greater in open than closed habitats (Salisbury 1942, 1974; Werner & Platt 1976). Consequently, fruits may be smaller, and fruit crops larger, in open habitats (also see Snow 1971). Tabulation of fruit sizes for bird-dispersed plants that were classified by Croat (1978) as being typical of young or old forests on Barro Colorado Island, Panama, shows that congeneric fruits are significantly smaller in young than old forests (Table 3). Furthermore, if all plant families typical of each habitat are included, the disparity in fruit size between habitats is even greater (Table 3). Most fruits typical of young forests are similar to or smaller than gape widths of common migrants, which vary from 0.6 cm for Tennessee Warblers to 1.3 cm for Wood Thrushes (Figure 4). However, most migrant gape widths are smaller than most fruits typical of old forests. Thus, migrants may, in part, select second-growth because of a greater probability of finding small fruits.

Fruit abundance

Numbers of fruits may be higher in second-growth than forest habitats because plants of open habitats generally have larger seed and fruit crop sizes (McDiarmid *et al.* 1977; Salisbury 1942, 1974), plants usually are more dense in young than in mature forest (Foster 1980, Hubbell 1979), and successional species may divert more energy to growth and leaf and fruit production (Foster 1980). I used tree census data from Knight (1975) to test the possibility that abundances of bird-dispersed fruit species, and particularly fruit species known to be eaten by migrants, are greater in young than old forest. Knight (1975) censused 13 forest sites on Barro Colorado Island, Panama and I classified 7 as young ($\leqslant$ 65 years old) and 6 as old ($\geqslant$ 80 years old) forest (Table 4). I calculated densities of tree species that produce bird-dispersed fruits and separated out those species known to be eaten by migrants (from Greenberg 1981a; Howe & DeSteven 1979; Leck 1972a, b; Morton 1971, 1980).

The results show that densities of bird-dispersed fruit species are indeed greater ($P < 0.05$, t-test) in young than old forest (Table 4). More importantly, the densities of fruit species eaten by migrants are markedly greater ($P < 0.02$, t-test) in young than old forest. Furthermore, fruit species eaten by migrants constitute a greater ($P < 0.02$, t-test) proportion of the available bird-dispersed fruit species in young than old forest.

All frugivorous migrants should not select young second-growth. Some

Table 3. Fruit size (in cm) of bird-dispersed plant species that are typical of young and old forests of Barro Colorado Island, Panama (from Croat 1978)

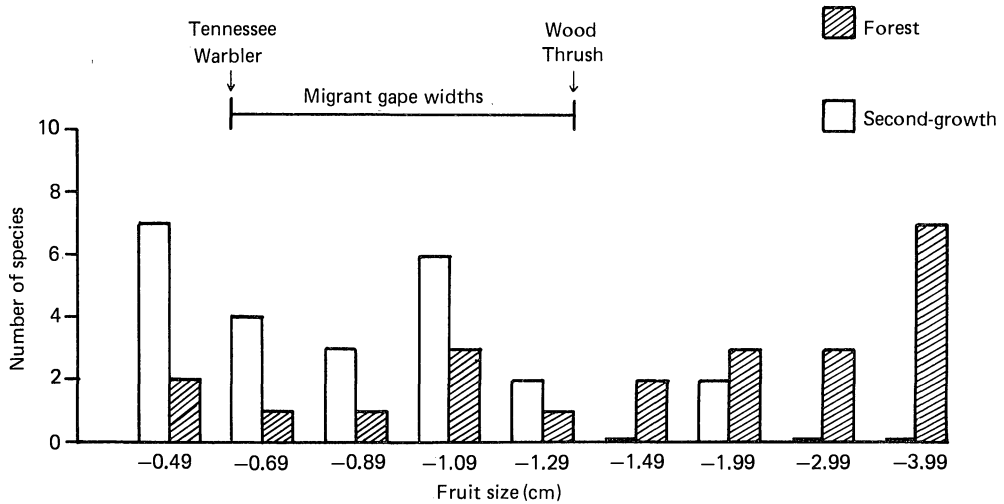| Young forest		Old forest	
Taxa	Fruit size	Taxa	Fruit size
Moraceae		Moraceae	
Ficus perforata	0.7	*Ficus tonduzii*	3.0
Melastomaceae		Melastomaceae	
Miconia argentea	0.6	*Miconia nervosa*	1.2
Annonaceae		Annonaceae	
Xylopia frutescens	1.2 × 0.7	*Xylopia macrantha*	3.75
Guatteria amplifolia	1.0	*Guatteria dumetorum*	2.5
		Anaxagorea panamensis	3.5
		Unonpsis pittieri	1.75
Olaceae		Olaceae	
Heisteria costaricensis	0.8	*Heisteria longipes*	1.0
Palmae		Palmae	
Cryosophila warscewiczii	1.5	*Bactris coloradonsis*	1.5
		Geonoma cuneata	0.8
Rubiaceae		Rubiaceae	
Psychotria carthagensis	0.6 × 0.3	*Psychotria granadensis*	0.4 × 0.4
P. brachybotyra	0.3 × 0.4	*P. capitata*	0.5 × 0.45
P. pubescens	0.55	*Hamelia axillaris*	0.55
Calycophyllum candidissimum	0.3 × 0.8		
Dilleniaceae		Dilleniaceae	
Doliocarpus dentatus	0.75	*Doliocarpus olivaceus*	1.75
D. major	1.15		
D. multiflorus	1.0		
Lauraceae		Lauraceae	
Nectandra purpurascens	1.5	*Nectandra cissiflora*	1.3
N. globosa	1.0	*Ocotea oblonga*	1.4 × 0.8
Ocotea cernua	1.5 × 1.0	*Ocotea skutchii*	5.0 × 2.25
Boraginaceae		Myristicaceae	
Tournefortia angustiflora	0.45	*Virola sebifera*	3.0
T. cuspidata	0.35	*V. surinamensis*	3.25
Heliotropium indicum	0.25	Melicaceae	
		Guarea multiflora	3.25
Malpighiaceae		*Trichilia cipo*	1.45
Byrsonima spicata	1.0		
Spachea membranacea	0.2 × 0.45	Burseraceae	
		Trattinickia aspera	1.0
Verbenaceae		*Protium panamensis*	2.8
Aegiphila panamensis	0.9 × 1.2	*P. costaricence*	1.75
Lantana camara	0.5	*P. tenuifolium*	2.5
Araliaceae		Guttiferae	
Didymopanax morototoni	0.5 × 0.9	*Toxomitopsis nicaraguensis*	2.0
Mean (±SE) fruit size			
Congeners only	0.83 ± 0.092	1.76 ± 0.347*	
All families	0.77 ± 0.074	1.96 ± 0.210*	

*P < 0.01.

Figure 4. Numbers of plant species per fruit size class in young forest versus old forest (see Table 4) and relative to the range of gape widths of migrant bird species.

pioneer fruit species are present in forests (see below) and fruiting lianas occur in forest canopies. Increased abundance of migrants in second-growth may lead to increased behavioural interference, exploitation competition, and attraction of predators, thereby decreasing profitability of these sites (Martin 1985). Consequently, some frugivorous migrants, or all frugivorous migrants at some times, should use forest and canopy fruits, as observed by Greenberg (1981b).

Second-growth is a term applied to forests of a wide range of ages. All 13 sites studied by Knight (1975) were second-growth, but clearly older second-growth forests can differ markedly from younger forests in their suitability to migrants. Many plant species typical of young forest (i.e. Table 4) are pioneer

abundances of such species decline with age of the forest, although they are not lost altogether because they will colonize light gaps (Brokaw 1982, Foster & Brokaw 1982). Of course, the forests can undoubtedly be too young as well: i.e. forests less than 5 years old may not have had enough time to establish an abundance of bird-dispersed fruit species. Thus, while the term 'second-growth' can encompass forests from 1 to 200 or more years old, this range includes a marked gradient in abundance of young forest plant species. For many frugivorous migrant species these young forest elements may well be most important to habitat selection during spring migration. Future considerations of the importance of second-growth forests to migrants should include age of the forest since old second-growth can differ from young second-growth in suitability to migrants.

Results from this study suggest that migrant species that concentrate in young lowland second-growth forest during spring migration may do so because (1) most are highly frugivorous during this period, (2) fruits supply high energy

Table 4. Densities (numbers/ha) of all plant species that produce fruits that are bird-dispersed (*Total fruit density*), plus densities for the subset that are known to be eaten by migrants (*Migrant fruit density*) and the percentage of total bird-dispersed fruit plants constituted by plants that produce fruits eaten by migrants. Plant species densities are calculated from Knight (1975) for 13 sites of varying ages

Site	Approximate age	Total fruit density	Migrant fruit density	Percent of total fruits
		Young forest		
1	15	1407	894	63.5
2	50	1079	648	60.1
3	65	1140	709	62.2
4	65	1894	1231	65.0
6	65	1226	434	35.4
12	50	1457	908	62.3
13	65	1724	1067	61.9
X̄		1418.1	841.6	58.6
SE		114.53	101.28	3.91
		Old forest		
5	80	1130	465	41.2
7	100–200	1420	788	55.5
8	100–200	798	398	49.9
9	100–200	1228	459	37.4
10	100–200	704	220	31.3
11	100–200	739	256	34.6
X̄		1003.2	431.0	41.6
SE		121.35	82.78	3.81

for migratory needs, and (3) young second-growth supplies a greater abundance of small fruits than older forests.

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