Duration of visits to fig trees of foraging avian frugivores in the Philippines

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Besuchsdauer auf Feigenbäumen nahrungssuchender Fruchtfresser der Philippinen. – Die Zeit, die fruchtfressende Vögel auf fruchtenden Bäumen verbringen, bestimmt die Effizienz dieser Besucher als Samenverbreiter. Die Aussicht eines verzehrten Samens, unter den Elternbaum zu fallen, wo die Samensterblichkeit erhöht ist, nimmt mit der Besuchsdauer zu. Qualitative Modelle von Howe (1979) sowie Pratt & Stiles (1983) sagten voraus, dass relativ hohe Körpergröße und Tarnfarbigkeit Vögel weniger feindanfällig machen und ihnen so ermöglichen, länger in einem Fruchtbaum zu verweilen (Körpergrößen- und Tarnungshypothese). Weiter sollten auch eng auf Früchte spezialisierte Vögel länger bleiben, da sie nicht woanders Nahrung suchen müssen, um ihren Speisezettel zu erweitern (Nahrungshypothese). Wir stellen Daten über die Besuchsdauer elf fruchtfressender Vogelarten auf Feigenbäumen auf Nord-Negros, Philippinen, vor. Die Ergebnisse sind vereinbar mit der Körpergrößen-, Tarnungs- und Nahrungshypothese. Doch erscheint die Besuchsdauer zusätzlich durch den Zusammenschluss mehrerer Arten mit nichtfruchtfressenden beeinflusst (Schwarmhypothese), so dass der Schwarmzusammenhalt die Besuchsdauer begrenzt. Wir erörtern die Angepasstheit des Schwarmverhaltens und machen die neue Annahme, dass der Zusammenhalt die Effekte von Feindkonfusion und Risikoverdünnung erhöht; ferner, dass den Schwarmmitgliedern durch kurze und in Raum und Zeit unvorhersagbare Besuche ihrer Nahrungsbäume ein zusätzlicher Vorteil dadurch entsteht, dass diese Feinden eine wenig verlässliche Beutequelle verheißen. Schließlich erlaubt die Betrachtung der Besuchsdauer, die Qualität der fruchtfressenden Arten als Samenverbreiter in neuem Licht zu sehen.

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Abstract

The amount of time fruit-eating birds spend in fruiting plants is an important aspect of behavior that affects a bird's effectiveness as a seed disperser. The chance that an ingested seed will be deposited beneath the parent tree where it suffers higher mortality increases with visit length. Qualitative models proposed by HOWE (1979) and PRATT & STILES (1983) predicted that relatively large body size and cryptic plumage should make birds less vulnerable to predation and enable them to spend more time in fruiting trees (body size and crypsis hypothesis). Furthermore, birds specialized on a narrow fruit diet should stay longer in fruiting plants because they do not have to leave plants to diversify their diet (diet hypothesis). We present data on duration of visits of eleven frugivorous bird species to fig trees of North Negros, Philippine Islands. The results reported here are compatible with the diet, body size, and crypsis hypothesis. However, it appears that visit length among these species is additionally confounded by their jointly traveling with non-frugivorous species (flocking hypothesis), and that the resulting flock cohesion may constrain visit duration. We discuss the adaptive nature of flocking behavior and propose first, that flock cohesion enhances the antipredation confusion and risk dilution effects promoting their permanence; second, that by paying only short and erratic visits in space and time to their food plants, flocks benefit additionally by making these trees a less predictable food patch from the predator's perspective. Finally, visit duration permits one to shed new light on the dispersal quality of avian frugivores in the context of their visit length.

Introduction

The behavior of frugivorous birds has important consequences for the selection of fruit traits of many plant species for which birds act as seed dispersers (e. g., PRATT & STILES 1983, HOWE 1986, WHEELWRIGHT 1991, GREEN 1993). The places where frugivores move and feed, their fruit-handling techniques, the frequency of their visits to the food plant, and the distances they travel after leaving the tree have been proposed to influence where seeds are dispersed, and hence influence the reproductive success of bird-dispersed plants (e. g., LEVEY 1987, MURRAY 1988). One major aspect of the behavior of fruit-eating birds that affects their suitability as seed dispersers is the amount of time they spend in fruiting plants during a foraging visit. The longer a bird's visit lasts, the more seeds will be deposited by defecation or regurgitation beneath the parent tree. These seeds and seedlings presumably (JANZEN 1971, CLARK & CLARK 1984, HOWE 1986, AUGSPURGER 1988) or actually (HOWE et al. 1985) suffer higher mortality. Shorter visits increase the likelihood that birds will carry seeds away from the parent plant.

Several hypotheses have been developed to predict the duration of visits by avian frugivores to their food plants. HOWE & ESTABROOK (1977) proposed that visit length should increase with the number of ripe fruits available. Animals should stay longer in „good" food patches. This argument holds for situations in which the bird's behavior is solely geared to its nutritional needs (HOWE 1979). However, fruit-rich patches attract not only fruit-eaters but also their predators, thus being a rich and predictable food patch from a predator's perspective (HOWE 1979). Howe's model predicts that birds that are small relative to their predators are especially vulnerable to predation and should therefore spend less time in the fruiting tree than larger, less vulnerable species (body size hypothesis). Extending Howe's emphasis on predation risk PRATT & STILES (1983) reasoned that cryptically colored birds are less subject to predation and should therefore stay longer in fruiting trees than more conspicuously colored birds (crypsis hypothesis). Also, frugivores with digestive adaptations specialized on a diet consisting of fruit should spend more time in the food plant than facultative frugivores that have to change their foraging sites more often to balance their diet (diet hypothesis). Finally, PRATT & STILES (1983) proposed that flocking species should pay only short visits to fruiting trees (flocking hypothesis), although they did not give any reasons why. Whereas they found positive evidence for the crypsis and diet hypothesis in their investigation, PRATT & STILES did not address the impact of flocking behavior on visit length.

Most hypotheses advanced to explain the selective advantage of flocking involve either reduced predation on or an increased food intake by the birds. Birds foraging in flocks may benefit from the „beater effect", i. e., prey that is flushed and missed by one bird can be grabbed by another (GILL 1994). Group foraging helps birds locate food by social facilitation because members can join successful individuals at rich clumps or concentrate their search efforts nearby (MURTON 1971, KREBS et al. 1972, KREBS 1973). Further, flocking behavior helps to evade predation by creating a dilution and/or confusion effect and providing group members benefits from one another's vigilance for danger (for reviews see POWELL 1985, KREBS & DAVIES 1993).

Flocking bird species, especially in tropical mixed-species flocks, are reported to move at fast and constant travel rates through the forest (e. g., PARTRIDGE & ASHCROFT 1976, POWELL 1979, HUTTO 1988, own observations). But despite the multitude of hypotheses about the adaptive significance of flocking behavior only little is said on how flocking affects the travel speed and thus the visit length of its members at particular food resources. E. g., POWELL (1974) proposed that in situations of thinly and/or homogeneously distributed food resources, feeding groups have to progress at a sufficient pace to avoid feeding competition.

Our study compares visit durations of avian frugivores in fruiting fig (*Ficus* sp.) trees on the Philippine island of Negros. We consider the results in the context of hypotheses related to body size (HOWE 1979), crypsis, and diet (PRATT & STILES 1983). We further investigate if visit length differs between flocking and less gregarious frugivorous bird species (flocking hypothesis) and discuss the adaptive nature of flocking behavior. Finally,

Table 1. Ecological and morphological characteristics of the eleven bird species observed feeding most frequently on figs in Negros.
Tab. 1. Ökologische und morphologische Kennzeichen der elf als Feigenfresser auf Negros am häufigsten beobachteten Vogelarten.

Bird species	Range of body mass[1]	General coloration	Diet	Foraging group size and flocking behavior
Non-Passeriformes				
Yellow-breasted Fruit Dove *Ptilinopus occipitalis*	185.0 – 278.0 g	green above yellow and gray below --> fairly cryptic	obligately frugivorous	foraging solitarily or in small groups
Pink-bellied Imperial-Pigeon *Ducula poliocephala*	510.0 – 564.0 g	green above gray below --> fairly cryptic	obligately frugivorous	foraging solitarily or in small groups
Hanging Parakeet *Loriculus philippensis*	32.3 – 39.5 g	green --> fairly cryptic	obligately frugivorous and granivorous	foraging solitarily or in small groups
Crimson-breasted Barbet *Megalaima haemacephala*	32.0 – 47.0 g	green above green and yellow below --> fairly cryptic	chiefly fruits	foraging solitarily or pairwise
Passeriformes				
Philippine Bulbul *Hypsipetes philippinus*	32.0 – 43.6 g	brown --> intermediate crypsis	fruits, invertebrates	foraging in small to medium sized single-species flocks
Stripe-headed Creeper *Rhabdornis mystacalis*	22.4 – 31.5 g	brown above white and brown below --> intermediate crypsis	chiefly invertebrates, supplementing diet with fruits	foraging primarily as a member of mixed-species flocks

Species	Body mass	Coloration / crypsis	Diet	Foraging behaviour
Plain-headed Creeper *Rhabdornis inornatus*	31.6 – 47.2 g	brown above gray below --> intermediate crypsis	chiefly invertebrates, supplementing diet with fruits	foraging primarily as a member of mixed-species flocks
Verditer Flycatcher *Eumyias panayensis*	17.7 – 21.7 g	blue --> least cryptic	chiefly invertebrates, supplementing diet with fruits	foraging primarily as a member of mixed-species flocks
Bicolored Flowerpecker *Dicaeum bicolor*	7.8 – 10.0 g	black glossed with blue above, white below --> least cryptic	fruits, nectar, invertebrates	foraging in medium sized single-species flocks, but primarily as members of mixed-species flocks
Orange-breasted Flowerpecker *Dicaeum trigonostigma*	5.9 – 8.4 g	dark blue above yellow and red below --> least cryptic	fruits, nectar, invertebrates	foraging in medium sized single-species flocks, but primarily as members of mixed-species flocks
Mountain White-eye *Zosterops montanus*	9.4 – 12.6 g	yellowish olive green above yellow and white below --> intermediate crypsis	chiefly invertebrates, supplementing diet with fruits	foraging in medium sized to large single-species flocks, sometimes as members of mixed-species flocks

[1] Data on body mass are taken from the CRC handbook of avian Body Masses (ed. by DUNNING, 1993)

we address the consequences of visit length for seed dispersal and attempt to assess the disperser quality of the avian frugivores under study.

Study area and Methods

We conducted this study in an upland tropical rainforest near Patag, Silay City district, on the island of Negros (10°41'N, 123°11'E), Philippines. This area is located on the northwest slope of Mt. Mandalagan at an average elevation of 1,000 m a. s. l. within a 24 km² montane oldgrowth forest (HAMANN in CURIO 1996). Research was conducted during the rainy season, which in this region lasts from May to mid January.

We made observations from mid-August through the end of November 1996. A total of 149 hours of observation (by M. H.) were spent in similar proportions at three individual trees of the genus *Ficus* during the peak of their fruiting periods. Over 75% of all observations took place between 06:00 and 11:00 and between 14:00 and 18:00. During the study, we recorded 15 species of birds feeding on fig fruits. Here, we focus on 11 of those species that together accounted for the vast majority of all observed visits by birds to fig trees (Table 1). All 11 bird species were residents for Negros. For each avian visit to a tree we recorded the species, visit length scored in 5 min-time-classes (see below), and fruit handling method (e. g., swallowing fruit whole, pecking parts out of it, dropping whole fruit, removing some pulp and dropping the remains). Because we could not identify birds individually, we could not control for repeat visits. Therefore, we ascribed each individual visit to a different bird. Quite often the moment when birds came in and/or flew out could not be detected because of the surrounding vegetation. We assumed therefore, that a bird's presence or absence was noticed soon after its entry into and/or its departure from the tree under scrutiny. Thus, we ranked the duration of a bird's visit into the corresponding 5 min-time-class. To be conservative, we decreased the impact of outliers by pooling all visits lasting longer than 60 min into the time class '> 60 min' (see Fig. 1). Differences in visit length between bird species were tested with the non-parametric Mann-Whitney U-Test. To compensate for the multitude of comparisons, a Bonferroni correction (SACHS 1988) was applied to adjust significance level (P_{adj}).

The three focal trees belonged to three different *Ficus* species, but they varied little in growth form (all were strangler figs) and crop size (personal judgement). Two of the trees had small (10.5 and 11.2 mm max. width), red fruits, whereas the fruits of the third were relatively large (19.4 mm mean max. width) and orange. We determined fruit size by measuring the maximum diameter of each of 17 to 25 fruits for each tree. To test the influence of fruit size and color on visit duration we applied a multiple regression analysis with stepwise variable selection on the data of four bird species for which reasonable numbers of observations in all three trees were obtained.
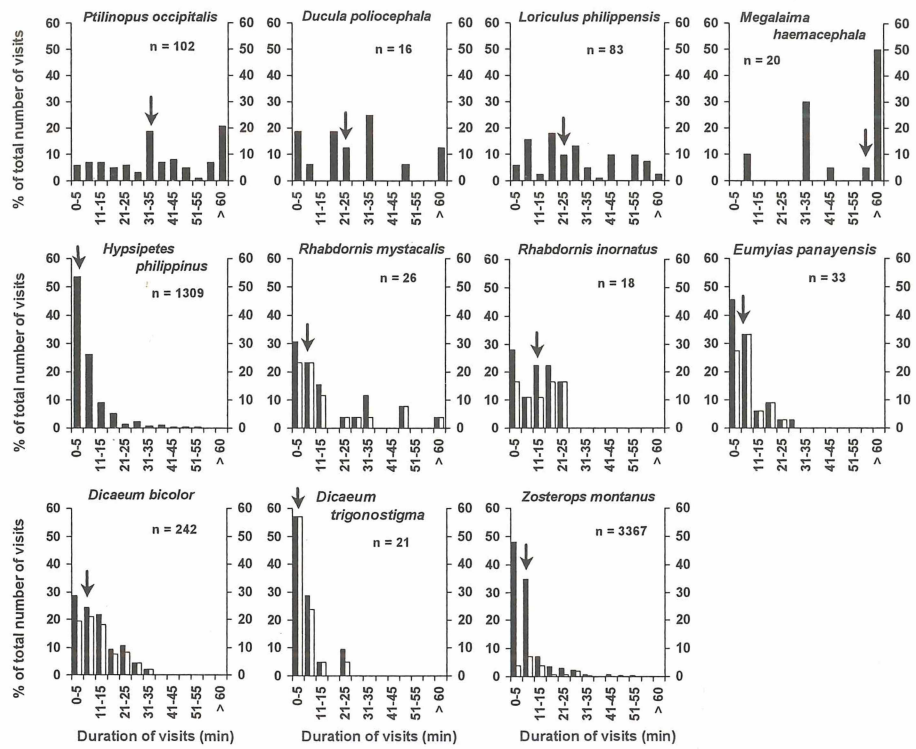
Fig. 1. Duration of visits to fruiting fig trees by various avian frugivores in the Northern Negros Forest Reserve. Black bars present the percentage of total number of visits by each frugivore species that lasted as long as the corresponding 5 min-time-class. White bars indicate the proportion of visits within a 5 min-time-class in which a bird was a member of a mixed-species flock. Arrows indicate time-classes in which the cumulative percentage of all shorter visits sums up to 50%. Data are pooled from three fig species, with one individual each. For further ecological and morphological characteristics of the frugivores see Table 1.

Fig. 1. Dauer des Aufenthalts fruchtfressender Vögel auf fruchtenden Feigenbäumen in der North Negros Forest Reserve. Schwarze Säulen = Prozentuale Verteilung der Besuchsdauer. Weiße Säulen = Anteile von Besuchen als Mitglied eines Mischschwarms. Pfeile kennzeichnen Zeiten, bis zu denen sich die kürzeren auf 50% aller Besuchsdauern summieren. Daten von drei Bäumen jeweils einer Art. Weitere ökologische und morphologische Kennzeichen der Arten siehe Tab. 1.

Statements made in this paper about the relative degree of crypsis of plumage color have to rely on subjective judgment and are inferred from the perspective of aerial predators (hawks). The most common raptors regularly recorded during the study period were the

Crested Goshawk (*Accipiter trivirgatus*) and the Serpent Eagle (*Spilornis cheela*). Both species are forest-dwelling raptors preying regularly on small to medium sized birds (GAMAUF et al. 1998). Whereas the Crested Goshawk hunts in the forest interior adopting a sit-and-wait strategy combined with short pursuit flights, the Serpent Eagle hunts above the forest canopy, relying on the soaring mode of hunting or launching attacks from perches in tree tops (GAMAUF et al. 1998).

Results

Table 1 presents the ecological and morphological characteristics of the eleven focal bird species, based on published data (DELACOUR & MAYR 1946, Baptista et al. 1997) and personal observations. The focal bird species vary in foraging group size, flocking behavior and in the traits highlighted by HOWE (1979) and PRATT & STILES (1983). All non-passerines were obligate or at least primary frugivores, and foraged alone or in small groups. The passerines in this study were only partially frugivorous and diversified their diet to different degrees by foraging on arthropods. While foraging, passerines often joined conspecific and/or mixed-species flocks. In our study the most cryptic species likely were the two fruit pigeons *Ptilinopus occipitalis* and *Ducula poliocephala*, further *Loriculus philippensis*, and *Megalaima haemacephala*, whose predominately green plumages blended well with the foliage. The brown plumage of *Rhabdornis* spp. and *Hypsipetes philippinus* matched the color of dead leaves or bark, presumably making birds perched in green foliage less cryptic. The remaining bird species (except *Zosterops montanus*) were more conspicuously colored and presumably not as well camouflaged as the former species. Yet even colorful plumages can appear relatively inconspicuous when birds forage in the shade of the foliage.
Except for *Rhabdornis* species and *Eumyias panayensis* all birds were seen to feed on fruits of all three *Ficus* trees. Fruits of the large-fruited fig species were presumably too large for the *Rhabdornis* species and *Eumyias panayensis* which always swallowed fruits whole. They plucked fruits from a perch or, in the case of *Eumyias*, took them on the wing. Conversely, birds of the genera *Dicaeum, Zosterops, Hypsipetes*, and *Loriculus* pecked pieces of flesh out of those fruits that were too large to be swallowed whole. Their large gape sizes allowed the Columbidae to swallow fruits of all fig species whole. The large-gaped *Megalaima haemacephala* plucked fruits whole and mashed them with its mandibles. All avian frugivores of this study can be considered potential dispersers for the fig species. The percentage of treated fruits dropped whole was for each bird species less than 20% and did not differ between fruit sizes. As a rule, fruits were consumed completely, even after prior handling. Bird species ingesting only parts of a fig, in which the rest was left on the tree or dropped, might still act as dispersers since even small pieces of flesh should contain some of the many tiny seeds inside. On very rare occasions, the *Rhabdornis* species, *Dicaeum bicolor* and *Hypsipetes*

philippinus carried a fruit in their bills away from the tree and out of sight of the observer. We never observed that seeds were regurgitated shortly after ingestion of fruit, nor that seeds were separated from the pulp and dropped under the tree.

No regression model analyzing the influence of fruit size and color on visit length could be fitted for *Ptilinopus occipitalis* (Multiple Regression: $b'_{(color)}$ = 0.29, P = 0.67; $b'_{(size)}$ = 0.57, P = 0.62) and *Megalaima haemacephala* (Multiple Regression: $b'_{(color)}$ = 0.2, P = 0.32; $b'_{(size)}$ = 0.19, P = 0.76). For *Dicaeum bicolor* (Multiple Regression: $b'_{(color)}$ = 0.25, P < 0.001; $b'_{(size)}$ = 0.52, P < 0.0001) and *Zosterops montanus* (Multiple Regression: $b'_{(color)}$ = 0.11, P < 0.001; $b'_{(size)}$ = 0.34, P < 0.001) we found a highly significant relationship of fruit size and color to visit duration, indicating prolonged visits in the fig tree with large and orange fruits. However, all visits of *Dicaeum bicolor* to this tree lasted less than 25 min, and 83.4% of all visits of *Zosterops montanus* less than 20 min, so that fruit size and color had, though significant, only a minor overall impact on the distribution of visit duration for the bird species considered (see Fig. 1). Therefore, we assume that our comparative approach is not severely influenced by the major interspecific differences in the fruit characteristics of the focal trees.

The distribution of visit lengths by passerine bird species is highly skewed toward shorter visits (Fig. 1). Half of the visits made by each species (except *Rhabdornis inornatus*, 39% $\leq$ 10 min) lasted less than 10 min, around 75% of the visits (except *Rhabdornis mystacalis*, 58% $\leq$ 20 min) were less than 20 min.

The chiefly frugivorous non-passerines often stayed much longer, so that the distribution of their visit lengths follows a rather platykurtic pattern. Extended visits were observed: two visits of *Ducula poliocephala* were around 1 ½ h; nine visits of *Ptilinopus occipitalis* lasted around 2 h, and two visits more than 3 ½ h. Half of the visits of *Megalaima haemacephala* lasted more than 1 h, with four visits lasting around 2 h, and two visits more than 4 h. These long visits included periods of rest between foraging bouts. In the Columbidae, periods of high foraging activity alternated with long periods of rest. In contrast, *Megalaima haemacephala* displayed a relatively cryptic behavior throughout. Moving slowly, it looked for fruits, often interrupting its search by periods of rest, in which it sometimes scanned the environs, probably for further food items. Conversely, all passerine birds were actively searching for food throughout their visits.

These results were confirmed by statistical comparisons. Each non-passerine species spent significantly more time per visit to a fig tree than did each passerine species (Mann-Whitney U-test, $P_{adj.}$ < 0.001) with the exception of *Ducula poliocephala*, which did not differ significantly from *Rhabdornis mystacalis*. Among the passerines, the cryptic *Rhabdornis* species stayed significantly longer per visit than the less camouflaged *Zosterops montanus* ($P_{adj.}$ < 0.01). However, both *Rhabdornis* species also stayed significantly longer than *Hypsipetes philippinus* of similar cryptic coloration ($P_{adj.}$ < 0.01).

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Discussion

Visit duration, functional explanation, and a new hypothesis
The results of this study are compatible with the predictions that diet, crypsis, and body size of frugivores tend to influence how long foraging birds spend in fruiting fig trees. HOWE's (1979) model that larger species are less vulnerable to predation and should thus spend more time in food trees may apply to the fruit pigeons, which were by far the largest species in this study. But because the fruit pigeons were also the most cryptic birds, body size may not have been the only determinant of visit length. The role of crypsis in lowering predation risk (PRATT & STILES 1983) may be more important since the smaller, but similarly cryptic *Loriculus philippensis* and *Megalaima haemacephala* also stayed long times visiting. Also, the more camouflaged *Rhabdornis* species tended to spend more time per visit than the other passerines, but differences in visit lengths were only slight (see cumulative percentage of visit lengths, Fig. 1). Presumably the species' brown plumage is rather an adaptation to searching for arthropods on the bark of trees and other factors, such as the need for a balanced diet and/or flocking behavior (see below), may mainly affect visit length of *Rhabdornis* in fruiting plants. The same reasoning may also account for the short visits of the intermediately cryptic passerines *Zosterops montanus* and *Hypsipetes philippinus*.
As hypothesized by PRATT & STILES (1983), all bird species in this study with extended visit duration were obligate or primary frugivores. Their specialized digestive apparatus allows them to sustain themselves exclusively on a diet of fruits so that they can afford to remain in a fruit-bearing plant between feeding bouts instead of searching for other food. Furthermore, after having consumed a large quantity of fruit, it may be more efficient to digest the bulky meal before setting out on some energetically demanding activity (PRATT & Stiles 1983). Finally, the lower metabolic rates of chiefly frugivorous birds were identified by FAABORG (1977) as a possible reason for their lower levels of activity relative to passerines, which may provide yet another reason for long visits. On the other hand, the insectivorous fruit-eating birds in this study stayed in the fruit tree only long enough to do some foraging, and left after a relatively short time. The nutritional inadequacy of fruits may force partially frugivorous birds to forage elsewhere for invertebrates or for fruits providing other nutrients.
However, it appears that besides a mixed diet and the lack of crypsis visit length is additionally confounded by flocking behavior, since the passerines of this study often joined single-species and/or mixed-species flocks, which travelled through the canopy in a uniform pattern. Before discussing the impact of flocking on visit length, we should consider our observations of grouping behavior in the context of the hypotheses proposed to explain the adaptedness of flocking behavior. Two main advantages, i. e., facilitation of foraging and protection from predation, have been ascribed to flocking behavior. By definition the „beater effect" may only apply to feeding assemblages foraging on arthropods (GILL 1994). However, we never observed that the frugivores

of single-species or mixed-species flocks were feeding on something else than fruits when visiting the fig trees. Hence, only the insectivores could have profited from any „beater effect" of the frugivores. However, we had the impression that the insectivorous members of mixed-species flocks stayed for even shorter periods in the fruiting tree and left them earlier. Thus, the frugivores apparently followed the insectivores and not vice versa.

Members of both single- and mixed-species feeding associations may profit by learning from one another about the location and nature of potential feeding places, as long as they are interested in the same type of food (KREBS et al. 1972, KREBS 1973). While this argument may account for the single-species assemblages of this study or for specific mixed feeding associations exploiting the same food, it does not provide a clear explanation why the frugivores of this study also coalesce with obligately insectivorous species. The latter problem may be resolved by hypotheses suggesting that flocking behavior decreases the risk of predation by creating a risk dilution and/or confusion effect or by increasing the overall vigilance in the group (for a review see POWELL 1985, KREBS & DAVIES 1993). This reasoning could account for both single- and mixed-species flocks of our study.

How could flocking affect visit length to fruiting trees? If flocking provides protection against predation or facilitates social learning, it should increase visit length because birds in a flock feel more secure or can exploit a food resource more effectively. The short visit lengths in single-species flocks observed in this study may then be due to the need to diversify their diet and flocking would have no direct impact on visit length. In mixed-species flocks, however, each frugivorous species presumably has a differently predisposing schedule by which to balance its nutritional demands. Nonetheless they moved together, and even travelled with uniform speed with insectivorous species which utilized totally different types of food. Therefore, we propose that in order to benefit from flocking, the birds coordinated their visit length with those of other flock members. Studies on mixed-species flocks of birds (PARTRIDGE & ASHCROFT 1977, RABENOLD & CHRISTENSEN 1979, HUTTO 1988) and primates (TERBORGH 1990) could demonstrate that there is considerable adjustment in the travel pace by participants in order to stay with the flock. BUSKIRK (1978) showed that in rainforests arthropods may be an evenly and thinly distributed food source that insectivores in mixed flocks exploit while traveling at some nearly constant speed to avoid feeding competition. The latter should not exist for frugivores exploiting a usually abundant food source. The fact that the obligate insectivores of this study (e. g., *Rhipidura cyaniceps*, *Parus elegans*, *Dendrocopus maculatus*, *Phylloscopus* sp.) included fig trees during foraging is best understood by their tendency to stay together in as large flocks as possible. Conversely, they did not compromise on their regular travel routine, so that the frugivores had to follow suite to reap the benefits of flock membership. The observation that the frugivores left the tree with birds of different diets after a relatively short time, although their clumped and superabundant fruit source was by far not depleted, suggests that benefits of flocking behavior were over-

riding. By thus staying together flock members enhance the confusion and risk dilution effects inherent in flocking. Furthermore, we propose that the uniformly quick travel pace results in short, erratic visits to fruit trees that lessen the probability of a predator encountering prey in any given fruiting tree and, thus, render hunting success less predictable in space and time (*erratic visitation hypothesis*). However, the diverse benefits of flocking are not mutually exclusive. It is conceivable that members of mixed-species flocks avoid predation by confusion, risk dilution *and* erratic visitation, but at the same time the insectivorous participants may profit from the insects flushed by the frugivores, whereas the mixed-diet frugivores benefit by following the insectivores because they will guide them to locations of arthropod food.

We are aware that the protocol of our study is not designed to compare directly the *erratic visitation hypothesis* with the several other established hypotheses to explain flocking (see Introduction). Yet it provides a new dimension to the adaptedness of mixed-species flocks and, thus, a new focus for future research. Information on the behavior of flocking birds in fruiting and non-fruiting trees, on differences in visit lengths between solitary versus flocking individuals of flock-forming species or on differences between individuals in single-species versus mixed-species flocks would be necessary to see if individuals modify their behavior in the company of other individuals. Furthermore, experimental studies (e. g., DOLBY & GRUBB 1998) are required to distinguish if flocking mainly functions as predator avoidance or for other reasons. That birds in our study site are subject to predation is born out by a *Ptilinopus occipitalis* being seized upon leaving the fig tree by a *Hieraaetus kienerii* that had perched in ambush nearby (SCHABACKER, pers. comm.).

How well frugivores qualify as seed-dispersers
How long a bird stays in a fruiting tree has important implications for seed dispersal. Visit duration at a tree determines whether a bird is likely to disperse the swallowed seeds or deposit them as fecal dropping or regurgitated pellet beneath the parent tree. According to our observations, we conclude that typical frugivores tend to be poorer dispersers because they exploit a fruiting tree by long visits, whereas the partially frugivorous passerines stay only for short periods. The latter species often join fast-travelling mixed- and/or single-species flocks which cover wide ranges, thus carrying seeds away from a parent tree and eventually depositing them at more appropriate germination sites (see Introduction).

However, it is evident that visit length becomes a clue to dispersal quality of a given bird species only when it is related to the time period a bird needs to expel the ingested seed. LEVEY & GRAJAL (1991) found that small seeds are retained longer in the gut than larger or regurgitated ones, and might travel farther from the parent plant. Therefore, with regard to visit length a given bird is not inherently a good or poor disperser (LEVEY 1987), since the resultant seed shadow may depend on seed size, fruit traits, and the bird's favored technique of seed ballast elimination (JOHNSON et al. 1985). To

answer questions about dispersal quality it is necessary to study specifically gut passage. There is evidence that in order to minimize the problem of a limited gut volume and to meet nutritional requirements the digestive system of highly frugivorous birds is adapted for fast fruit processing, thus obtaining short gut transit times (JOHNSON et al. 1985, LEVEY 1986, WORTHINGTON 1989, KARASOV & LEVEY 1990). Fruit pigeons of the genera *Ducula* and *Ptilinopus* have short and wide guts which allow them to process bulky fruits fairly quickly (CADOW 1933, BOWMAN 1994), whereas for the partially frugivorous *Dicaeum hirundinaceum* and *Zosterops lateralis* KEAST (1958) reports passage times for mistletoe seeds of 25-60 min and 30-80 min, respectively; and *Hypsipetes philippinus* was found to process seeds of nine tree species in 8 to 27 min (arithmetic means, SCHABACKER 2000). From the bird's perspective, passage rates such as these are likely more suitable for a high-protein and/or lipid diet than for a fruit diet being low in nutrient content but high in bulk (LEVEY & GRAJAL 1991). If these data can be generalized and related to the observed visit lengths of this study, it appears that the chance for chiefly frugivorous birds to deposit seeds below the parent tree is higher than in the partially frugivorous passerines. Furthermore, there is evidence (COLLAR 1997, BAPTISTA et al. 1997) that members of the Psittacidae and of the genera *Ducula* and *Ptilinopus* may harm or even destroy seeds while processing fruits. Hence, these groups may be poorer dispersers for yet another reason (but see BÖHNING-GAESE et al. 1995). From the plant's perspective, the obligate fruit-eaters may therefore not be the best seed-dispersers.

Acknowledgments

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