



Bird Assemblage and Visitation Pattern at Fruiting *Elmerrillia tsiampaca* (Magnoliaceae) Trees in Papua New Guinea

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ABSTRACT

Most tropical trees produce fleshy fruits that attract frugivores that disperse their seeds. Early demography and distribution for these tree species depend on the effects of frugivores and their behavior. Anthropogenic changes that affect frugivore communities could ultimately result in changes in tree distribution and population demography. We studied the frugivore assemblage at 38 fruiting *Elmerrillia tsiampaca*, a rain forest canopy tree species in Papua New Guinea. *Elmerrillia tsiampaca* is an important resource for frugivorous birds at our study site because it produces abundant lipid-rich fruits at a time of low fruit availability. We classified avian frugivores into functional disperser groups and quantified visitation rates and behavior at trees during 56 canopy and 35 ground observation periods. We tested predictions derived from other studies of plant–frugivore interactions with this little-studied frugivore assemblage in an undisturbed rain forest. *Elmerrillia tsiampaca* fruits were consumed by 26 bird species, but most seeds were removed by eight species. The most important visitors (Columbidae, Paradisaeidae and *Rhyticeros plicatus*) were of a larger size than predicted based on diaspore size. Columbidae efficiently exploited the structurally protected fruit, which was inconsistent with other studies in New Guinea where structurally protected fruits were predominantly consumed by Paradisaeidae. Birds vulnerable to predation foraged for short time periods, consistent with the hypothesis that predator avoidance enhances seed dispersal. We identified seven functional disperser groups, indicating there is little redundancy in disperser groups among the regular and frequent visitors to this tropical rain forest tree species.

Key words: Columbidae; frugivore; *Gymnophaps albertisii*; Paradisaeidae; seed dispersal; tropical wet forest.

MOST TROPICAL TREE SPECIES produce fleshy fruits and rely on frugivorous vertebrates for seed dispersal (Snow 1981, Howe 1993, Herrera 2002). Both the composition of the visiting frugivore assemblage and the behavior and visitation pattern of frugivores affect the number of seeds removed and the quality of dispersal (Howe 1977, Bleher & Böhning-Gaese 2001, Westcott *et al.* 2005). Anthropogenic factors, such as hunting or habitat fragmentation, that alter the frugivore community can have cascading effects on seed dispersal, forest structure, and regeneration patterns (Hamann & Curio 1999, Meehan *et al.* 2002, Moran *et al.* 2009). To understand the potential effects of a modification of the frugivore community on the dispersal success of a tree species, it is essential to study tree species-specific frugivore assemblages in large undisturbed reserves with a complete coterie of frugivores (Corlett 1998, Githiru *et al.* 2002, Marsden *et al.* 2006).

Many factors influence frugivore use of different tree species, such as fruit crop size, fruiting phenology, and the size, structure, and chemical composition of the fruit (Mack 1993, Voigt *et al.* 2004, Saracco *et al.* 2005). These factors also influence the behavior of frugivores within a fruiting tree, with important consequences for dispersal success (Moermond & Denslow 1983, Levey 1987, Wheelwright 1993, Dennis & Westcott 2006). For example, short foraging visits that may be caused by the risk of predation in a tree

species with abundant fruits are more beneficial for seed dispersal than longer visits that result in defecation or regurgitation of indigestible seeds in the high-mortality zone underneath the parent tree (Howe 1979, Howe & Vande Kerckhove 1979, Pratt & Stiles 1983, Wheelwright 1991). Given the fruit morphology and fructification strategy of a tree species, the main frugivore group and their behavior in a fruiting tree can often be predicted (Voigt *et al.* 2004). Testing such predictions is important to understand the generality of theories explaining plant–frugivore interactions.

Most tree species in the tropics rely on a diverse group of frugivores, and mutualistic relationships between plants and seed dispersers are generally diffuse (Fuentes 1995, Herrera 2002, Stanton 2003, Burns 2006). In restricted dispersal systems, however, such as rain forests on New Guinea characterized by the absence of primates, certain forest trees with structurally protected fruits may depend on a single taxonomic group as seed dispersers (Beehler 1983, Pratt & Stiles 1985, Beehler 1988, Beehler & Dumbacher 1996). In particular, Beehler and Dumbacher (1996) found that some structurally protected fruits were consumed solely by members of the family Paradisaeidae (birds of paradise), whereas other prominent frugivores of the family Columbidae (doves and pigeons) consumed mostly unprotected fruits (Frith *et al.* 1976, Pratt & Stiles 1985). Here, we focus on a tree species that produces dehiscent arillate fruits to test whether its fruits are primarily consumed by Paradisaeidae or Columbidae.

We chose a common rain forest canopy tree, *Elmerrillia tsiampaca* (Magnoliaceae; Schlechter 1913), as our study system,

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due to the documented importance of this species to frugivorous birds in Papua New Guinea (Mack & Wright 1996, 2005; Brown & Hopkins 2002). This tree species ranges from lowlands to at least 1200 m on both the northern and southern flanks of the Central Cordillera (Womersley 1978). Mature *E. tsiampaca* fruit for 3–4 wk and produce abundant dehiscent syncarpic fruits with *ca* 22 diaspores/infructescence, resulting in tens of thousands of diaspores per tree. Diaspores are small (7–9 mm), scentless, red, and high in lipid content (Wright 1998, Brown & Hopkins 2002). They contain one seed (3–4 mm), and ripen in rapid succession while infructescences are still attached to the tree.

In this study, we first describe the natural frugivore assemblage at *E. tsiampaca* in a montane rain forest in Papua New Guinea to provide a baseline against which potential changes resulting from forest alteration can be measured (Ratnarison & Forget 2005, Marsden *et al.* 2006, Kirika *et al.* 2008). We used a functional classification of frugivores (Dennis & Westcott 2006) to assess the degree of redundancy in this specific dispersal system. Our second goal was to explore whether the taxonomic composition and the behavior of the frugivore assemblage at *E. tsiampaca* trees in an undisturbed rain forest are consistent with predictions of plant–frugivore relationships (Table 1). Specifically, we predicted that: (1) *E. tsiampaca* would be visited by a diverse avian frugivore assemblage of small- to medium-sized opportunistic frugivores (Howe & Estabrook 1977, Wheelwright 1985, Fleming *et al.* 1993, Schupp 1993); (2) birds of paradise would be the most frequent visitors due to their efficient handling of *E. tsiampaca* fruit (Pratt & Stiles 1985, Beehler & Dumbacher 1996); and (3) small frugivores vulnerable to avian predators would visit for shorter time intervals than large, less vulnerable frugivores. We combine the information of visitation frequency and behavior of all species to identify potential seed dispersers that are important for the dispersal strategy of *E. tsiampaca* in rain forests in New Guinea.

METHODS

STUDY AREA.—The study site is located at the former Crater Mountain Biological Research Station, within the 2700 km² Crater

Mountain Wildlife Management Area, on the southern scarp of the central mountain range of Papua New Guinea (6°43' S, 145°05' E). The study area covers *ca* 4 km² at 850–1300 m asl. It lies within an extensive tract of continuous primary rain forest with high plant diversity (Wright *et al.* 1997). Local landowners have a moratorium on hunting and tree cutting over the entire study area that has been in effect since 1989. Rainfall is high and aseasonal, with *ca* 6400 mm/yr (Wright *et al.* 1997). Forest temperature range is 18°–26°C. Despite a lack of distinct seasons, the majority of tree species fruit during May–August with a pronounced lean season with few fruiting species in January–March (Mack & Wright 1996, 2005; Wright 2005).

STUDY SPECIES AND LOCAL AVIFAUNA.—*Elmerrillia tsiampaca* is one of the first tree species of the annual fruiting season to produce a large fruit crop, starting in April and lasting through June with most trees bearing ripe fruit synchronously (Wright 2005). During the time of *E. tsiampaca* fructification overall forest fruit mass is low (70 kg/ha, compared with 130 kg/ha during peak fruiting season; Wright 2005), and there is no other tree species in the study area that offers a similarly lipid-rich fruit at the same time as *E. tsiampaca* (Wright 1998). Mature *E. tsiampaca* are scattered throughout the study area, with slightly higher densities on upper slopes and ridgelines than in valley bottoms. Mean density has never been quantified but was estimated at about 2–3 mature trees/ha. To our knowledge, fruiting during this study was typical (based on 4 yr of personal observation).

Prior field observations indicated that *E. tsiampaca* fruit is consumed by several bird species in our study area (Mack & Wright 1996). Of 170 bird species recorded in the study area, 18 were strict frugivores and an additional 61 were mixed feeders that also consume fruit (Mack & Wright 1996, 2005). Several frugivorous species breed during the peak fruiting season and their breeding period thus overlaps with the time of *E. tsiampaca* fructification (Symes & Marsden 2005). Most species are local residents, but several Columbidae migrate seasonally from adjacent forest areas at higher or lower elevations (Mack & Wright 1996, 2005; Symes & Marsden 2007). Frugivorous

TABLE 1. Fruit traits of *Elmerrillia tsiampaca* in a lower montane tropical rain forest in Papua New Guinea, and the predicted effects on the assemblage and visitation pattern of avian frugivores to fruiting trees of that species.

Fruit trait	State in <i>E. tsiampaca</i>	Predicted effect on avian frugivores	References
Fruit size	Small (7–9 mm)	Generalist frugivores of small–medium size	Pratt and Stiles (1985), Howe (1993), Mack (1993)
Fruit structure and presentation	Protected in dehiscent capsules	Generalist frugivores, strong-billed or footed, mostly Paradisaecidae	Moermond and Denslow (1983), Pratt and Stiles (1985), Beehler and Dumbacher (1996)
Number of seeds	One per diaspore, 22 per infructescence	Generalist frugivores, ‘gulpers’	Moermond and Denslow (1985), Levey (1987)
Fruit crop size	Large (> 1000/tree)	Short visitation patterns	Howe (1979), Pratt and Stiles (1983), Wheelwright (1991), Saracco <i>et al.</i> (2005)
Fruiting duration	4–6 wk	Generalist frugivores and omnivores; dominant species	Howe (1993), Schupp (1993)

bird species in the study area can be highly social or solitary, and for most species knowledge about their dietary breadth or their potential to disperse viable seeds is incomplete.

Ten raptor species have been recorded in the study area (Mack & Wright 1996), among which three Accipitrids, two Falconids, and three eagles are potential predators of frugivorous bird species up to 2 kg (Diamond 1972, Beehler *et al.* 1986).

FIELD OBSERVATIONS.—In March 2004 we selected 38 *E. tsiampaca* trees that were distributed across the study area and spaced 50–300 m apart to avoid possible clumping effects. We selected trees with immature fruits and a majority of the canopy visible from a ground observation point. Focal trees were situated near ridge-tops, on steep slopes, or near valley bottoms, represented all aspects, and a wide range of microhabitats. We recorded bird visitation during 56 observation periods for a total of 129 h spanning the entire 2004 fruiting season between April and late June 2004. Observations were carried out during daylight at 0600–1800 h local time, and observation periods generally lasted 2 h. We visited focal trees up to eight times on different days, and rotated observation periods between mornings (0600–1100 h), noon (1100–1400 h), and afternoons (1400–1800 h) so that most trees were observed at least once during each time period. Observations were terminated during heavy rain, and total observation time per focal tree was 2–16 h (median: 8 h) spread over the fruiting season.

During observation periods we recorded the identity of all bird species visiting the focal trees, and the amount of fruits in each tree (in three categories: low, intermediate, and high, to reflect the availability of roughly hundreds, thousands, and tens of thousands of diaspores, respectively). Every 10 min we censused all birds in the entire visible canopy for a total of 719 censuses of *E. tsiampaca* canopy visitors (morning: $N = 449$; noon: $N = 93$; afternoon: $N = 177$).

Behavioral observations of birds were conducted on a random subset of all individuals visiting a focal tree. We conducted behavioral scans at 1-min intervals to maintain independence of the data set, and recorded the bird species, its activity (fruit picking, scanning/resting, aggression, other), and the length of its visit in the tree. As exact recording of visitation time proved very difficult (Pratt & Stiles 1983), we recorded visitation time in six categories: 0–20, 21–60 s, 1–3, 3–5, 5–10, > 10 min. For foraging birds we counted the number of diaspores consumed per time to estimate fruit consumption rate.

In addition to canopy observations we conducted observations of ground-foraging bird species from hides set up under fruiting *E. tsiampaca* trees. These observations were carried out at 12 focal trees during 35 observation periods lasting 2–3 h each. Each focal tree was observed at least once during the morning and once during the afternoon. For ground-foragers we recorded only those species that were observed to consume either *E. tsiampaca* fruit or seeds. We did not quantify behavior or number of diaspores consumed.

ANALYSIS.—We assessed temporal and spatial consistency of visitation for each species recorded feeding on *E. tsiampaca* fruit to assess their reliability as potential seed dispersers (Schupp 1993). We calculated temporal consistency as the proportion of observation

periods during which a species was recorded in a focal tree, based on 56 observation periods (for ground foragers $N = 35$). Spatial distribution was calculated as the proportion of focal trees ($N = 38$, for ground foragers $N = 12$) in which a species was recorded during the study period. We divided species into four groups for each of the spatial and temporal distribution: (1) rare visitors (< 0.10); (2) irregular visitors (0.11–0.20); (3) regular visitors (0.21–0.30); and (4) frequent visitors (> 0.30). We then used the key provided by Dennis and Westcott (2006) to assign each frugivore species to a functional disperser group, based on its general diet, movements, size, and habitat. We extracted species-specific information on those factors from the literature (Diamond 1972, Beehler *et al.* 1986, Mack & Wright 1996, Symes & Marsden 2007, Dunning 2008).

Fruit consumption rate (ingested diaspores/min) was compared among species by nonparametric Mann–Whitney U tests. We compared behavioral patterns and residency time among species, size classes, and between trees with different fruit abundance using nonparametric Kruskal–Wallis tests, and corrected for multiple pair wise comparisons using a Bonferroni-type adjustment (Benjamini & Hochberg 1995). To test our hypothesis that smaller frugivores vulnerable to predation would visit fruiting trees for shorter periods we calculated a Spearman correlation coefficient between residency time and average body size of species. We report results as mean \pm SD.

RESULTS

AVIAN ASSEMBLAGE AND FRUIT CONSUMERS.—We observed 61 bird species in *E. tsiampaca* trees and another four foraging on the forest floor underneath *E. tsiampaca* trees during the study period. Twenty-six species were observed eating diaspores of *E. tsiampaca* (see Table S1). During 530 censuses (74%) no birds were present in the canopy of the focal fruiting tree, and > 10 birds were counted on only 21 occasions (3%). Most species occurred solitary or in small groups. The only bird species that consistently appeared in large flocks was *Gymnophaps albertisii* with an average flock size of 15 ± 11 birds (range 1–45; $N = 63$). Columbidae accounted for 71 percent of all birds encountered during censuses, and Paradisaeidae accounted for 5 percent. Thirteen percent of the birds observed were unidentified due to poor light conditions or foliage obstruction.

Trees with a high fruit abundance had only marginally more avian visitors (1.5 ± 4.7 birds/census) than trees with intermediate (1.2 ± 3.5) and low fruit abundances (0.8 ± 3.5 , $H = 5.2$, $df = 2$, $P = 0.08$).

The majority of frugivores (69%) were rare or irregular visitors in both time and space (Table S1). Two species (*Paradisaea raggiana* and *G. albertisii*) were recorded in > 30 percent of focal trees and during > 50 percent of all observation periods (Table S1). Among the eight regular and frequent visitors were two species of Paradisaeidae, and five species of Columbidae (Table S1), one of which (*Gallicolumba rufigula*) was classified as a digestive predator. The eight regular and frequent visitors belonged to seven different functional disperser groups. Large within-forest frugivores were the only functional group represented by two species (Table S1).

BEHAVIOR OF FRUGIVORES.—To explore whether visitation patterns at *E. tsiampaca* trees conformed with predictions from the predation hypothesis we assessed the time birds remained in a fruiting *E. tsiampaca* tree for 649 bird visits. Most commonly, birds stayed 1–3 min (28%). About 70 percent of all visits lasted 1–10 min, and only 74 birds (11.4%) remained longer than 10 min in a fruiting tree. Visitation time did not differ among trees with different fruit crop size ($H = 0.31$, $df = 2$, $P = 0.86$), or at different times of the day ($H = 3.03$, $df = 5$, $P = 0.70$), but varied with the size of frugivores; birds visiting fruiting *E. tsiampaca* trees for brief periods were on average smaller than birds staying for longer time periods ($r_s = 0.29$, $P < 0.001$; Fig. 1).

Birds visiting fruiting trees were mostly picking fruit (45% of all behavioral scans, $N = 1050$), or scanning and resting (47%) while present in *E. tsiampaca*. All other behaviors were recorded only occasionally (< 7%), and aggressive interactions between frugivores were rare (0.6%). Behavior differed among different visitation times ($\chi^2 = 56.5$, $df = 5$, $P < 0.001$): fruit picking was the most common behavior for birds staying between 20 s and 10 min, whereas shorter and longer visits were mostly by scanning or resting birds (Fig. 1). The only long-term forager was *Rhyticeros plicatus* (450 diaspores in a single 40-min foraging bout).

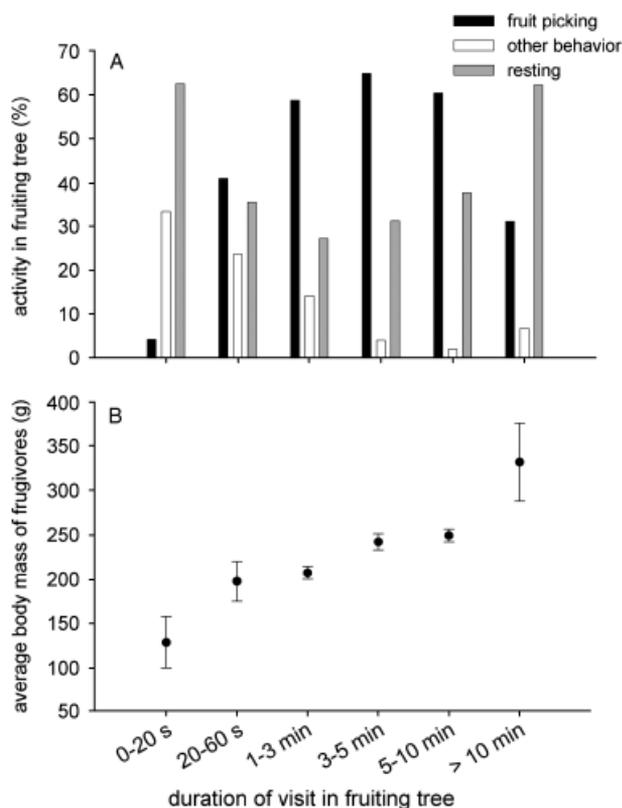


FIGURE 1. Proportion of activities (A) and average body mass (\pm SE) of avian visitors (B) to fruiting *Elmerillia tsiampaca* trees in a lower montane tropical rain forest in Papua New Guinea in relation to the duration of their visit. Body mass data for recorded frugivores were derived from Dunning (2008).

The proportion of time that birds spent foraging while present in *E. tsiampaca* trees varied substantially among species. Of the regular and frequent visitors (Table S1), *G. albertisii* spent a significantly higher proportion of time picking fruit than birds of paradise and smaller fruit doves (Table 2).

All frugivores visiting *E. tsiampaca* trees picked single diaspores and swallowed them whole, and only *Trichoglossus haematodus*, *Eclectus roratus*, and *Cacatua galerita* were observed to manipulate single diaspores in the beak for 40–120 s. In four species we were able to assess the amount of diaspores consumed per time. Both *R. plicatus* (13.5 ± 2.0 diaspores/min) and *G. albertisii* (20.3 ± 9.0) were significantly more efficient in consuming diaspores than *Ptilinopus superbis* (6.4 ± 3.8 ; $z = -2.17$, $P = 0.031$, and $z = -4.05$, $P < 0.001$, respectively). The two *P. raggiana* observed during fruit picking removed 11.2 and 18 diaspores/min.

DISCUSSION

COMPOSITION OF THE FRUGIVORE ASSEMBLAGE.—The assemblage of birds visiting *E. tsiampaca* trees during the fruiting period was mostly comprised of rare and irregular visitors. Avian frugivore assemblages at fruiting rain forest trees range from 22 to 45 species (McDiarmid *et al.* 1977, Moran *et al.* 2004, Farwig *et al.* 2006, Kirika *et al.* 2008). In Papua New Guinea, frugivore assemblages at rain forest tree species ranged between 3 and 28 species (Pratt & Stiles 1985, Beehler & Dumbacher 1996, Brown & Hopkins 2002). The diverse assemblage of 26 species consuming *E. tsiampaca* fruit conforms to our expectation of a broad frugivore guild.

Most of the species were medium- to large-sized within-forest frugivores that usually scatter or clump-disperse a diverse diet of seeds over short to long distances (Dennis & Westcott 2006). The eight most common frugivores included seven functional disperser groups, suggesting that *E. tsiampaca* seeds are dispersed in a variety of ways. A diverse coterie of dispersers promotes seed dispersal across a variety of landscapes and habitat types. Small-scale forest modification in Papua New Guinea can affect the frugivore community (Mack & Wright 1996, Marsden *et al.* 2006), and pigeons and ground-foraging frugivores appear to be especially

TABLE 2. Percentage of 1-min scan observations during which regular and frequent visitors were observed foraging when in *Elmerillia tsiampaca* trees in Papua New Guinea. N indicates number of scan observations. Superscript letters indicate significant difference at $P < 0.05$.

Species	N	% foraging
<i>Gymnophaps albertisii</i>	542	55.6 ^a
<i>Cracticus cassicus</i>	36	50.0 ^b
<i>Cicinnurus magnificus</i>	24	45.8 ^b
<i>Paradisaea raggiana</i>	40	43.9 ^b
<i>Ptilinopus ornatus</i>	34	34.3 ^c
<i>Ptilinopus superbis</i>	120	32.5 ^c
<i>Ducula zoeae</i>	35	17.7 ^d
<i>Ptilinopus rivoli</i>	30	13.3 ^d

vulnerable to human persecution and forest modification (Steadman 1997, Boyer 2008). Loss of a single frugivore species could mean the loss of a functional disperser group represented by that species, and thus affect the dispersal of *E. tsiampaca* seeds (Moran *et al.* 2009).

Our study showed a much higher visitation frequency of Columbidae (71.1% of all visitors) than Paradisaeidae (Beehler 1983, Pratt & Stiles 1985, Beehler 1988, Beehler & Dumbacher 1996, Brown & Hopkins 2002). Pratt and Stiles (1985) hypothesized that fruit pigeons are at a competitive disadvantage to birds of paradise in removing arillate seeds from protective capsules. However, *G. albertisii* had the highest frequency of foraging and also the highest rate of fruit consumption, and did not appear to be at a disadvantage compared with birds of paradise. The apparent lack of interference competitive interactions for *E. tsiampaca* fruit in this study could be a result of the large fruit crops, which may allow fruit pigeons to forage despite the presence of more efficient foragers. Hence, we conclude that Columbidae are not restricted to structurally unprotected fruit types as suggested by Pratt and Stiles (1985), but that structurally protected dehiscent fruit may comprise a significant part of their diet.

By providing an important component in the diet of *G. albertisii*, the fruit of *E. tsiampaca* may be a keystone resource. *Gymnophaps albertisii* performs long daily commuting flights (Symes & Marsden 2007) and immigrates seasonally into the study area specifically to consume *E. tsiampaca* fruit (Mack & Wright 1996, 2005). Highly frugivorous birds are known to track seasonally abundant resources across the landscape (Chaves-Campos *et al.* 2003, García & Ortiz-Pulido 2004, Hampe 2008), and higher fruit availability in an area generally attracts a higher number of frugivores to that area (Guitian & Munilla 2008). *Elmerrillia tsiampaca* might therefore act as a species that attracts frugivores to an area, and facilitates frugivory and seed dispersal for subsequently fruiting tree species with a less attractive fruit crop (Saracco *et al.* 2004).

The attractiveness of *E. tsiampaca* fruit may be its large fruit crop and high lipid content of diaspores (Wright 1998, Brown & Hopkins 2002). Highly frugivorous bird species favor fruit with high lipid and protein contents (Stiles 1993). The high availability of lipid-rich diaspores in *E. tsiampaca* may explain the size distribution of frugivores consuming its fruit. We found that the most frequent consumers of *E. tsiampaca* fruit were birds of medium to large size (body mass 80–2400 g; Table S1). Thus, while large birds are not confined to eat large fruit (Dennis & Westcott 2006), the consumption of *E. tsiampaca* fruit by relatively large birds indicates that *E. tsiampaca* assumes an important role in meeting nutritional demands even for large forest frugivores.

Because of their relatively large size, most birds in our study were able to swallow the entire *E. tsiampaca* diaspore including the seed, which is generally beneficial for dispersal of viable seeds (Levey 1987). The only nongulping species were three parrots, which are known to crack seeds, and two ground dove species known to grind seeds in the gizzard (Diamond 1972, Diamond *et al.* 1999, Symes *et al.* 2006). Parrots generally do not have a gallbladder and may therefore not be able to digest the lipid-rich pulp

(Martinez del Rio & Restrepo 1993, Stiles 1993, Levey & Martinez del Rio 2001). The long fruit handling time of these species suggests that they extract the seed from the diaspore and they were classified as seed predators rather than dispersers (Dennis & Westcott 2006).

FRUGIVORE PREDATION AVOIDANCE.—Fruiting trees were unoccupied for 75 percent of the time, and residency time for visitors was generally short. The only birds that stayed in a fruiting *E. tsiampaca* tree for > 15 min were either very cryptic (roosting fruit doves) or too large for most predators (*R. plicatus*). The visitation pattern observed at *E. tsiampaca* trees is thus consistent with the short residency times predicted by the predation hypothesis and consistent with other studies where frugivores stayed in a fruiting tree for only short time intervals (Pratt & Stiles 1983, Wheelwright 1991, Barnea *et al.* 1993, Nogales *et al.* 1999).

IMPORTANT DISPERSERS OF *E. TSIAMPACA*.—The two most common visitors, *G. albertisii* and *P. raggiana*, generally stayed only for short periods of time, and we never observed *G. albertisii* roosting or preening in *E. tsiampaca* trees. It is likely that most seeds are voided away from the parent tree. Roosting trees used by *G. albertisii* were of different species and mostly located on upper slopes or ridgelines, which appeared to facilitate rapid downhill escapes when a roosting flock was flushed. If defecation of previously ingested seeds occurs primarily during roosting, the usage of trees on upper slopes for roosting might lead to nonrandom uphill dispersal of *E. tsiampaca* seeds, an important benefit of seed dispersal in mountainous terrain (Mack 1995).

Another potentially important disperser of *E. tsiampaca* seeds is *R. plicatus*, which consumed large numbers of *E. tsiampaca* diaspores during each visit. Despite the long visits (> 40-min foraging bouts), hornbills are likely effective long-distance seed dispersers due to their long gut retention times and large-scale movements (Kinnaird 1998, Holbrook & Smith 2000, Kitamura *et al.* 2008).

Two ground foraging frugivores, *Otidiphaps nobilis* and *Casuaris bennetti*, might also play an important role in dispersal of *E. tsiampaca* seeds. Although not recorded in our study, *C. bennetti* has been identified as an important dispersal agent in the study area (Mack 1995), and fallen *E. tsiampaca* fruit comprised 3 percent of their diet in some years (Wright 1998, 2005). The *E. tsiampaca* fruiting season coincides with the time when *C. bennetti* chicks start foraging with their parent. Droppings of *C. bennetti* chicks were composed entirely of *E. tsiampaca* seeds at this time (A. L. Mack, unpubl. data), and suggest that this small, nutritious fruit might be particularly important for cassowary chicks.

CONCLUSION

We showed that in a pristine forest environment a wide variety of avian frugivores consumes *E. tsiampaca* fruit, and that Columbidae were the most common consumer of the structurally protected dehiscent fruit. The majority of frugivore species visited rarely, and most of the fruit were removed by a small number of species. Visits

to *E. tsiampaca* were generally short, presumably to avoid predators as we did not find interference competition among frugivores. As most species gulped *E. tsiampaca* fruit the short visitation pattern makes it likely that most of the ingested seeds are effectively dispersed from the parent tree by avian consumers. The most frequent visitors that may act as dispersers of *E. tsiampaca* seeds belonged to different functional disperser groups, and a reduction of the natural frugivore community may thus adversely affect the seed dispersal strategy of *E. tsiampaca*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Bird species observed to consume Elmerillia tsiampaca fruit in a lower montane tropical rain forest in Papua New Guinea during the 2004 fruiting season.*

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