Disappearance of insectivorous birds from tropical forest fragments

Çağan H. Şekercioğlu*⁺, Paul R. Ehrlich*, Gretchen C. Daily*, Deniz Aygen[‡], David Goehring[§], and Randi F. Sandí[¶]

*Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020; [‡]Coastal Virginia Wildlife Observatory, Cape Charles, VA 23310; and [§]Department of Ecology and Evolutionary Biology, Princeton University, [¶]Copal de Agua Buena, Coto Brus 8257, Costa Rica

Contributed by Paul R. Ehrlich, November 19, 2001

Determining the impact of forest disturbance and fragmentation on tropical biotas is a central goal of conservation biology. Among tropical forest birds, understory insectivores are particularly sensitive to habitat disturbance and fragmentation, despite their relatively small sizes and freedom from hunting pressure. Why these birds are especially vulnerable to fragmentation is not known. Our data indicate that the best determinant of the persistence of understory insectivorous birds in small fragments is the ability to disperse through deforested countryside habitats. This finding contradicts our initial hypothesis that the decline of insectivorous birds in forest fragments is caused by impoverished invertebrate prey base in fragments. Although we observed significantly fewer insectivorous birds in smaller fragments, extensive sampling of invertebrate communities (106,082 individuals) and avian diets (of 735 birds) revealed no important differences between large and small fragments. Neither habitat specificity nor drier fragment microclimates seemed critical. Bird species that were less affected by forest fragmentation were, in general, those that used the deforested countryside more, and we suggest that the key to their conservation will be found there.

orest understory insectivores, in general, have high habitat specificity, low mobility, and are more confined to forest interior than other forest passerine guilds, especially in the tropics where forest fragmentation and its consequences are most dramatic (1-5). Although over a dozen hypotheses have been proposed to explain the disappearance of insectivorous bird species from forested habitats around the world (2, 6), four of these are particularly relevant to explaining the decline of understory insectivores. The food scarcity hypothesis states that small fragments are impoverished in prey preferred by understory insectivores (6-8). The microclimate hypothesis proposes that these birds are particularly sensitive physiologically to changes in microclimate associated with forest fragmentation (2, 9). The habitat specificity hypothesis states that the loss of some microhabitat elements (such as army ant swarms, curled leaves, and dead trees) from fragments may affect many understory insectivores negatively (2, 6). Insectivores are more sensitive to such subtle changes because, unlike fruits, flowers, and seeds, invertebrates actively avoid insectivores and, as a result, insectivorous birds have evolved into many specialized niches and seek prey in certain microhabitats. Finally, according to the limited dispersal hypothesis, understory insectivores, because of their relatively sedentary habits and possible psychological avoidance of clearings (1, 10), may be less likely to disperse into more favorable habitats after forest fragmentation and may disappear from fragments as a result of stochastic events and other negative consequences of fragmentation.

Changes in invertebrate communities as a result of forest fragmentation are well documented (11–13). Leaf-litter and soil-dwelling invertebrates decline as a result of desiccation in small forest fragments and generalist edge species that prefer the dense vegetation near fragment edges increase in number (12). Because many understory insectivores forage in the dark and humid leaf litter in relatively open understory and avoid dense vegetation (2), these changes can diminish the birds' prey base.

If the food scarcity hypothesis is correct and a reduced resource base is the main reason for the decline of insectivorous understory birds in smaller forest fragments, these fragments should exhibit some combination of lower invertebrate abundance and biomass. In addition, food limitation may be apparent in the quantity and composition of invertebrates in the birds' diets. Given the centrality of food availability to the reproductive success of songbirds in general (14), we decided to test the food scarcity hypothesis in tropical humid forest, where it has received relatively little attention (15).

Methods

Research Site. We tested our predictions by sampling birds, bird diets, and invertebrates in large and small forest fragments near Las Cruces, southern Costa Rica. Data were collected between 1 July 1999-15 September 2000, in Las Cruces Forest and three smaller forest fragments (8°47'N, 82°57'W). These fragments are Pacific premontane (elevation 1,100 m) humid forest surrounded by pastures, plantations of coffee and other crops, and human settlements. The fragments have been isolated since the mid-1950s. Las Cruces Forest is the largest midelevation fragment in the region [227 hectares (ha)]; in it, we established three study transects (referred to below as "forest transects") separated from each other by 400-1000 m. The small primary forest fragments (4-5 ha) studied were 400-2,300 m from Las Cruces Forest and there was a study transect in each small fragment (referred to below as "fragment transects"). Each of the six transects was 200-m long and within 150 m of the forest edge, to control for "edge effects" (16).

Sampling Birds. We mist-netted in each transect with 12 12-m, 36-mm mesh nets, for a total of 82,944 m h divided evenly between forest and fragment transects, following published methodology (17).

Sampling Invertebrates. We sampled invertebrates with pitfall traps [Bioquip (Gardena, CA) product no. 2838A] filled with equal parts of ethylene glycol and water, sticky traps, 30 cm \times 30 cm plastic sheets covered with Tangle-Trap (Bioquip product no. 2870C), and timed searches. With this combination, we were able to sample both passive and actively moving invertebrates on various substrates. The traps were placed randomly along transects. The 1-week pitfall traps were active for 1 week, 2-week sticky traps were active for 2 weeks, and other traps were active for 1 day. For searches, each 200-m transect was divided into 40 5-m sections. Two people spent 5 min searching each section for invertebrates in flight, in the leaf litter, and on vegetation; invertebrates longer than 5 mm were captured with nets and forceps and placed in 70% alcohol. We identified all invertebrates to order and measured their lengths. For 1-week pitfall traps and searches, we measured only invertebrates longer than

[†]To whom reprint requests should be addressed. E-mail: cagan@stanford.edu.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.



5 mm and obtained the cumulative dry weight of all of the specimens in each order for each sample-day.

Bird Diet. We obtained diet samples from insectivorous and omnivorous birds by using nonlethal 1.5% potassium antimony tartarate, based on established protocol (18). The first author examined each regurgitate under a stereo microscope and estimated the number, length, and weight of prey items eaten based on a reference collection and published regressions of weight on length (19). Invertebrates were identified to order, except *Formicidae* (ants), which were identified to family. For 14 understory insectivorous species that occurred both in forest and fragment transects, we had at least four diet samples from each treatment. That is the minimum number thought to offer adequate representation of the diet of a species within a given time period (20), and for 11 of these species, we had at least 10 diet samples from each treatment.

Vegetation. At 30 randomly selected points in each transect, we measured canopy closure by taking photos of the canopy from ground-level with a 17-mm lens and later analyzing them with Adobe Systems (Mountain View, CA) PHOTOSHOP. We assessed distribution of canopy height by measuring the height of the highest vegetation above these points with a rangefinder.

Results

Bird Community. We mist-netted 1.202 birds in forest transects and 1,096 birds in fragment transects, representing 116 species (nomenclature based on ref. 21). Overall daily capture rates did not differ between forest and fragment transects (t = 1.50, P =0.137), but certain guilds and forest-dependence classes showed pronounced differences (Fig. 1). Most large and specialized insectivorous species, such as black-faced antthrush (Formicarius analis) and ruddy woodcreeper (Dendrocincla homochroa), did not occur along fragment transects and many of the remaining insectivores, such as white-breasted wood-wren (Henicorhina leucosticta) and white-throated spadebill (Platyrinchus mystaceus), occurred there in significantly lower numbers than along forest transects (see Table 2, which is published as supporting information on the PNAS web site, www.pnas.org). Insectivorous species were significantly fewer in the fragments than in Las Cruces Forest (t = 3.08, P = 0.028), especially those species feeding on large invertebrates and small vertebrates (t = 4.01,P = 0.008); insectivores feeding on small invertebrates tended to be fewer as well (t = 2.45, P = 0.058). Both sampled and estimated species richness was higher along forest transects for all species and for insectivores (Fig. 1C). As in previous studies (1, 3, 4), we observed significantly fewer species and individuals of understory insectivores in small fragments and none of the ground-foraging or army ant-following species were observed in those fragments.

Fig. 1. Comparisons of abundance and species richness of birds captured with mist nets. The asterisks indicate a significant difference (P < 0.05). (A) More insectivorous birds were captured along forest transects (t = 2.67, P =0.0089), and more omnivorous (t = 2.70, P = 0.0081) and granivorous (t = 2.18, P = 0.0315) birds were captured along fragment transects. Guild assignments were based on ref. 22. (B) More high forest-dependent species were captured along forest transects (t = 3.63, P = 0.0005) and more low forest-dependent species (t = 2.40, P = 0.019) were captured along fragment transects. High, intermediate, and low forest-dependent classes correspond to forestdependent, forest generalist, and nonforest species in ref. 23. (C) Observed and estimated species richness values are based on methods provided in ESTIMATES (ref. 24, http://viceroy.eeb.uconn.edu/EstimateS). OBS, observed number of species; ACE, abundance-based coverage estimator; ICE, incidencebased coverage estimator; BTS, bootstrap; CH, Chao; JK, Jackknife; MM, Michaelis-Menten. SEs for Chao1, Chao2, and Jackknife1 methods are included.



Invertebrate Community. Individuals/sample, average length, and dry biomass/sample of invertebrates varied between forest and fragment transects with no overall pattern (Fig. 2). When we compared these variables for some invertebrate orders and classes, we again found no overall differences between forest and fragment transects (Table 1). Overall, numbers of individuals/sample and dry biomass/sample values were about 15% lower in forest samples, but the differences were not significant. Of 319 independent *t* tests comparing individuals/sample, average length, and dry biomass/sample values between forest and fragment transects for different invertebrate taxa sampled with various methods, 69 tests were significant and greater values were almost equally distributed between forest (35/69) and fragment transects (34/69). These tests do not pose a multiple comparison problem because the null hypothesis for each test was different (25).

There were, however, two discernible trends. First, all eight significantly greater values for Diptera were from fragment transects. Second, a number of mainly forest floor/leaf-litter groups [such as Annelida, Blattaria, Collembola, Decapoda (forest crabs), Dermaptera, Isopoda, Mollusca, and Thysanura], which comprised 7.3% of the individuals and 12.5% of the biomass sampled, were somewhat better represented along forest transects. There were also significantly more army ant (*Eciton burchelli*) swarms during searches along forest transects (7 of 8 encounters, binomial test, P = 0.0313).

Bird Diet. In bird diet samples, Coleoptera, Orthoptera, Formicidae, and Arachnida were the most common prey, comprising about 75% of the individuals found in diet samples. The taxonomic distribution of prey items in forest and fragment diet samples did not differ significantly for any bird group (all $\chi^2 < 11.91$, all P > 0.99).

Overall, estimated dry weight of invertebrates was not significantly different between forest and fragment diet samples (F = 2.60, P = 0.108; two-factor ANOVA with origin of sample and species as factors).

The average number of prey items/diet sample (all t < 1.64, all P > 0.156) and estimated dry weight (19) of consumed prey (all t < 1.60, all P > 0.111) values, although greater in general in forest samples, did not differ significantly between forest and fragment samples for any of the 14 species with enough diet samples from both treatments (Table 3, which is published as supporting information on the PNAS web site). Even though the average lengths of invertebrates in diet samples were greater in the forest samples of 11 species, the values differed significantly only for *Henicorhina leucosticta* (P = 0.016) and *Sittasomus griseicapillus* (P = 0.008).

When we compared the diet samples obtained in Las Cruces Forest of insectivorous species present and absent from small fragments, prey taxonomic distribution did not differ significantly for insectivores with large prey ($\chi^2 = 0.58$, P > 0.99) or with small prey ($\chi^2 = 0.36$, P > 0.99). Nor did the estimated dry weight of consumed prey of insectivores with large prey (t =0.005, P = 0.996) or with small prey (t = 0.262, P = 0.793).

Vegetation Structure. Neither canopy closure (F = 0.414, P > 0.5) nor canopy height distribution ($\chi^2 = 15.15, P > 0.1$) differed

Fig. 2. Comparisons of average number, length, and dry weight of invertebrates captured. For sample sizes, see Table 1. With 1-week pitfall traps and searches, only invertebrates ≥ 5 mm were taken into consideration. The asterisks indicate a significant difference (P < 0.001). (A) Average number of invertebrates captured/sample. (B) Average length of invertebrates captured (mm). (C) Average dry weight of invertebrates/sample (mg). For sticky traps and 1-day pitfall traps, dry weight was estimated by using the appropriate regression equations (19).

Table 1. The distribution of significantly greater values of invertebrate measures between forest and fragment transects

		Individuals/sample		Average inver	tebrate length	Dry biomass/sample		
Sampling method	No. captured	Forest	Fragment	Forest	Fragment	Forest	Fragment	
1-day sticky (36)	9,630		Diptera Hemiptera Hymenoptera	Arachnida Coleoptera	Diptera Hymenoptera Isopida		Hymenoptera	
2-week sticky (18)	47,356	Collembola	Orthoptera	Coleoptera Collembola Hymenoptera Orthoptera Thysanoptera	Diptera Lepidoptera	Collembola	lsoptera	
Ground sticky (12)	19,970		Diptera	Arachnida Coleoptera Collembola	Diptera Orthoptera	Coleoptera Collembola	Diptera	
1-day pitfall (16)	4,206	Collembola	Orthoptera Diptera	Coleoptera	Formicidae Hymenoptera	Coleoptera Collembola	Diptera Hymenoptera Orthoptera	
1-week pitfall (36)	9,801	Chilopoda Decapoda Dermaptera	Coleoptera Hemiptera	Annelida Blattaria Orthoptera	Coleoptera Formicidae Hymenoptera	Blattaria Decapoda Dermaptera	Coleoptera	
Search (8)	15,119	Coleoptera Hemiptera Hymenoptera Isopoda	Lepidoptera		Coleoptera Formicidae Orthoptera	Arachnida Dermaptera Isopoda Phasmida	Homoptera Lepidoptera	

Values next to sampling methods indicate number of samples from each transect. Dry biomass values for sticky traps and 1-day pitfall traps were estimated by using appropriate regression equations (19).

significantly between forest and fragment transects. Average canopy closure was around 80% for all transects.

Discussion

Although there were significantly fewer understory insectivores in small fragments, invertebrate abundance, average length, and dry biomass values along forest and fragment transects were surprisingly close. We obtained similar results from examination of bird diets, with no significant differences in diet composition, biomass, or prey items per sample, and only 2 of 14 bird species exhibited significant differences in average length of invertebrates eaten. Even though the significant reduction in army ant swarms in small fragments may affect the three army ant-following species negatively, the food scarcity hypothesis does not seem to be supported as the primary cause of the disappearance of understory insectivorous birds from small forest fragments around Las Cruces. This finding differs from the findings of two recent studies in the temperate zone where increased food abundance in larger forest fragments was positively correlated with the abundance and reproductive performance of the two understory insectivorous bird species studied (7, 8).

The microclimate hypothesis, which states that sedentary understory insectivores react more unfavorably to microclimate fluctuations in forest fragments than more mobile species that are frequently exposed to different microclimates, was not tested by our observations. We tried to control for microclimate differences by sampling only near forest edges, but this does not preclude the possibility that understory insectivores in larger fragments may forage near edges and seek shelter in the forest interior when climatic conditions become intolerable.

With respect to the habitat specificity hypothesis, some understory insectivorous species may have disappeared from fragments because of the reduction or disappearance of some critical habitat elements, such as army ant swarms. However, the small fragment where we sometimes observed army ant swarms (although only once during invertebrate sampling) was also missing army ant-following bird species absent from other fragments, and a number of bird species missing from small fragments feed on invertebrate resources that were not significantly different between forest and fragments sites. Thus, this hypothesis is tentatively rejected.

Dispersal, crucial in the colonization of habitat islands (26, 27), may be the key mechanism that makes it more likely that small and short-lived bird species will go extinct as a result of habitat fragmentation compared with large and long-lived species (28, 29). Likewise, the limited dispersal capabilities of understory insectivores (1, 2) may be the most important factor in their sensitivity to fragmentation. At our site, presence of a bird species in the deforested open countryside around forest fragments was the best determinant of its occurrence in smaller fragments, in agreement with the limited dispersal hypothesis. Of the 18 species (15 insectivorous) we caught significantly more times along Las Cruces Forest transects than along fragment transects, only two (one insectivorous) were detected in nonforest habitats in a separate study (30). In that study, the average detection rate in nonforest for these 18 species was 0.0005 individuals/person-hour (3 of 5,007 observations) and none of the six insectivorous species feeding on large prey were found in nonforest habitats. Conversely, of the 12 species we caught significantly more frequently along fragment transects (three insectivorous, all feeding on small prey), 9 were present in nonforest (30), and the average detection rate in nonforest was 0.296 individuals/person-hour (1,172 of 5,007 observations). Only one of these nine species was insectivorous and it accounted for 1.8% of the observations. These detection rates were significantly different (Mann–Whitney U test, P = 0.004), and insectivores, especially those feeding on large prey, were significantly under-represented both in forest fragments and in nonforest habitats.

There was also a significant positive correlation ($r^2 = 0.714$, P < 0.0001) between the number of species of a bird family present in nonforest habitats (30) and the number of species of that bird family present in small fragments (Fig. 3). Thus, ability to move through



Fig. 3. Increased species diversity of a bird family in the nonforest matrix correlates with increased species diversity in small fragments ($r^2 = 0.714$, P < 0.0001). Families that are not well sampled with mist nets, such as Accipitridae, Strigidae, Trogonidae, and Cotingidae, were not included. The data for all of the species in the study region were provided by James Zook (unpublished data). Note that the four families in the superfamily Furnarioidea, which is particularly sensitive to forest disturbance (2), have the lowest values and are marked with circles.

and possibly forage in deforested habitats around forest fragments may link small populations that would otherwise be isolated and vulnerable to edge effects and stochastic events. This mobility may greatly enhance the "rescue effect" (31) and thus improve the survival chances of forest-dependent organisms in forest fragments, as was observed in previous studies (1, 32). In addition, forest bird species frequently detected in the matrix surrounding forest fragments are also likely to be more tolerant of ecological changes in fragments, such as those resulting from edge effects (16, 33), and may be more capable of occasionally foraging and even nesting in some matrix habitats near fragments.

Thus, the limited dispersal hypothesis is best supported by our study. Inability to use deforested countryside habitats, rather than

- 1. Stouffer, P. C. & Bierregaard, R. O. (1995) Ecology 76, 2429-2445.
- 2. Canaday, C. (1996) Biol. Conserv. 77, 63-77.
- 3. Stratford, J. A. & Stouffer, P. C. (1999) Conserv. Biol. 16, 1416-1423.
- 4. Kattan, G. H., Alvarez-Lopez, H. & Giraldo, M. (1994) Conserv. Biol. 8, 138-146.
- 5. Thiollay, J. M. (1992) Conserv. Biol. 6, 47-63.
- Ford, H. A., Barrett, G. W., Saunders, D. A. & Recher, H. F. (2001) *Biol. Conserv.* 97, 71–88.
- 7. Burke, D. M. & Nol, E. (1998) Auk 115, 96-104.
- 8. Zanette, L., Doyle, P. & Tremont, S. M. (2000) Ecology 81, 1654-1666.
- 9. Karr, J. R. & Freemark, K. E. (1983) Ecology 64, 1481-1494.
- 10. Greenberg, R. (1988) Can. J. Zool. 67, 1194-1199.
- Didham, R. K., Ghazoul, J., Stork, N. E. & Davis, A. J. (1996) Trends Ecol. Evol. 11, 255–260.
- Didham R. K. (1997) in *Tropical Forest Remnants*, eds. Laurance, W. F. & Bierregaard, R. O. (University of Chicago Press, Chicago), pp. 55–70.
- Ricketts, T. H., Daily, G. C., Ehrlich, P. R. & Fay, J. P. (2001) Conserv. Biol. 15, 378–388.
- 14. Martin, T. E. (1987) Annu. Rev. Ecol. Syst. 18, 453-488.
- 15. Ahumada, J. A. (2001) Auk 118, 191-210.
- 16. Restrepo, C. & Gómez, N. (1998) Ecol. Appl. 8, 170-183.
- 17. Karr, J. R. (1979) Inland Bird Banding 51, 1-10.
- 18. Poulin, B., Lefebvre, G. & McNeil, R. (1994) Condor 96, 98–104.
- 19. Schoener, T. W. (1980) Ann. Entomol. Soc. Am. 73, 106-109.

food scarcity in fragments, seems to be the major cause of the decline of understory insectivores in forest fragments around Las Cruces. The actual mechanism of decline, whether it is increased nest predation, changes in microclimate, negative stochastic effects caused by small population size, or a combination thereof, remains to be elucidated. Although forest fragmentation and other forms of habitat disturbance may reduce the breeding success of most forest bird species equally, possibly as a result of increased nest predation of all species (33), more sedentary species may be less able than other birds to "commute" through nonforest from their breeding territories to small fragments containing sufficient resources. Such regular "commuting" from nesting areas to foraging areas that are unsuitable for nesting has been observed in frugivorous bats in Mexican lowland tropical forest fragments (M. Evelyn, unpublished data). Increased mobility increases the chances of renesting in fragments if conditions become more favorable, making it less likely that more vagile species will become locally extinct. In addition, forest bird species that are likely to move through nonforest habitats are more likely to occasionally use those habitats for foraging and nesting, mitigating the effects of fragmentation. Sedentary behavior can also explain the decline of understory insectivores in unfragmented but otherwise disturbed forests (2, 5).

More research comparing the movement, foraging, and breeding patterns of understory insectivores and other guilds in both forest fragments of various sizes and in open countryside is needed to reveal the actual mechanism(s) of the disappearance of understory insectivores. Meanwhile, better integration of agricultural/human-dominated habitats into conservation strategies, such as linking forest fragments with shade coffee plantations, fence rows, and windbreaks composed of native tree species, may make deforested areas more hospitable to understory insectivores and other fragmentation-sensitive groups by enabling them to disperse between forest fragments and prevent local extinctions.

We thank the Costa Rican government and the Organization for Tropical Studies for allowing us to work at Las Cruces Biological Research Station (LCBRS), the staff of LCBRS for their support, and Tom Davis, Forrest Fleischmann, Angelina Sanderson, Jason Sandí, Jeisson Sandí, Audrey Tapia, and Parker VanValkenburgh for their help with field work. We thank Walter Loewenstern and Thomas Brokaw for graduate fellowships, the Bing undergraduate research fund, Sigma Xi Grant-in-Aid of Research, the Winslow Foundation, and Peter and Helen Bing for support. We appreciate critical comments from Richard Bierregaard, Carol Boggs, Chris Canaday, Marcus Feldman, Oliver Komar, William Laurance, Gary Luck, Harold Mooney, Phillip Stouffer, and Peter Vitousek.

- Cooper, R. J., Martinat, P. J. & Whitmore, R. C. (1990) in Avian Foraging: Theory, Methodology and Applications, eds. M. L., Ralph, C. J., Verner, J. & Jehl, J. R., Jr. (Cooper Ornithol. Soc., Los Angeles), pp. 104–109.
- 21. Clements, J. F. (2000) Birds of the World: A Checklist (Ibis, Vista, CA).
- Karr, J. K., Robinson, S. K., Blake, J. G. & Bierregaard, R. O., Jr. (1990) in *Four* Neotropical Rainforests, ed. Gentry, A. H. (Yale Univ. Press, New Haven, CT), pp. 237–269.
- Stiles, F. G. (1985) in Conservation of Tropical Forest Birds, eds. Diamond, A. W. & Lovejoy, T. E. (ICBP Technical Publication, Cambridge, U.K.), pp. 141–185.
- Colwell, R. K. (2001) ESTIMATES 6.0b1: Statistical Estimation of Species Richness and Shared Species from Samples (Univ. of Connecticut, Storrs, CT).
- Fisher, L. D. & van Belle, G. (1993) Biostatistics: A Methodology for the Health Sciences (Wiley, New York), pp. 596–629.
- Paradis, E., Baillie, S. R., Sutherland, W. J. & Gregory, R. D. (1998) J. Anim. Ecol. 67, 518–536.
- 27. Brown, J. H. & Kodric-Brown, A. (1977) Ecology 58, 445-449.
- 28. Beissinger, S. (2000) Proc. Natl. Acad. Sci. USA 97, 11688-11689.
- Owens, I. P. F. & Bennett, P. M. (2000) Proc. Natl. Acad. Sci. USA 97, 12144–12148. (First Published September 26, 2000; 10.1073/pnas.200223397)
- 30. Hughes, J. B., Daily, G. C. & Ehrlich, P. R. Ecol. Lett., in press.
- 31. Invargsson, P. K. (2001) Trends Ecol. Evol. 16, 62-63.
- 32. Laurance, W. F. (1991) Conserv. Biol. 5, 79-89.
- 33. Paton, P. W. C. (1994) Conserv. Biol. 8, 17-26.

Family and Latin name	English name	For1	For2	For3	Frag1	Frag2	Frag3
Falconidae							
Micrastur ruficollis	Barred Forest-falcon	1				1	
Odontophoridae							
Odontophorus guttatus	Spotted Wood-quail		1				
Columbidae							
Columbina talpacoti	Ruddy Ground-dove			1			
Leptotila verreauxi	White-tipped Dove				1		2
Leptotila cassini	Gray-chested Dove	3	1	3	6	1	3
Geotrygon chiriquensis	Chiriqui Quail-dove						1
Geotrygon montana	Ruddy Ouail-dove		1	1	1		
Psittacidae							
Pionus senilis	White-crowned Parrot					1	
Strigidae						-	
Pulsatrix perspicillata	Spectacled Owl				1		
Trochilidae					-		
Eutoxeres aquila	White-tipped Sicklebill	5	6	11	7	4	7
Glaucis aenea	Bronzy Hermit	1	÷			-	
Phaethornis guy	Green Hermit	58	24	24	28	11	23
Phaethornis striigularis	Stripe-throated Hermit	9	14	7	7	1	5
Phaechroa cuvierii	Scaly-breasted Hummingbird		1	1	1	2	1
Campylonterus	Violet Sabrewing	5	3	9	1	-	1
hemileucurus	, loter Sucre wing	C	U	-			-
Florisuga mellivora	White-necked Jacobin						1
Chlorostilbon canivetii	Canivet's Emerald	1			1		
Elvira chionura	White-tailed Emerald	3	2	12	2	5	3
Thalurania colombica	Violet-crowned Woodnymph	6	3	4		3	2
Amazilia tzacatl	Rufous-tailed Hummingbird	4	4	15	16	14	24
Polyerata amabilis	Charming Hummingbird	5	3	8	3	1	5
Saucerottia edward	Snowy-bellied Hummingbird		2	7	3		1
Heliodaxa jacula	Green-crowned Brilliant			4			
Heliothryx barroti	Purple-crowned Fairy		1				
Trogonidae							
Trogon collaris	Collared Trogon			2			
Momotidae							
Momotus momota	Blue-crowned Motmot			2	2	1	2
Galbulidae							
Galbula ruficauda	Rufous-tailed Jacamar		1	2			
Ramphastidae							
Aulacorhynchus prasinus	Emerald Toucanet			1			
Pteroglossus frantzii	Fiery-billed Aracari					3	1
Picidae							
Veniliornis fumigatus	Smoky-brown Woodpecker				4	1	
Furnariidae	,				-	-	
Synallaxis brachvura	Slaty Spinetail			1			
Premnoplex brunnescens	Spotted Barbtail			4			

Table 2. List of birds captured with mist nets during the study

Family and Latin name	English name	For1	For2	For3	Frag1	Frag2	Frag3
Xenops minutus	Plain Xenops	1	2	2	1	1	2
Xenops rutilans	Streaked Xenops	-	-	-		-	-
Hyloctistes subulatus	Striped Woodhaunter	1					
Automolus ochrolaemus	Buff-throated Foliage-gleaner	5	8	11	4	6	10
Automolus rubiginosus	Ruddy Foliage-gleaner	8	8	14	•	2	11
Sclerurus mexicanus	Tawny-throated Leaftosser	Ũ	1			-	
Sclerurus guatemalensis	Scalv-throated Leaftosser	3	•	1			
Dendrocolaptidae		U		•			
Dendrocincla anabatina	Tawny-winged Woodcreeper	2	3				
Dendrocincla homochroa	Ruddy Woodcreeper	5	2	3			
Sittasomus griseicanillus	Olivaceous Woodcreeper	2	-	9	2	6	4
Glyphorhynchus spirurus	Wedge-billed Woodcreeper	5	6	7	11	9	2
Xiphorhynchus	Spotted Woodcreeper	1	1	, 1	11		1
ervthronygius	sponed woodereeper	1	1	-			1
Lepidocolantes soulevetii	Streak-headed Woodcreeper						1
Campylorhamphus pusillus	Brown-billed Scythebill	2	1	2	3		-
Thampophilidae		-	•	-	U		
Dysithamnus mentalis	Plain Antvireo	5	12	3			6
Myrmotherula schisticolor	Slaty Antwren	3	7	5	1	4	6
Microrhonias auixensis	Dot-winged Antwren	5	,	1	1	•	0
Cercomacra tyrannina	Dusky Anthird	2		1	1	1	
Gymnonityhs leucasnis	Bicolored Anthird	8	4	3	1	1	
Formicariidae	Dicolored Antonia	0	т	5			
Formicarius analis	Black-faced Antthrush	12	1	Λ			
Grallaria quatimalensis	Scaled Antritta	12	т	т			
Cotingidae	Seared Antpitta	1					
Cotinga ridawayi	Turgoise Cotings					1	
Dipridaa	Turquise Counga					1	
Manacus aurantiacus	Orange collared Manakin	2	1		1		7
Corapino altera	White ruffed Manakin	25	20	70	21	35	117
Corupipo uliera	Plue grouped Manakin	21	11	24	21	2	117
Fipra coronaia	Blue-clowned Manakin	21	11	24	/	3	17
Microsoftag alagain aug	Oshra hallind Elwastahan	14	12	11	17	11	40
Mionecies oleagineus	Olive stringd Elyesteher	14	15	11 6	17	11	40
Mionectes olivaceus	Slate come d Elucatel er	1		0			2
Leptopogon superciliaris	Slaty-capped Flycatcher	1		4	2		2
Zimmerius vilissimus	Paitry Tyrannulet	2		1	2		1
Lopnotriccus pileatus	Scale-crested Pygmy-tyrant	3		2	1	2	1
Rhynchocyclus brevirostris	Eye-ringed Flatbill	1	1	1	4	3	4
Platyrinchus coronatus	Golden-crowned Spadebill	1	1	1	•		
Platyrinchus mystaceus	White-throated Spadebill	5	4	8	2	l	4
Myiobius sulphureipygius	Sulphur-rumped Flycatcher	3	1	5		3	15
Empidonax traillii	Willow Flycatcher				1		
Attila spadiceus	Bright-rumped Attila		1	1			1
Myiarchus tuberculifer	Dusky-capped Flycatcher				2		
Pachyramphus	White-winged Becard					1	4
polychopterus			~				
Schiffornis turdinus	Thrush-like Schiffornis		3				
Troglodytidae					_		
Thryothorus rutilus	Rufous-breasted Wren	1			2		1
Thryothorus semibadius	Riverside Wren	2	3	1			
Troglodytes aedon	House Wren				1	1	

Family and Latin name	English name	For1	For2	For3	Frag1	Frag2	Frag3
Henicorhina leucosticta	White-breasted Wood-wren	37	38	30	11	8	22
Henicorhina leucophrys	Grav-breasted Wood-wren	1	50	50	11	0	3
Microcerculus marginatus	Scaly-breasted Wren	1	5	2			6
Turdidae	Seary-breasted with	-	5	2			0
Myadestes melanons	Black-faced Solitaire			1			1
Catharus aurantiirostris	Orange hilled Nightingale thrush	18	24	12	28	27	22
Turdus aravi	Clay colored Robin	3	2 4 1	12	20	27	12
Turdus assimilis	White threated Thrush	5	6	15 2	3	2	5
Poliontilidae	winte-unoated Thrush	5	0	2	5	2	5
Pamphoogenus melanumus	Long billed Gnotwron	4	1				2
Viroopidoo	Long-billed Gliatwren	4	1				2
Hylophilus ochraceicens	Towny crownod Groonlat	1					
Demilidee	Tawity-crowned Greennet	1					
Parula nitianumi	Tropical Darula			1			
Faruta pittayumi Saiumua nauahangaanaia	Northern Waterthruch			1			
Seturus novedoracencis	Northern Waterthrush			4			
Seturus motacilia	Slate threated Dedetert	5	4	2 10	0	1	2
Myioborus miniatus	State-throated Redstart	5	4	18	9	1	3
Basileuterus culicivorus	Golden-crowned Warbler	1	I		0	-	1
Basileuterus rufifrons	Rufous-capped Warbler	I ~	-		8	5	1
Basileuterus fulvicauda	Buff-rumped Warbler	5	1	4	1	1	2
Coerebidae		_			-		_
Coereba flaveola	Bananaquit	7		1	2		7
Thraupidae							
Eucometis penicillata	Gray-headed Tanager	6	1	5	13	1	5
Habia rubica	Red-crowned Ant-tanager	3	5	1	_	1	12
Ramphocelus costaricencis	Cherrie's Tanager				5		1
Thraupis episcopus	Blue-gray Tanager				5		
Euphonia luteicapilla	Yellow-crowned Euphonia				1	2	
Euphonia laniirostris	Thick-billed Euphonia	2	1				1
Euphonia elegantissima	Elegant Euphonia		3				
Euphonia imitans	Spot-crowned Euphonia	1					2
Tangara icterocephala	Silver-throated Tanager		2	13	17	10	2
Tangara guttata	Speckled Tanager			1	1		
Tangara gyrola	Bay-headed Tanager			2	2		
Dacnis venusta	Scarlet-thighed Dacnis			1			
Emberizidae							
Volatinia jacarina	Blue-black Grassquit		1				
Sporophila corvina	Variable Seedeater	6	3	1	7	2	13
Sporophila corvina	Yellow-bellied Seedeater						1
Oryzoborus funereus	Thick-billed Seed-finch					1	6
Tiaris olivacea	Yellow-faced Grassquit	2		2	2		1
Atlapetes albinucha	White-naped Brush-finch				2		
Buarremon brunneinucha	Chesnut-capped Brush-finch	1	1	5	7	3	
Buarremon torauatus	Stripe-headed Brush finch	2	-	1	11	1	7
Arremon aurantiirostris	Orange-billed Sparrow	29	21	12	7	12	, 30
Zonotrichia capensis	Rufous-collared Sparrow		-1		,	1	20
Cardinalidae	tarous contaroa opariow					1	
Saltator striatipectus	Streaked Saltator				5		3
Saltator maximus	Buff-throated Saltator	3	1	1	15	7	7
Cvanocompsa cvanaoides	Blue-black Grosbeak	8	11	5	2	, 1	, 11
Cyanocompsu cyanaoides	Dide older Olobour	0	11	5	4	1	11

Family and Latin name	English name	For1	For2	For3	Frag1	Frag2	Frag3
Total		410	327	465	339	230	527

For1, For2, and For3 are the transects in the Las Cruces Forest, and Frag1, Frag2,

and Frag3 are the transects in the small forest fragments. The taxonomy is based on ref.

21.

Supporting information for Sekercioglu *et al.* (2002) *Proc. Natl. Acad. Sci. USA* **99** (1), 263–267. (10.1073/pnas.012616199)

Species	Forest-dependence
Sittasomus griseicapillus	Intermediate
Glyphorhynchus spirurus	Intermediate
Automolus ochrolaemus	Intermediate
Automolus rubiginosus	High
Dysithamnus mentalis	High
Myrmotherula schisticolor	High
Myiobius sulphureipygius	High
Henichorhina leucosticta	High
Microcerculus luscinia	High
Myioborus miniatus	Intermediate
Phaeothlypis fulvicauda	Low
Habia rubica	High
Eucometis penicillata	High
Atlatepes atricapillus	Intermediate

Table 3. Fourteen understory insectivorous species from which we obtained at least four diet samples in each treatment