

## EDGE RESPONSES OF TROPICAL AND TEMPERATE BIRDS

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**ABSTRACT.**—Tropical birds may differ from temperate birds in their sensitivity to forest edges. We provide predictions about the proportions of tropical and temperate species that should avoid or exploit edges, and relationships between natural-history characters and edge responses. We conducted exploratory meta-analyses from 11 studies using 287 records of 220 neotropical and temperate species' responses to edges to address our predictions. A higher proportion of neotropical species were edge-avoiders compared with temperate species and a higher proportion of temperate species were edge-exploiters compared with neotropical species. Edge-avoiding responses were positively associated with being an insectivore for neotropical birds, and with being of small body mass and a latitudinal migrant for temperate birds. Temperate edge-exploiters were less likely to be insectivores and migrants than temperate birds that were not edge-exploiters. A greater proportion of neotropical birds than temperate birds may be at risk from forest fragmentation if edge-avoidance is a reasonable indicator of an inability to adapt to land-cover change. Future progress in our understanding of forest bird responses to edges is dependent upon greater standardization of methods and designing studies in the context of recent theoretical developments. *Received 27 October 2005. Accepted 30 August 2006.*

The conversion of forest to other land-cover types leads to creation of edges (Murcia 1995). Species' responses to land-cover change and edge creation in temperate forests may not be generalizable to tropical forests (Sisk and Battin 2002, Stratford and Robinson 2005). Negative edge responses may be stronger in tropical than temperate systems leading to greater effects of fragmentation in tropical compared to temperate systems (Harris and Reed 2002, Fahrig 2003). Stronger responses could manifest themselves as a greater proportion of species showing negative responses to edges in the tropics, or as relatively greater negative influences of edge on population

densities of species in the tropics. Here we focus on the possibility that a greater proportion of species is negatively influenced by edges in the tropics.

A recent theoretical framework suggests that species' resource requirements are an important component in understanding why some species have positive or negative responses to edge while no responses are observed for other species (Ries and Sisk 2004). We use the term resource broadly to encompass requirements such as food and the environmental conditions that an organism is able to tolerate, including, for example, light levels and temperature. We assume that resource requirements are typically narrower for tropical forest species than for temperate forest species (Marra and Remsen 1997). We consider the implications of this assumption for the proportions of species with negative and positive responses to edges in the two regions. We also explore whether insectivory and being a latitudinal migrant are associated with edge-avoidance to examine whether some consistencies exist regarding particular natural-history characters and edge responses. Edge effects are important mechanistic explanations for the negative effects of fragmentation (e.g., Didham et al. 1998, Laurance et al. 2002) and analyses to address these issues will aid in the search for patterns regarding edge response. We used data from the literature to examine five predictions.

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*A Higher Proportion of Tropical Species Should Be Edge-avoiders Compared with Temperate Species.*—Humid tropical forest environments, particularly in the understory, show less seasonal variability in microclimate than many other environments (e.g., Karr 1976). Tropical forests provide some resources year-round that are not found as consistently in the temperate zone (e.g., small arthropods [Greenberg 1995], fruit and nectar [Poulsen 2002]). The species inhabiting such environments are likely to be more narrow in their resource requirements than those inhabiting temperate forest (Stratford and Robinson 2005). Temperate species experience a greater range of environmental conditions during a year than most resident species of the humid tropics because of the substantial environmental differences that exist between winter and summer in the temperate zone (Karr 1976). Temperate species are physiologically capable of tolerating conditions that lineages of tropical forest species have not encountered for many generations (Stevens 1989, Stratford and Robinson 2005). Temperate species that migrate latitudinally typically encounter and use a wider range of resources (e.g., Rodewald and Brittingham 2004) than those likely to be encountered by sedentary residents of humid tropical forests. Many microclimatic differences between edge and interior cease to exist in the winter in the temperate zone, effectively eliminating non-edge habitat (Young and Mitchell 1994). In contrast, edge-interior differences in tropical humid forests should be present year-round. Thus, we expect a larger proportion of tropical than temperate species should avoid edges because more tropical species will have a lower capacity to use/tolerate the resources available in edges, which often differ from those farther from edges (Chen et al. 1993, Fox et al. 1997, Williams-Linera et al. 1998).

*A Higher Proportion of Temperate Species Should Be Edge-exploiters Compared with Tropical Species.*—Báldi (1996) suggested that historically higher levels of patchiness in temperate landscapes compared with tropical landscapes have resulted in a greater proportion of species adapted to edge in temperate regions compared with tropical regions. Báldi (1996) emphasized patchiness on a regional scale but if temperate landscapes showed

greater patchiness than tropical landscapes on a local scale as well, we would expect that more temperate than tropical species have adapted to use resources from different and adjacent habitats. This complementary resource distribution (e.g., nest sites in one habitat and foraging sites in another) has been suggested as an important mechanism leading to positive edge responses (Ries and Sisk 2004). This prediction is distinct in that a greater proportion of avoiders in one region compared with a second region does not necessarily lead to a greater proportion of exploiters in the second region. This is because all species do not necessarily exhibit avoidance or exploitation of edges but may not respond to edges.

*Insectivores Are More Likely to Show Edge-avoiding Responses Than Non-insectivores in Both Regions.*—Insectivores are often specialized in their food preferences and/or foraging techniques (Snow 1976, Rosenberg 1990, Marra and Remsen 1997), necessitating a reliance on specific substrates in particular habitats with particular environmental conditions (e.g., dead leaves in understory forest). Some groups of insects may be more abundant in forest edge than interior but many groups are less abundant, with the overall effect that edge insect communities may be significantly different from interior communities (Didham et al. 1998). We expect that insect communities of the forest edge will provide lower-quality resources than insect communities of the forest interior for insectivorous birds, given their relatively high level of specialization. Nectarivores, frugivores, and granivores use food resources that are often dispersed in space and time (Karr 1976, Stiles 1985, Levey 1988a, Stiles and Skutch 1989, Blake and Loiselle 1991), making mobility and use of environments with varying conditions more likely than for many insectivores. Omnivores are flexible in their food choices, helping to buffer them from environmental variability (Karr 1976). Thus, we expect insectivores are more likely to avoid edges. We expect this effect to be stronger in the tropics because of the greater foraging and food choice specialization demonstrated by tropical compared to temperate insectivores (Marra and Remsen 1997).

*Non-insectivores are More Likely to Show Edge-exploiting Responses than Insectivores*

TABLE 1. Temperate studies used in analyses were between 29° N and 44° N and tropical studies were between 2° S and 9° N.

Reference	Location	Latitude	Records ( <i>n</i> )
<b>Temperate</b>			
Brand and George (2001)	Humboldt County, CA	41° N	14
Germaine et al. (1997)	Green Mountain NF, VT	44° N	24
King et al. (1997)	White Mountain NF, VT	44° N	5
Kroodsmma (1984)	Oak Ridge, Roane, and Anderson counties, TN	36° N	17
Noss (1991)	Alachua County, FL	29° N	26
Ortega and Capen (2002)	Green Mountain NF, VT	44° N	29
Sisk (1992)	San Mateo County, CA	37° N	25
Strelke and Dickson (1980)	Nacogdoches and Cherokee counties, TX	32° N	10
<b>Tropical</b>			
Laurance (2004)	Amazonas State (north of Manaus), Brazil	2° S	100
Restrepo and Gómez (1998)	Ricaurte Municipality, Nariño Dep., Colombia	1° N	23
Sisk (1992)	Coto Brus, Puntarenas, Costa Rica	9° N	14

*in Both Regions.*—Plants favored by non-insectivores, including fruit and nectar producers, are often more common in high-light areas like gaps and edges, than in intact forest (Stiles 1975, Levey 1988b, Rodewald and Brittingham 2004). Thus, where resources are concentrated at edges, it is predicted that species that rely on these resources (i.e., frugivores and nectarivores), will exploit edges (Ries and Sisk 2004).

*Latitudinal Migrants in Temperate Regions are More Likely to Show Edge-avoiding Responses Than Non-migrants.*—Migrants appear to be less resistant to land-cover and climate changes than non-migrant species of temperate regions and have shown declines with habitat and climatic changes (e.g., Flather and Sauer 1996, Lemoine and Böhning-Gaese 2003). The mechanisms responsible for their susceptibility to disturbance are unclear, but Stevens (1989) and O'Connor (1992) suggested that migrants are less able to withstand environmental variability than non-migrants of temperate regions. Thus, we expect migrants will be more inclined to avoid edge than non-migrants.

We did not develop a specific prediction involving body size. Some work suggests larger birds may be more sensitive to land-cover disturbance or less likely to use edge than smaller birds (e.g., Thiollay 1995, Brand 2004). However, large species may be able to use edge habitat briefly and easily leave. The travel and time costs for a small species to enter and leave edge habitat that turns out to be unsuitable may be

higher relative to energy reserves than for large species. Thus, we investigated whether body size was associated with edge response in both regions to examine if any patterns existed that could guide future work.

#### METHODS

We searched Biological Abstracts from 1969 through early 2005 (Biological Abstracts 1969–2005) and two reviews (Kremsater and Bunnell 1999, Sisk and Battin 2002) to select 11 studies (Table 1) that estimated either abundance or density of individual species as a function of distance from an abrupt forest edge (i.e., forest-clearcut edges, forest-field edges or forest-road edges). We excluded studies that measured nest predation, nest success, or reported only species richness or abundance of avian guilds. We also excluded studies conducted at gradual edges (e.g., forest-shrubland edges) except in one case (Noss 1991), where data from several edge types were pooled but the majority of edge types were abrupt. We initially included studies from the Paleotropics as well, but these studies were few in number and we had difficulty finding natural history information for a number of the species. These studies were excluded from the final analyses. We classified the studies into those conducted in the Neotropics (between 2° S and 10° N latitude) and those conducted in the temperate zone (between 29° and 44° N latitude). We considered temperate species to be those that spent all or part of the year at or above 29° latitude and neotropical

species to be those that did not meet this criterion.

We constructed two, separate binary response variables—avoiders (avoider = 1, non-avoider = 0) and exploiters (exploiter = 1, non-exploiter = 0)—to examine edge avoidance and exploitation as distinct ecological phenomena. Each species was included in each of these two response variables because we viewed these responses as independent. If a species is not an avoider, this does not predispose it to be an exploiter. Some species could have no response to edges. Thus, for our edge-avoidance analyses, non-avoiders were any species that did not exhibit edge avoidance (e.g., both exploiters and species with no response) in each region. Non-exploiters consisted of avoiders and species with no response in each region for our edge-exploitation analyses.

We designated each species in each study as an avoider (significantly greater abundance or density away from edges), an exploiter (significantly greater abundance or density at edges), or as having no response (no increase or decrease in abundance at edges) based on the conclusions reached by the authors of each original study except in three cases (Strelke and Dickson 1980, Quintela 1985, and Sisk 1992–neotropical data). We conducted our own goodness-of-fit tests with *G*-statistics and Williams' corrections (Sokal and Rohlf 1995) for these studies to make designations. We excluded species' records if the expected values used for designations were less than five (Siegel and Castellan 1988).

A number of species in the temperate data set had multiple records because they were detected in more than one study. Thus, we developed three temperate data sets that differ in conservatism. The most conservative data set is the "reduced temperate data set" ( $n = 54$  species,  $n = 54$  records) that includes only species where all studies agreed as to the designation for that species (i.e., avoider, neutral, or no response). The "one-designation temperate data set" ( $n = 83$  species,  $n = 83$  records) is less conservative because we included all species and assigned only one designation to each, including those that demonstrated one type of directional response (avoid or exploit) but exhibited no response in one or more of the studies. For example, if a species was designated as an avoider

by two studies but showed no response in a third study, it was considered an avoider in the one-designation temperate data set. We excluded only one species from this data set (Red-eyed Vireo, [*Vireo olivaceus*]) because it had conflicting designations (i.e., both avoid and exploit) in different studies. We created and analyzed this data set because species designated as an avoider or exploiter by at least one study showed an avoid- or exploit-response in at least some situations. Some of the multiple designations likely reflected real differences in responses (Ries and Sisk 2004), but some of the no response results may have been a result of small sample sizes. Because of the exploratory nature of these analyses, we wanted to detect potential patterns if they existed. The third data set is the "full temperate data set" ( $n = 83$  species,  $n = 150$  records, Appendix) which includes all species (except the Red-eyed Vireo for the same reason given above) with all their designations. This data set most accurately reflects the variability in the designations of the species across the different studies.

The neotropical data set contained only one species with conflicting designations, the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) and we removed the records for this species. The neotropical data set had 137 species with 137 total records (Appendix).

We tabulated the number of species exhibiting each edge response (avoider or non-avoider, and exploiter or non-exploiter) in each region to compare proportions of avoiders/non-avoiders and exploiters/non-exploiters in the temperate and neotropical regions. We are aware of the limitations of simple tabulations (Wang and Bushman 1999, Gates 2002) but the 11 studies used a variety of distances, sampling techniques, and statistical techniques that prevented us from calculating effect sizes (Chalfoun et al. 2002). We used the reduced and one-designation temperate and neotropical data sets in contingency tables, with *G*-tests of significance and Williams' correction (Sokal and Rohlf 1995) for these analyses. We did not use the full data set because, for contingency table analyses, a species has to be designated as having only one response.

We classified species as primarily insectivores (insectivore = 1, other = 0) based on DeGraaf et al. (1985) for temperate species. We used information from Hilty and Brown

(1986), Stiles and Skutch (1989), Karr et al. (1990), Restrepo and Gómez (1998), del Hoyo et al. (1999), Renjifo (1999), and del Hoyo et al. (2003, 2004, 2005) to classify neotropical species. We classified temperate species by latitudinal migration patterns (neotropical migrant = 1, short-distance migrant or resident = 0) using Robbins et al. (1989) and range maps (Cornell Laboratory of Ornithology Online Bird Guide [2003]). We took body mass estimates from Dunning (1993). When separate estimates were given for males and females, we used the mean of the two values. We investigated the relationships between natural-history variables and species' responses to edges by conducting separate analyses (four analyses) for each combination of response type (avoid or exploit) and geographic region (temperate and neotropical) using the one-designation and full data sets. The reduced data set was too small to use for these analyses.

Our full data set contained many different species from the same families and multiple records of some species. The avoid/exploit response may be similar for closely related species (or for multiple records of the same species). Our data would not be truly independent if this was the case and we included random effects for both species and family in a generalized mixed linear model (GLIMMIX macro in SAS, Littell et al. 1996) to control for taxonomically clustered data (e.g., Sol et al. 2005). Similarly, the exploit/avoid responses could be correlated within studies and we included study as a random effect. Insectivory and migratory traits were included as fixed effects. This approach adjusts for possible correlations within each of the groups of repeated observations (*sensu* Sol et al. 2005). We also conducted the analyses without the random effects to allow for comparisons between results.

We were unable to test for interactions between the natural-history variables, given the sample sizes. Instead we conducted *t*-tests to examine whether body mass differed for insectivores and non-insectivores using the neotropical and one-designation temperate data sets. We also used a *t*-test to examine whether body mass differed for migrants and non-migrants using the one-designation temperate data set.

We did not use Bonferroni corrections in our analyses because of recent work indicating these corrections reduce power to unrea-

sonable levels (Roback and Askins 2005). We considered  $\alpha = 0.10$  as our significance level for all analyses because of the low power of our tabulation techniques and because of the exploratory nature of our analyses.

Species' designations and natural-history characters are available from the first author. Species and family assignments generally follow the American Ornithologists' Union (2006) and Remsen et al. (2006).

## RESULTS

A higher proportion of species was classified as edge-avoiders in the neotropical data set compared with either the reduced or one-designation temperate data sets (temperate: 13%, neotropical: 50%,  $G = 24.10$ ,  $P < 0.001$ ,  $n = 191$ ,  $df = 1$ ; temperate: 17%, neotropical: 50%,  $G = 25.08$ ,  $P < 0.001$ ,  $n = 220$ ,  $df = 1$ , respectively). Proportions of species classified as edge-exploiters were equivalent in both regions when using the reduced temperate data set (temperate: 33%, neotropical: 31%,  $G = 0.13$ ,  $P = 0.72$ ,  $n = 191$ ,  $df = 1$ ) while a higher proportion of species was classified as edge-exploiters for the temperate zone when using the one-designation temperate data set (temperate: 48%, neotropical: 31%,  $G = 6.67$ ,  $P = 0.01$ ,  $n = 220$ ,  $df = 1$ ).

Temperate avoiders and non-avoiders did not differ in diet (insectivore or not,  $P = 0.29$ ), body mass ( $P = 0.16$ ), or whether they were a migrant or not ( $P = 0.53$ ) for the one-designation data set, without random effects. Results were similar when random effects were included (Table 2). Using the full temperate data set, avoiders were significantly smaller than non-avoiders, without random effects ( $P = 0.10$ ), and more likely to be latitudinal migrants than non-avoiders, with or without random effects ( $P = 0.05$  and  $P = 0.05$ , respectively, Table 3). Exploiters were less likely to be insectivores than non-exploiters for the one-designation temperate data set, with or without random effects ( $P = 0.08$  and  $P = 0.08$ , respectively, Table 2). Exploiters were less likely to be migrants than non-exploiters for the full temperate data set when random effects were not included in the analyses ( $P = 0.07$ , Table 3).

Neotropical avoiders were more likely to be insectivores than non-avoiders, with or without random effects ( $P = 0.10$  and  $P = 0.02$ , re-

TABLE 2. One-designation temperate data set. None of the natural-history variables differed for avoiders ( $n = 14$  species) and non-avoiders ( $n = 69$  species). Exploiters ( $n = 40$  species) were less likely to be insectivores than non-exploiters ( $n = 43$  species).  $P$ -values are from mixed models containing the natural-history variable and random effect for family.

Variable	Avoider	Non-avoider	Random effects $P$ -value	No random effects $P$ -value
Body mass, mean $\pm$ SE	17.9 $\pm$ 4.9	35.7 $\pm$ 5.5 <sup>a</sup>	0.16	0.16
Insectivore, % of species	50.0	34.8	0.29	0.29
Latitudinal migrant, % of species	57.1	47.8	0.53	0.53
	Exploiter	Non-exploiter		
Body mass, mean $\pm$ SE	36.7 $\pm$ 5.8	28.8 $\pm$ 7.3 <sup>a</sup>	0.42	0.42
Insectivore, % of species	27.5	46.5	0.08	0.08
Latitudinal migrant, % of species	42.5	55.8	0.23	0.23

<sup>a</sup>  $n = 68$  (avoiders) and  $n = 42$  (exploiters) for the body mass analysis because we omitted one extreme outlier (*Corvus corax*).

spectively, Table 4). The difference in  $P$ -values with and without random effects is due to a family effect with study having no effect. Body mass did not differ for neotropical avoiders and non-avoiders, with or without random effects ( $P = 0.81$  and  $P = 0.63$ , respectively, Table 4). Neither diet (insectivore or not) nor body mass differed for neotropical exploiters and non-exploiters, with random effects ( $P = 0.20$ ,  $P = 0.72$ , respectively, Table 4). Results were similar without random effects.

Temperate migrants had a smaller body mass than non-migrants and temperate insectivores had a smaller body mass than non-insectivores ( $t = -2.88$ ,  $P < 0.01$ ,  $n = 82$ ,  $df = 80$  and  $t = -4.54$ ,  $P < 0.001$ ,  $n = 82$ ,  $df = 80$ , respectively). Neotropical insectivores also were smaller than non-insectivores ( $t = -2.38$ ,  $P < 0.01$ ,  $n = 136$ ,  $df = 134$ ).

## DISCUSSION

A higher proportion of neotropical species were edge-avoiders compared with temperate species while a higher proportion of temperate compared with neotropical species showed edge-exploiting responses. These patterns may help explain the apparent higher bird species richness at edges in the temperate zone (reviewed in Kremsater and Bunnell 1999, Sisk and Battin 2002) compared to the reduced bird species richness at tropical forest edges (Lovejoy et al. 1986, Dale et al. 2000, Watson et al. 2004). These patterns also suggest that forest fragmentation and edge creation may be more detrimental to neotropical species than temperate species, if edge-avoidance indicates a species' ability to withstand land-cover changes.

Work in both temperate and neotropical re-

TABLE 3. Full temperate data set. Avoiders ( $n = 22$  records) were more likely to be latitudinal migrants and had smaller body mass than non-avoiders ( $n = 128$  records). Exploiters ( $n = 44$  records) were less likely to be latitudinal migrants than non-exploiters ( $n = 106$  records).  $P$ -values are from mixed models containing the natural-history variable and random effects for family, species nested within family, and study.

Variable	Avoider	Non-avoider	Random effects $P$ -value	No random effects $P$ -value
Body mass, mean $\pm$ SE	20.0 $\pm$ 3.5	33.3 $\pm$ 3.4 <sup>a</sup>	0.17	0.10
Insectivore, % of species	40.9	35.9	0.64	0.66
Latitudinal migrant, % of species	72.7	49.20	0.05	0.05
	Exploiter	Non-exploiter		
Body mass, mean $\pm$ SE	35.5 $\pm$ 5.4	29.6 $\pm$ 3.5 <sup>a</sup>	0.60	0.37
Insectivore, % of species	29.5	39.6	0.35	0.25
Latitudinal migrant, % of species	40.9	57.5	0.14	0.07

<sup>a</sup>  $n = 127$  (avoiders) and  $n = 106$  (exploiters) for the body mass analysis because we omitted one extreme outlier (*Corvus corax*).

TABLE 4. Tropical data set. Avoiders ( $n = 68$  species) were more likely to be insectivores than non-insectivores. There were 69 species of non-avoiders, 42 species of exploiters, and 95 species of non-exploiters.  $P$ -values are from mixed models containing the natural-history variable and random effects for family and study.

Variable	Avoider	Non-avoider	Random effects $P$ -value	No random effects $P$ -value
Body mass, mean $\pm$ SE	36.8 $\pm$ 6.1 <sup>a</sup>	32.5 $\pm$ 6.4	0.81	0.63
Insectivore, % of responses	58.8	37.7	0.10	0.02
	Exploiter	Non-exploiter		
Body mass, mean $\pm$ SE	40.0 $\pm$ 10.3	32.3 $\pm$ 4.5 <sup>a</sup>	0.72	0.43
Insectivore, % of responses	38.1	52.6	0.20	0.12

<sup>a</sup>  $n = 67$  (avoiders) and  $n = 94$  (non-exploiters) for the body mass analysis because body mass for one species, *Sclerurus caudacutus*, was not available.

gions has shown increased food resources for birds (e.g., fruit, insects, and cones) in edge or gap habitats compared with interior forest (temperate region: Jokimäki et al. 1998, Brotons and Herrando 2003, Rodewald and Brittingham 2004; tropics: Levey 1988b, Restrepo et al. 1999). Some studies have shown increased pollination and fruit consumption at edges compared to interior (Galetti 2003, Montgomery et al. 2003). However, it is possible that temperate birds are more able to take advantage of extra food in edges than neotropical birds because they are more flexible in their resource use than neotropical birds. Rodewald and Brittingham (2004) showed positive relationships between resources available in edges and bird abundances in a temperate area while frugivore abundance was not related to fruit abundance in a neotropical study (Restrepo et al. 1999).

Other factors may help explain differences in the proportion of edge-avoiders and edge-exploiters in the two regions. If edge-to-interior differences in food resources are greater in temperate regions than the Neotropics, temperate birds may have more to gain by exploiting forest edges than neotropical birds. It is also possible that temperate birds' longer history of living in patchy landscapes (Báldi 1996) has provided selective pressure to be able to exploit edge resources. In contrast, the relatively narrow environmental conditions under which many present-day neotropical species, particularly forest species, evolved (Stevens 1989), may have diminished their ability to use habitat (edges) that results from land-cover change processes including forest fragmentation (Stratford and Robinson 2005). Finally, if temperate birds' more synchronous

annual cycles cause more competition for resources during the nesting season, there may be a greater impetus for them to exploit differences that exist between edge and interior, compared with neotropical species. Data to formally address these ideas are needed.

Our finding that a higher proportion of neotropical avoiders were insectivores, compared with non-avoiders, has been indicated in other studies (Restrepo and Gómez 1998, Kremsater and Bunnell 1999, Dale et al. 2000, Beier et al. 2002, but see Watson et al. 2004). Body mass did not differ for neotropical avoiders and non-avoiders, but insectivores had a significantly smaller mass than non-insectivores. This suggests that insectivory and body size may interact so that small insectivores are particularly likely to avoid edge. The relationship between insectivory and edge-avoidance was somewhat weaker when family was included as a random effect in the analysis. This finding suggests the relationship between insectivory and edge-avoidance may be driven, at least in part, by edge-avoidance by particular families of birds (e.g., the formicariids). The mechanisms that drive these patterns need to be investigated. Neotropical insectivores may avoid edge because they tend to have narrow diets, narrow ranges of tolerable environmental conditions, and use specialized microhabitats that are not available in forest edge (Rosenberg 1990, Canaday 1996, Lindell et al. 2004). Small birds may experience higher predation risk at edges or may spend large amounts of energy if they venture into unsuitable edge habitat and then have to leave. Investigations of the types of resources used by small neotropical insectivores, and the availability of these resources in edge and in-

terior habitats, would help resolve this question. Experimental manipulations of resources such as food and light in edge and interior habitat are also needed.

The lack of a relationship between insectivory and edge-avoidance in temperate birds suggests that insectivory is not as great a driver or indicator of edge response as it is for neotropical birds. Temperate insectivores may be less specialized than neotropical insectivores and able to use a wider range of habitat types including edge. We found that migrants are more likely to avoid edge than non-migrants in the temperate zone (similar to Flather and Sauer [1996] and Sisk and Battin [2002]), indicating they may be more susceptible as a group than temperate residents to land-cover change. Temperate migrants were also smaller than temperate non-migrants, raising the possibility of an interaction between migratory behavior, body mass, and edge-avoidance.

A lower percentage of exploiters compared with non-exploiters were insectivores for the neotropical and the two temperate data sets. However, only the one-designation temperate data set showed a significant difference. The data are suggestive, if not conclusive, that species that use resources besides insects are better able to take advantage of edge resources and/or that resources that tend to be abundant in edges, compared to interior, are more useful to non-insectivores. Previous work indicates that frugivorous species are more edge-tolerant than many insectivorous species (Restrepo and Gómez 1998, Dale et al. 2000, Beier et al. 2002), although this pattern is not always strong (Beier et al. 2002) nor consistent geographically (Watson et al. 2004).

We assessed edge avoidance and edge exploitation primarily as behavioral responses (i.e., habitat selection), driven by distributions of resources. We assume that in most cases organisms are able to select appropriate habitat and this process drives much of the variation in abundance as a function of distance to edge. However, differing predation rates on individuals in edge compared to interior, or differing nest success as a result of predation or microclimate (e.g., McCollin 1998, Flaspohler et al. 2001) may influence abundance as a function of edge through demographic processes, particularly in cases where mis-

matches occur between what an organism perceives to be suitable habitat and what actually is suitable habitat, (i.e., ecological traps) (Gates and Gysel 1978). These processes have received substantial attention in the temperate zone but studies to investigate these processes in the Neotropics are limited and should be a priority in the future (Bátary and Báldi 2004).

We examined food resources as a first step in documenting potential relationships between edge avoidance or exploitation and the use of particular resources while we did not examine such associations with regard to nest site resources. This was partially a result of our expectation that food resources, given they are vital to every day survival while nest sites are only critical during some seasons of the year, would be more likely to show such associations, and partially a result of the lack of data on nest sites for many neotropical species. Recent work supports the idea that food requirements, particularly being an insectivore, predispose neotropical birds to being susceptible to environmental disturbance while nest site requirements do not (Sigel et al. 2006). We suggest that future work explore such potential associations because relationships with regard to resources besides food could be more subtle or complex.

Edge effects are widely recognized (Kremasater and Bunnell 1999, Ries et al. 2004), and well documented for a range of organisms and abiotic variables (e.g., Laurance et al. 2002). We were surprised at the small number of studies that addressed density and abundance of birds as a function of distance to edge. Investigators have used a range of techniques to investigate edge effects. The three neotropical studies all involved mist netting yet the investigators used different distance intervals and/or different numbers of distance categories over which to measure edge effects. We were able to counter these differences to some extent by using a similar statistical technique (*G*-tests of goodness-of-fit) to assess whether distance to edge was associated with abundance. A number of species with multiple records were classified differently by different investigators. For example, Red-eyed Vireos were detected in six studies and classified as both avoiders and exploiters, while in some studies no response was detected. It is difficult to know which multiple designations represent

meaningful biological variation among populations or study sites and which are simply a result of different sampling designs. There are indications that abiotic and vegetation edge effects vary over relatively small distances near edge, and that edge effects may penetrate several hundred meters into forest (Laurance et al. 2002). We suggest intervals of 25–50 m (based on the species under consideration) to a maximum distance into forest of at least 500 m is likely to be the most useful in documenting edge effects in species abundances. Future progress in understanding patterns and processes of edge responses is highly dependent upon greater standardization among studies with regard to distance intervals, field techniques, and statistical techniques.

We also suggest that studies compare edge effects at different times of year. All of the temperate studies, except one (Noss 1991), sampled exclusively during the nesting season. However, recent work suggests that temporal effects may help explain some of the observed variation of edge responses within species (Ries et al. 2004). Patterns may be different during winter when it could be beneficial for many species to avoid edge in temperate regions (e.g., Dolby and Grubb 1999).

Our results are drawn from studies in the New World and at one general edge type. Recent work suggests that responses to edges may vary geographically (e.g., Watson et al. 2004) and among edge types (Ries and Sisk 2004). A recent theoretical framework (Ries and Sisk 2004) emphasizes the importance of considering the relative availability of resources in adjacent patch types to be able to predict the edge-responses of particular species. Increasing the geographical range of future edge studies, standardizing methodologies, and incorporating theoretical developments into study design will increase our understanding of the influences of edges on populations and communities.

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#### LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 2006. Check-list of North American birds. [www.aou.org/checklist/index.php3/](http://www.aou.org/checklist/index.php3/) (accessed 7 June 2006).
- BÁLDI, A. 1996. Edge effects in tropical versus temperate forest bird communities: three alternative hypotheses for the explanation of differences. *Acta Zoologica Academiae Scientiarum Hungaricae* 42:163–172.
- BATÁRY, P. AND A. BÁLDI. 2004. Evidence of an edge effect on avian nest success. *Conservation Biology* 18:389–400.
- BEIER, P., M. VAN DRIELEN, AND B. L. KANKAM. 2002. Avifaunal collapse in West African forest fragments. *Conservation Biology* 16:1097–1111.
- BIOLOGICAL ABSTRACTS. 1969–2005. The Thomson Corporation, Philadelphia, Pennsylvania, USA.
- BLAKE, J. G. AND B. A. LOISELLE. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. *Auk* 108:114–130.
- BRAND, L. A. 2004. Prediction and assessment of edge response and abundance for desert riparian birds in southeastern Arizona. Dissertation. Colorado State University, Fort Collins, USA.
- BRAND, L. A. AND T. L. GEORGE. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. *Auk* 118:678–686.
- BROTONS, L. AND S. HERRANDO. 2003. Effect of increased food abundance near forest edges on flocking patterns of Coal Tit *Parus ater* winter groups in mountain coniferous forests. *Bird Study* 50:106–111.
- CANADAY, C. 1996. Loss of insectivorous birds along a gradient of human impact in Amazonia. *Biological Conservation* 77:63–77.
- CHALFOUN, A. D., F. R. THOMPSON, AND M. J. RATNASWAMY. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16:306–318.
- CHEN, J., J. R. FRANKLIN, AND T. A. SPIES. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219–237.
- CORNELL LABORATORY OF ORNITHOLOGY. 2003. Online bird guide. [www.birds.cornell.edu/programs/AllAboutBirds/](http://www.birds.cornell.edu/programs/AllAboutBirds/) (accessed July 2005).
- DALE, S., K. MORT, R. SOLVANG, AND A. J. PLUMPTRE. 2000. Edge effects on the understory bird community in a logged forest in Uganda. *Conservation Biology* 14:265–276.
- DEGRAAF, R. M., N. G. TILGHMAN, AND S. H. ANDERSON. 1985. Foraging guilds of North American birds. *Environmental Management* 9:493–536.
- DEL HOYO, J., A. ELLIOTT, AND D. A. CHRISTIE (EDITORS). 2003. Handbook of the birds of the world.

- Volume 8. Broadbills to tapaculos. Lynx Edicions, Barcelona, Spain.
- DEL HOYO, J., A. ELLIOTT, AND D. A. CHRISTIE (EDITORS). 2004. Handbook of the birds of the world. Volume 9. Cotingas to pipits and wagtails. Lynx Edicions, Barcelona, Spain.
- DEL HOYO, J., A. ELLIOTT, AND D. A. CHRISTIE (EDITORS). 2005. Handbook of the birds of the world. Volume 10. Cuckoo-shrikes to thrushes. Lynx Edicions, Barcelona, Spain.
- DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL (EDITORS). 1999. Handbook of the birds of the world. Volume 5. Barn-owls to hummingbirds. Lynx Edicions, Barcelona, Spain.
- DIDHAM, R. K., P. M. HAMMOND, J. H. LAWTON, P. EGGLETON, AND N. E. STORK. 1998. Beetle species responses to tropical forest fragmentation. *Ecological Monographs* 68:295–323.
- DOLBY, A. A. AND T. C. GRUBB, JR. 1999. Effect of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. *Condor* 101:408–412.
- DUNNING, JR., J. B. 1993. CRC Handbook of avian body masses. CRC Press, Boca Raton, Florida, USA.
- FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.
- FLATHER, C. H. AND J. R. SAUER. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology* 77:28–35.
- FLASPOHLER, D. J., S. A. TEMPLE, AND R. N. ROSENFELD. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. *Ecological Applications* 11:32–46.
- FOX, B. J., J. E. TAYLOR, M. D. FOX, AND C. WILLIAMS. 1997. Vegetation changes across edges of rainforest remnants. *Biological Conservation* 82:1–13.
- GALETTI, M., C. P. ALVES COSTA, AND E. CAZETTA. 2003. Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. *Biological Conservation* 111:269–273.
- GATES, J. E. AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.
- GATES, S. 2002. Review of methodology of quantitative reviews using meta-analyses in ecology. *Journal of Animal Ecology* 71:547–557.
- GERMAINE, S. S., S. H. VESSEY, AND D. E. CAPEN. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. *Condor* 99:708–718.
- GREENBERG, R. 1995. Insectivorous migratory birds in tropical ecosystems: the breeding currency hypothesis. *Journal of Avian Biology* 26:260–264.
- HARRIS, R. J. AND J. M. REED. 2002. Behavioral barriers to non-migratory movements of birds. *Annales Zoologici Fennici* 39:275–290.
- HILTY, S. L. AND W. L. BROWN. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, USA.
- JOKIMÄKI, J., E. HUHTA, J. ITÄMIES, AND P. RAHKO. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Canadian Journal of Forest Research* 28:1068–1072.
- KARR, J. R. 1976. Seasonality, resource availability, and community diversity in tropical bird communities. *American Naturalist* 110:973–994.
- KARR, J. R., S. K. ROBINSON, J. G. BLAKE, AND R. O. BIERREGAARD, JR. 1990. Birds of four neotropical forests. Pages 237–269 in *Four neotropical rainforests* (A. H. Gentry, Editor). Yale University Press, New Haven, Connecticut, USA.
- KING, D. I., C. R. GRIFFIN, AND R. M. DEGRAAF. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. *Wilson Bulletin* 109:239–245.
- KREMSATER, L. L. AND F. L. BUNNELL. 1999. Edge effects: theory, evidence and implications to management of western North American forests. Pages 117–153 in *Forest fragmentation: wildlife and management implications* (J. A. Rochelle, L. A. Lehmann, and J. Wisniewski, Editors). Brill, Boston, Massachusetts, USA.
- KROODSMA, R. L. 1984. Effect of edge on breeding forest bird species. *Wilson Bulletin* 96:426–436.
- LAURANCE, S. G. W. 2004. Responses of understory rain forest birds to road edges in central Amazonia. *Ecological Applications* 14:1344–1357.
- LAURANCE, W. F., T. E. LOVEJOY, H. L. VASCONCELOS, E. M. BRUNA, R. K. DIDHAM, P. C. STOUFFER, C. GASCON, R. O. BIERREGAARD, S. G. LAURANCE, AND E. SAMPAIO. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16:605–618.
- LEMOINE, N. AND K. BÖHNING-GAESE. 2003. Potential impact of global climate change on species richness of long-distance migrants. *Conservation Biology* 17:577–586.
- LEVEY, D. J. 1988a. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58:251–269.
- LEVEY, D. J. 1988b. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69:1076–1089.
- LINDELL, C. A., W. H. CHOMENTOWSKI, AND J. R. ZOOK. 2004. Characteristics of bird species using forest and agricultural land covers in southern Costa Rica. *Biodiversity and Conservation* 13:2419–2441.
- LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Inc., Cary, North Carolina, USA.
- LOVEJOY, T. E., R. O. BIERREGAARD, JR., A. B. RYLANDS, J. R. MALCOLM, C. E. QUINTELA, L. H. HARPER, K. S. BROWN, JR., A. H. POWELL, G. V. N. POWELL, H. O. R. SCHUBART, AND M. B. HAYS. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in *Conservation biology: the science of scarcity and diver-*

- sity (M. E. Soulé, Editor). Sinauer, Sunderland, Massachusetts, USA.
- MARRA, P. P. AND J. V. REMSEN, JR. 1997. Insights into the maintenance of high species diversity in the Neotropics: habitat selection and foraging behavior in the understory birds of tropical and temperate forests. *Ornithological Monographs* 48:445–483.
- MCCOLLIN, D. 1998. Forest edges and habitat selection in birds. *Ecography* 21:247–260.
- MONTGOMERY, B. R., D. KELLY, A. W. ROBERTSON, AND J. J. LADLEY. 2003. Pollinator behaviour, not increased resources, boosts seed set on forest edges in a New Zealand Loranthaceous mistletoe. *New Zealand Journal of Botany* 41:277–286.
- MURCIA, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10:58–62.
- NOSS, R. F. 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth hammock. *Natural Areas Journal* 11:34–47.
- O'CONNOR, R. J. 1992. Population variation in relation to migrancy status in some North American birds. Pages 64–74 in *Ecology and conservation of neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, Editors). Smithsonian Institution Press, Washington, D.C., USA.
- ORTEGA, Y. K. AND D. E. CAPEN. 2002. Roads as edges: effects on birds in forested landscapes. *Forest Science* 48:381–390.
- POULSEN, B. O. 2002. A comparison of bird richness, abundance and trophic organizations in forests of Ecuador and Denmark: are high-altitude Andean forests temperate or tropical? *Journal of Tropical Ecology* 18:615–636.
- QUINTELA, C. E. 1985. Forest fragmentation and differential use of natural and man-made edges by understory birds in central Amazonia. Thesis. University of Chicago, Chicago, Illinois, USA.
- REMSSEN, JR., J. V., A. JARAMILLO, M. NORES, J. F. PACHECO, M. B. ROBBINS, T. S. SCHULENBERG, F. G. STILES, J. M. C. DA SILVA, D. F. STOTZ, AND K. J. ZIMMER. 2006. A classification of the bird species of South America. [www.museum.lsu.edu/~Remsen/SACCBaseline.html](http://www.museum.lsu.edu/~Remsen/SACCBaseline.html) (accessed 7 June 2006).
- RENJIFO, L. M. 1999. Compositional changes in a sub-andean avifauna after long-term forest fragmentation. *Conservation Biology* 13:1124–1139.
- RESTREPO, C. AND N. GÓMEZ. 1998. Responses of understory birds to anthropogenic edges in a neotropical montane forest. *Ecological Applications* 8:170–183.
- RESTREPO, C., N. GÓMEZ, AND S. HEREDIA. 1999. Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a neotropical montane forest. *Ecology* 80:668–685.
- RIES, L. AND T. D. SISK. 2004. A predictive model of edge effects. *Ecology* 85:2917–2926.
- RIES, L., R. J. FLETCHER, JR., J. BATTIN, AND T. D. SISK. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35:491–522.
- ROBACK, P. J. AND R. A. ASKINS. 2005. Judicious use of multiple hypothesis tests. *Conservation Biology* 19:261–267.
- ROBBINS, C. S., J. R. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences, USA* 86:7658–7662.
- RODEWALD, P. G. AND M. C. BRITTINGHAM. 2004. Stop-over habitats of landbirds during fall: use of edge-dominated and early-successional forests. *Auk* 121:1040–1055.
- ROSENBERG, K. V. 1990. Dead-leaf foraging specialization in tropical forest birds: measuring resource availability and use. *Studies in Avian Biology* 13:360–368.
- SIEGEL, N. G. AND N. J. CASTELLAN. 1988. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York, USA.
- SIGEL, B. J., T. W. SHERRY, AND B. E. YOUNG. 2006. Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. *Conservation Biology* 20:111–121.
- SISK, T. D. 1992. Distribution of birds and butterflies in heterogeneous landscapes. Dissertation. Stanford University, Palo Alto, California, USA.
- SISK, T. D. AND J. BATTIN. 2002. Habitat edges and avian ecology: geographic patterns and insights for western landscapes. *Studies in Avian Biology* 25:30–48.
- SISK, T. D., N. M. HADDAD, AND P. R. EHRLICH. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecological Applications* 7:1170–1180.
- SNOW, D. W. 1976. *The web of adaptation: bird studies in the American tropics*. Quadrangle, Times Book Co., New York, USA.
- SOKAL, R. R. AND F. J. ROHLF. 1995. *Biometry*. Third Edition. W. H. Freeman and Company, New York, USA.
- SOL, D., R. P. DUNCAN, T. M. BLACKBURN, P. CASSEY, AND L. LEFEBVRE. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences, USA* 102:5460–5465.
- STEVENS, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133:240–256.
- STILES, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285–301.
- STILES, F. G. 1985. Seasonal patterns and coevolution in the hummingbird-flower community of a Costa Rican subtropical forest. *Ornithological Monographs* 36:757–785.
- STILES, F. G. AND A. F. SKUTCH. 1989. *A guide to the birds of Costa Rica*. Cornell University Press, Ithaca, New York, USA.

- STRATFORD, J. A. AND W. D. ROBINSON. 2005. Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. *Frontiers in Ecology and the Environment* 3:91–98.
- STRELKE, W. K. AND J. G. DICKSON. 1980. Effect of forest clear-cut edge on breeding birds in east Texas. *Journal of Wildlife Management* 44:559–567.
- THIOLLAY, J.-M. 1995. The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. *Conservation Biology* 9:335–353.
- WANG, M. C. AND B. J. BUSHMAN. 1999. Integrating results through meta-analytic review using SAS software. SAS Institute, Inc., Cary, North Carolina, USA.
- WATSON, J. E. M., R. J. WHITTAKER, AND T. P. DAWSON. 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. *Biological Conservation* 120:311–327.
- WILLIAMS-LINERA, G., V. DOMINGUEZ-GASTELU, AND M. E. GARCIA-ZURITA. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conservation Biology* 12:1091–1102.
- YOUNG, A. AND N. MITCHELL. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation* 67:63–72.

APPENDIX. Records used in analyses to examine relationships between natural-history characters and edge-avoidance or edge-exploitation. The species represent numerous families in both the neotropical and temperate data sets.

Scientific name	Family	Study <sup>a</sup>	Avoid	Exploit
Neotropical data set				
<i>Crypturellus variegatus</i>	Tinamidae	L	0	1
<i>Geotrygon montana</i>	Columbidae	L	1	0
<i>Campylopterus largipennis</i>	Trochilidae	L	0	1
<i>Florisuga mellivora</i>	Trochilidae	L	1	0
<i>Heliothryx auritus</i>	Trochilidae	L	1	0
<i>Phaethornis bourcieri</i>	Trochilidae	L	0	1
<i>Phaethornis superciliosus</i>	Trochilidae	L	0	1
<i>Thalurania furcata</i>	Trochilidae	L	1	0
<i>Aglaiocercus coelestis</i>	Trochilidae	R	1	0
<i>Coeligena wilsoni</i>	Trochilidae	R	0	1
<i>Haplophaedia lugens</i>	Trochilidae	R	0	1
<i>Ocreatus underwoodii</i>	Trochilidae	R	0	1
<i>Phaethornis syrmatophorus</i>	Trochilidae	R	0	0
<i>Campylopterus hemileucurus</i>	Trochilidae	S	0	0
<i>Phaethornis guy</i>	Trochilidae	S	0	0
<i>Trogon rufus</i>	Trogonidae	L	1	0
<i>Trogon violaceus</i>	Trogonidae	L	1	0
<i>Chloroceryle aenea</i>	Alcedinidae	L	1	0
<i>Momotus momota</i>	Momotidae	L	1	0
<i>Galbula albirostris</i>	Galbulidae	L	0	1
<i>Jacamerops aureus</i>	Galbulidae	L	0	1
<i>Bucco capensis</i>	Bucconidae	L	0	1
<i>Bucco tamatia</i>	Bucconidae	L	0	1
<i>Malacoptila fusca</i>	Bucconidae	L	1	0
<i>Monasa atra</i>	Bucconidae	L	1	0
<i>Nonnula rubecula</i>	Bucconidae	L	1	0
<i>Ramphastos vitellinus</i>	Ramphastidae	L	1	0
<i>Campephilus rubricollis</i>	Picidae	L	0	1
<i>Celeus elegans</i>	Picidae	L	0	1
<i>Veniliornis cassini</i>	Picidae	L	0	1
<i>Automolus infuscatus</i>	Furnariidae	L	1	0
<i>Automolus ochrolaemus</i>	Furnariidae	L	1	0
<i>Automolus rubiginosus</i>	Furnariidae	L	1	0
<i>Philydor erythrocerum</i>	Furnariidae	L	1	0
<i>Sclerurus caudacutus</i>	Furnariidae	L	1	0
<i>Sclerurus mexicanus</i>	Furnariidae	L	1	0
<i>Sclerurus rufigularis</i>	Furnariidae	L	1	0
<i>Synallaxis rutilans</i>	Furnariidae	L	0	1
<i>Xenops minutus</i>	Furnariidae	L	0	1
<i>Campylorhamphus procurvoides</i>	Furnariidae	L	0	0
<i>Deconychura longicauda</i>	Furnariidae	L	1	0

## APPENDIX. Continued.

Scientific name	Family	Study <sup>a</sup>	Avoid	Exploit
<i>Deconychura stictolaema</i>	Furnariidae	L	1	0
<i>Dendrocincla fuliginosa</i>	Furnariidae	L	0	1
<i>Dendrocincla merula</i>	Furnariidae	L	1	0
<i>Dendrocolaptes certhia</i>	Furnariidae	L	0	1
<i>Hylexetastes perrotii</i>	Furnariidae	L	0	1
<i>Sittasomus griseicapillus</i>	Furnariidae	L	0	1
<i>Xiphorhynchus pardalotus</i>	Furnariidae	L	0	1
<i>Premnoplex brunnescens</i>	Furnariidae	R	1	0
<i>Premnornis guttuligera</i>	Furnariidae	R	0	0
<i>Syndactyla subalaris</i>	Furnariidae	R	0	0
<i>Dendrocincla homochroa</i>	Furnariidae	S	0	0
<i>Xiphorhynchus erythropygus</i>	Furnariidae	S	0	0
<i>Cercomacra tyrannina</i>	Thamnophilidae	L	1	0
<i>Cymbilaimus lineatus</i>	Thamnophilidae	L	0	1
<i>Frederickena viridis</i>	Thamnophilidae	L	1	0
<i>Gymnopithys rufigula</i>	Thamnophilidae	L	1	0
<i>Hylophylax naevius</i>	Thamnophilidae	L	0	1
<i>Hylophylax poecilinotus</i>	Thamnophilidae	L	1	0
<i>Hypocnemis cantator</i>	Thamnophilidae	L	0	1
<i>Myrmeciza ferruginea</i>	Thamnophilidae	L	1	0
<i>Myrmornis torquata</i>	Thamnophilidae	L	1	0
<i>Myrmotherula axillaris</i>	Thamnophilidae	L	0	1
<i>Myrmotherula guttata</i>	Thamnophilidae	L	1	0
<i>Myrmotherula gutturalis</i>	Thamnophilidae	L	1	0
<i>Myrmotherula longipennis</i>	Thamnophilidae	L	1	0
<i>Myrmotherula menetriesii</i>	Thamnophilidae	L	1	0
<i>Percnostola rufifrons</i>	Thamnophilidae	L	0	1
<i>Pithys albifrons</i>	Thamnophilidae	L	1	0
<i>Thamnomanes ardesiacus</i>	Thamnophilidae	L	1	0
<i>Thamnomanes caesius</i>	Thamnophilidae	L	1	0
<i>Thamnophilus murinus</i>	Thamnophilidae	L	0	1
<i>Dysithamnus mentalis</i>	Thamnophilidae	S	0	0
<i>Gymnopithys leucaspis</i>	Thamnophilidae	S	1	0
<i>Myrmotherula schisticolor</i>	Thamnophilidae	S	1	0
<i>Formicarius analis</i>	Formicariidae	L	1	0
<i>Formicarius colma</i>	Formicariidae	L	1	0
<i>Grallaria varia</i>	Formicariidae	L	1	0
<i>Hylopezus macularius</i>	Formicariidae	L	1	0
<i>Myrmothera campanisona</i>	Formicariidae	L	1	0
<i>Grallaricula flavirostris</i>	Formicariidae	R	0	0
<i>Conopophaga aurita</i>	Conopogidae	L	1	0
<i>Attila spadiceus</i>	Tyrannidae	L	0	1
<i>Corythopsis torquatus</i>	Tyrannidae	L	1	0
<i>Hemitriccus zosterops</i>	Tyrannidae	L	0	1
<i>Myiobius barbatus</i>	Tyrannidae	L	1	0
<i>Onychorhynchus coronatus</i>	Tyrannidae	L	1	0
<i>Platyrinchus coronatus</i>	Tyrannidae	L	1	0
<i>Platyrinchus platyrhynchos</i>	Tyrannidae	L	1	0
<i>Platyrinchus saturatus</i>	Tyrannidae	L	1	0
<i>Rhynchocyclus olivaceus</i>	Tyrannidae	L	1	0
<i>Rhytipterna simplex</i>	Tyrannidae	L	1	0
<i>Terenotriccus erythrurus</i>	Tyrannidae	L	0	1
<i>Tolmomyias assimilis</i>	Tyrannidae	L	1	0
<i>Mionectes striaticollis</i>	Tyrannidae	R	0	0
<i>Myiophobus flavicans</i>	Tyrannidae	R	0	0
<i>Myiotriccus ornatus</i>	Tyrannidae	R	1	0
<i>Pseudotriccus pelzelni</i>	Tyrannidae	R	1	0
<i>Mionectes olivaceus</i>	Tyrannidae	S	0	0
<i>Platyrinchus mystaceus</i>	Tyrannidae	S	1	0
<i>Snowornis cryptolophus</i>	Cotingidae	R	1	0
<i>Pipreola riefferii</i>	Cotingidae	R	0	0
<i>Phoenicircus carniflex</i>	Cotingidae	L	1	0
<i>Corapipo gutturalis</i>	Pipridae	L	0	1

## APPENDIX. Continued.

Scientific name	Family	Study <sup>a</sup>	Avoid	Exploit
<i>Lepidothrix serena</i>	Pipridae	L	0	1
<i>Pipra erythrocephala</i>	Pipridae	L	0	1
<i>Pipra pipra</i>	Pipridae	L	0	1
<i>Machaeropterus deliciosus</i>	Pipridae	R	0	0
<i>Masius chrysopterus</i>	Pipridae	R	0	0
<i>Corapipo altera</i>	Pipridae	S	0	0
<i>Schiffornis turdina</i>	Tityridae	L	1	0
<i>Laniocera hypopyrra</i>	Tityridae	L	0	1
<i>Pachyrhamphus marginatus</i>	Tityridae	L	1	0
<i>Hylophilus ochraceiceps</i>	Vireonidae	L	1	0
<i>Cyphorhinus arada</i>	Troglodytidae	L	1	0
<i>Microcerculus bambla</i>	Troglodytidae	L	0	1
<i>Thryothorus coraya</i>	Troglodytidae	L	0	1
<i>Troglodytes aedon</i>	Troglodytidae	L	0	1
<i>Henicorhina leucophrys</i>	Troglodytidae	R	0	0
<i>Henicorhina leucosticta</i>	Troglodytidae	S	0	0
<i>Microbates collaris</i>	Poliotilidae	L	1	0
<i>Catharus fuscescens</i>	Turdidae	L	1	0
<i>Turdus albicollis</i>	Turdidae	L	1	0
<i>Myadestes ralloides</i>	Turdidae	R	0	0
<i>Catharus ustulatus</i>	Turdidae	S	0	0
<i>Myadestes melanops</i>	Turdidae	S	0	0
<i>Basileuterus tristriatus</i>	Parulidae	R	0	0
<i>Oporornis formosus</i>	Parulidae	S	0	0
<i>Lanio fulvus</i>	Thraupidae	L	0	1
<i>Tachyphonus cristatus</i>	Thraupidae	L	0	0
<i>Tachyphonus surinamus</i>	Thraupidae	L	0	1
<i>Chlorospingus semifuscus</i>	Thraupidae	R	0	1
<i>Arremon taciturnis</i>	Emberizidae	L	1	0
<i>Buarremon brunneinucha</i>	Emberizidae	R	1	0
<i>Cyanocopsa cyanooides</i>	Cardinalidae	L	0	0
<i>Saltator grossus</i>	Cardinalidae	L	0	1
<i>Euphonia xanthogaster</i>	Fringillidae	R	0	0
Temperate data set				
<i>Callipepla californica</i>	Odontophoridae	S	0	1
<i>Zenaida macroura</i>	Columbidae	S	0	0
<i>Coccyzus americanus</i>	Cuculidae	K	0	0
<i>Coccyzus americanus</i>	Cuculidae	St	0	0
<i>Coccyzus americanus</i>	Cuculidae	N	0	1
<i>Calypte anna</i>	Trochilidae	S	0	0
<i>Archilochus colubris</i>	Trochilidae	G	0	0
<i>Picoides pubescens</i>	Picidae	K	0	0
<i>Picoides pubescens</i>	Picidae	N	0	0
<i>Picoides villosus</i>	Picidae	K	0	0
<i>Picoides villosus</i>	Picidae	O	0	0
<i>Colaptes auratus</i>	Picidae	S	0	1
<i>Colaptes auratus</i>	Picidae	N	0	0
<i>Picoides nuttallii</i>	Picidae	S	0	1
<i>Dryocopus pileatus</i>	Picidae	N	0	0
<i>Melanerpes carolinus</i>	Picidae	K	0	0
<i>Melanerpes carolinus</i>	Picidae	N	0	1
<i>Sphyrapicus varius</i>	Picidae	G	0	0
<i>Sphyrapicus varius</i>	Picidae	N	0	0
<i>Sphyrapicus varius</i>	Picidae	O	0	0
<i>Empidonax virescens</i>	Tyrannidae	K	1	0
<i>Empidonax virescens</i>	Tyrannidae	N	1	0
<i>Myiarchus cinerascens</i>	Tyrannidae	S	0	1
<i>Sayornis phoebe</i>	Tyrannidae	N	0	0
<i>Contopus virens</i>	Tyrannidae	St	0	1
<i>Myiarchus crinitus</i>	Tyrannidae	St	0	1
<i>Myiarchus crinitus</i>	Tyrannidae	N	0	0
<i>Empidonax minimus</i>	Tyrannidae	G	0	0

## APPENDIX. Continued.

Scientific name	Family	Study <sup>a</sup>	Avoid	Exploit
<i>Empidonax minimus</i>	Tyrannidae	O	0	1
<i>Empidonax difficilis</i>	Tyrannidae	B	1	0
<i>Contopus sordidulus</i>	Tyrannidae	S	0	0
<i>Vireo solitarius</i>	Vireonidae	G	1	0
<i>Vireo solitarius</i>	Vireonidae	O	0	0
<i>Vireo huttoni</i>	Vireonidae	S	0	0
<i>Vireo griseus</i>	Vireonidae	N	0	1
<i>Vireo flavifrons</i>	Vireonidae	N	0	0
<i>Cyanocitta cristata</i>	Corvidae	K	0	0
<i>Cyanocitta cristata</i>	Corvidae	St	0	0
<i>Cyanocitta cristata</i>	Corvidae	O	0	0
<i>Corvus corax</i>	Corvidae	B	0	0
<i>Aphelocoma californica</i>	Corvidae	S	0	1
<i>Cyanocitta stelleri</i>	Corvidae	B	0	1
<i>Tachycineta thalassina</i>	Hirundinidae	S	0	1
<i>Poecile atricapillus</i>	Paridae	G	0	0
<i>Poecile atricapillus</i>	Paridae	O	0	0
<i>Poecile carolinensis</i>	Paridae	K	0	0
<i>Poecile carolinensis</i>	Paridae	St	0	1
<i>Poecile carolinensis</i>	Paridae	N	0	1
<i>Poecile rufescens</i>	Paridae	B	0	0
<i>Poecile rufescens</i>	Paridae	S	0	0
<i>Baeolophus inornatus</i>	Paridae	S	1	0
<i>Baeolophus bicolor</i>	Paridae	K	0	0
<i>Baeolophus bicolor</i>	Paridae	St	0	0
<i>Baeolophus bicolor</i>	Paridae	N	0	1
<i>Psaltriparus minimus</i>	Aegithalidae	S	0	1
<i>Sitta canadensis</i>	Sittidae	B	1	0
<i>Sitta canadensis</i>	Sittidae	O	0	0
<i>Sitta carolinensis</i>	Sittidae	S	0	1
<i>Sitta carolinensis</i>	Sittidae	K	0	0
<i>Sitta carolinensis</i>	Sittidae	O	0	0
<i>Certhia americana</i>	Certhiidae	B	1	0
<i>Certhia americana</i>	Certhiidae	G	0	0
<i>Certhia americana</i>	Certhiidae	O	0	0
<i>Thryomanes bewickii</i>	Troglodytidae	S	0	0
<i>Thryothorus ludovicianus</i>	Troglodytidae	N	0	1
<i>Troglodytes troglodytes</i>	Troglodytidae	B	1	0
<i>Troglodytes troglodytes</i>	Troglodytidae	G	0	0
<i>Troglodytes troglodytes</i>	Troglodytidae	O	1	0
<i>Regulus satrapa</i>	Regulidae	B	0	0
<i>Regulus satrapa</i>	Regulidae	O	0	0
<i>Regulus calendula</i>	Regulidae	N	0	1
<i>Polioptila caerulea</i>	Sylviidae	S	0	0
<i>Polioptila caerulea</i>	Sylviidae	K	0	0
<i>Turdus migratorius</i>	Turdidae	B	0	0
<i>Turdus migratorius</i>	Turdidae	G	0	0
<i>Turdus migratorius</i>	Turdidae	N	0	0
<i>Turdus migratorius</i>	Turdidae	O	0	1
<i>Catharus guttatus</i>	Turdidae	G	1	0
<i>Catharus guttatus</i>	Turdidae	N	0	0
<i>Catharus guttatus</i>	Turdidae	Ki	1	0
<i>Catharus guttatus</i>	Turdidae	O	1	0
<i>Catharus ustulatus</i>	Turdidae	B	0	1
<i>Catharus ustulatus</i>	Turdidae	O	0	0
<i>Ixoreus naevius</i>	Turdidae	B	1	0
<i>Catharus fuscescens</i>	Turdidae	G	0	0
<i>Catharus fuscescens</i>	Turdidae	O	0	0
<i>Sialia mexicana</i>	Turdidae	S	0	0
<i>Hylocichla mustelina</i>	Turdidae	G	0	1
<i>Hylocichla mustelina</i>	Turdidae	K	0	0
<i>Hylocichla mustelina</i>	Turdidae	N	1	0

## APPENDIX. Continued.

Scientific name	Family	Study <sup>a</sup>	Avoid	Exploit
<i>Chamaea fasciata</i>	Timaliidae	S	0	1
<i>Chamaea fasciata</i>	Timaliidae	B	0	0
<i>Dumetella carolinensis</i>	Mimidae	N	0	1
<i>Mimus polyglottos</i>	Mimidae	S	0	1
<i>Bombycilla cedrorum</i>	Bombycillidae	O	0	1
<i>Setophaga ruticilla</i>	Parulidae	G	0	0
<i>Setophaga ruticilla</i>	Parulidae	O	0	1
<i>Mniotilta varia</i>	Parulidae	G	0	0
<i>Mniotilta varia</i>	Parulidae	St	0	0
<i>Mniotilta varia</i>	Parulidae	N	0	0
<i>Mniotilta varia</i>	Parulidae	O	0	1
<i>Dendroica fusca</i>	Parulidae	G	0	0
<i>Dendroica fusca</i>	Parulidae	O	0	0
<i>Dendroica caerulescens</i>	Parulidae	G	0	1
<i>Dendroica caerulescens</i>	Parulidae	Ki	0	1
<i>Dendroica caerulescens</i>	Parulidae	O	0	0
<i>Dendroica virens</i>	Parulidae	G	1	0
<i>Dendroica virens</i>	Parulidae	Ki	0	0
<i>Dendroica virens</i>	Parulidae	O	1	0
<i>Wilsonia canadensis</i>	Parulidae	O	0	0
<i>Dendroica pensylvanica</i>	Parulidae	G	0	0
<i>Dendroica pensylvanica</i>	Parulidae	O	0	1
<i>Geothlypis trichas</i>	Parulidae	G	0	0
<i>Geothlypis trichas</i>	Parulidae	O	0	0
<i>Dendroica occidentalis</i>	Parulidae	B	1	0
<i>Wilsonia citrina</i>	Parulidae	N	1	0
<i>Oporornis formosus</i>	Parulidae	K	0	0
<i>Oporornis philadelphia</i>	Parulidae	G	0	0
<i>Parula americana</i>	Parulidae	N	0	1
<i>Vermivora celata</i>	Parulidae	S	1	0
<i>Seiurus aurocapilla</i>	Parulidae	G	1	0
<i>Seiurus aurocapilla</i>	Parulidae	K	1	0
<i>Seiurus aurocapilla</i>	Parulidae	N	0	0
<i>Seiurus aurocapilla</i>	Parulidae	Ki	0	0
<i>Seiurus aurocapilla</i>	Parulidae	O	1	0
<i>Dendroica pinus</i>	Parulidae	St	0	0
<i>Dendroica pinus</i>	Parulidae	N	0	1
<i>Wilsonia pusilla</i>	Parulidae	B	0	0
<i>Dendroica coronata</i>	Parulidae	O	0	0
<i>Piranga olivacea</i>	Thraupidae	G	0	0
<i>Piranga olivacea</i>	Thraupidae	K	0	0
<i>Piranga rubra</i>	Thraupidae	Ki	0	0
<i>Piranga olivacea</i>	Thraupidae	O	0	0
<i>Piranga rubra</i>	Thraupidae	K	0	1
<i>Piranga rubra</i>	Thraupidae	St	0	0
<i>Piranga rubra</i>	Thraupidae	N	0	1
<i>Pipilo crissalis</i>	Emberizidae	S	0	1
<i>Junco hyemalis</i>	Emberizidae	S	0	1
<i>Junco hyemalis</i>	Emberizidae	G	0	0
<i>Junco hyemalis</i>	Emberizidae	O	0	1
<i>Pipilo erythrophthalmus</i>	Emberizidae	S	0	0
<i>Pipilo erythrophthalmus</i>	Emberizidae	K	0	1
<i>Zonotrichia albicollis</i>	Emberizidae	G	0	1
<i>Cardinalis cardinalis</i>	Cardinalidae	K	0	1
<i>Cardinalis cardinalis</i>	Cardinalidae	St	0	0
<i>Cardinalis cardinalis</i>	Cardinalidae	N	0	1
<i>Pheucticus ludovicianus</i>	Cardinalidae	G	0	0
<i>Pheucticus ludovicianus</i>	Cardinalidae	O	0	0
<i>Carduelis psaltria</i>	Fringillidae	S	0	0
<i>Carpodacus purpureus</i>	Fringillidae	S	0	1

<sup>a</sup> B = Brand and George (2001), G = Germaine et al. (1997), K = Kroodsmma (1984), Ki = King et al. (1997), L = Laurance (2004), N = Noss (1991), O = Ortega and Capen (2002), R = Restrepo and Gómez (1998), S = Sisk (1992), St = Strelke and Dickson (1980).