

Avian response to landscape pattern: The role of species' life histories

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Abstract

We suggest that the life histories of species within communities may differ among geographic locations and that communities from distinct biomes may respond uniquely to a given trajectory of landscape change. This paper presents initial tests relevant to these hypotheses. First, the representation of various life-history guilds in avifaunas from the Eastern Deciduous (EDF) and Pacific Northwest (PNW) forests were compared. Three guilds contained more species in the EDF community (large patch and/or habitat interior guild, small patch and/or edge guild, and fragmentation-sensitive guild). The guild of predators requiring large forest tracts was better represented in the PNW. Next, the relative sensitivity of each community to habitat change was ranked based on the life-history traits of their species. The EDF avifauna had a significantly higher index of sensitivity to both forest fragmentation and to landscape change in general. Among the birds with high scores for sensitivity to landscape change were several species that have received little conservation attention thus far including some associated with open-canopy habitats. Lastly, the validity of using life histories to predict community response to landscape change was supported by the fact that the sensitivity scores for PNW species correlated significantly with independent data on species population trends. While more rigorous analyses are suggested, we conclude that knowledge of life histories is useful for predicting community response to landscape change and that conservation strategies should be uniquely tailored to local communities.

1. Introduction

A rapidly growing body of knowledge involves the effects of landscape dynamics on patterns of species diversity. Several landscape metrics have been found to explain variation in patterns of biodiversity including habitat size (Forman *et al.* 1976; Galli *et al.* 1976; Ambuel and Temple 1983; Freemark and Merriam 1986; Robbins *et al.* 1989), isolation (MacClintock *et al.* 1977; Lynch and Whitcomb 1978; Urban *et al.* 1988), boundary characteristics (Kroodsma 1982; Gates and Gysel 1978; Brittin-

gham and Temple 1983; Wilcove 1985; Harris 1988), patch juxtaposition (Harris 1984), and patch diversity (Roth 1976).

Forested landscapes undergoing fragmentation have received particular attention. The progressive reduction of total forest area and mean patch size may elicit a suite of ecological responses involving microclimate (Ranney *et al.* 1981), disturbance (Franklin and Forman 1987), decomposition (Klein 1989), nutrient cycling (Ryszkowski 1992), pollination (Jennersten 1988), vegetation structure and composition (Ranney *et al.* 1981), and predation

(Gates and Gysel 1978; Wilcove 1985; Small and Hunter 1988). Perhaps best known are the effects of forest fragmentation on forest birds and mammals: studies primarily from the Eastern Deciduous Forest of North America indicate that species associated with forest interiors generally decline while those specializing on forest edges increase in abundance (Whitcomb *et al.* 1981; Noss 1983; Terborgh 1989; Merriam and Wegner 1992). Fragmentation is the prevalent trajectory of landscape change in several human-dominated forest regions of the world. The negative consequences of fragmentation have been a rallying point for ecologists and conservationists for the last decade, with the concepts developed in the few regions that are well studied being exported to others where local data are often lacking.

We have suggested elsewhere (Hansen *et al.* 1992) that forest fragmentation and its associated consequences are a subset of a more general phenomenon that drives patterns of biodiversity. Two key components of the phenomenon are the life-history attributes of the species that occupy an area and the local trajectory of landscape change. Hansen *et al.* (1992) simulated three common landscape trajectories in human-dominated systems and showed that patterns of avian habitat diversity differ under each. In this paper we examine the role of species' life histories in community response to landscape change.

Whitcomb *et al.* (1981) were among the first to document correlations between bird life-history traits and use of specific landscape features. They found that species sensitive to fragmentation in the Eastern Deciduous Forest were neotropical migrants, specialized in forest interior habitats, nested on or near the ground in open nests, and had relatively low reproductive potential. These life-history traits could be associated with, respectively, constrained time for finding nest sites (hence limited access to isolated habitat patches), low habitat availability (especially in small patches), and high vulnerability to brood parasitism and nest predation (especially in forest edges) (Urban *et al.* 1988). These findings suggest that life-history traits represent a mechanism that underlies habitat selection within a species. Extending this assertion, the

suite of life histories present across all species in a community may influence the community response to landscape change.

Life-history traits set constraints on the types of resources that can be used profitably. Some cavity-nesting birds, for example, have extremely low densities in landscapes devoid of the standing dead trees they require for nesting (Zarnowitz and Manuwal 1985). Life histories also constrain the spatial and temporal scales at which resources can be exploited. The guild of forest interior birds described by Whitcomb *et al.* (1981) is apparently unable to breed successfully in small forest patches, partially because their open nests placed near the forest floor make them susceptible to predators and brood parasites associated with forest edges (Terborgh 1989). Similarly, species with low reproductive rates or dispersal abilities are unable to reach and/or use resource patches created by ephemeral disturbances before the resources are exhausted (Pianka 1970).

The life-history traits of a species are, of course, influenced by its environment. They are a product of natural selection and other evolutionary forces and thus reflect the long-term interplay of species demography and environment (Stearns 1977; Lande 1982). Moreover, behavioral plasticity allows organisms to adjust life-history strategies to current environmental conditions. The range of possible strategies open to an organism, however, is fixed or constrained in ecological time by its genotype (Begon *et al.* 1986). Thus, knowledge of life history should offer a good approximation of the habitat and landscape settings likely to be suitable for a species.

This leads us to two hypotheses that are rather intuitive but, nonetheless, important. The first is that long-term environmental, demographic, and genetic factors are likely to cause communities from different geographic locations to have unique suites of life-history strategies. The second hypothesis is that such differences in life histories will cause communities from distinct biomes to respond uniquely to a given trajectory of landscape change. An important implication for conservation is that caution is needed when extrapolating the community dynamics observed in one system to other systems.

Differences in either landscape patterns or life history attributes may cause such extrapolations to be erroneous. A second implication is that knowledge of local landscape patterns and local life histories may allow prediction of future animal community dynamics. Such a predictive capacity would greatly improve our ability to manage species diversity.

In this paper we report initial tests that are relevant to these hypotheses. We compare the life-history structures of avifaunas from the Eastern Deciduous (EDF) and Pacific Northwest (PNW) forest by examining the number of species present in each of several life-history guilds. We then predict, based on the life-history traits of the species that comprise each community, the relative sensitivity of each community to forest fragmentation and to landscape change in general. Finally, we consider the relationships between the population trends of some birds species from the PNW and their life-history strategies.

2. Methods

The EDF bird community used in the analysis was that described by Whitcomb *et al.* (1981) for a three-county area of central Maryland. The region was dominated by oak-hickory-chestnut (*Quercus*, *Carya*, *Castanea*) forest in pre-settlement times. Land-use practices reduced forest cover to somewhat below 20% by the late nineteenth century. In 1981, 22% of Whitcomb's study area was wooded, mostly with forest under 50 years old. The remaining area was primarily agricultural, rural residential, or suburban. Several other important studies of forest fragmentation were done in the vicinity, including MacClintock *et al.* (1977), Whitcomb *et al.* (1977), and Robbins *et al.* (1989).

The other avifauna examined is that of the wet temperate coniferous forests of western Oregon and Washington. These forests are characterized by the large size of dominant trees; in many cases local species are the largest representatives of their genera (Waring and Franklin 1979). Biomass accumulations are among the highest described in any system (Franklin 1988). The pre-settlement distur-

bance regime in the region maintained a complex mosaic of seral stages, and large standing and fallen trees that survived disturbance provided considerable structural diversity to all seral stages (Franklin *et al.* 1986; Hansen *et al.* 1991). Natural forests on most private lands in the region have been converted to managed tree farms or agricultural lands over the past century (Harris 1984). Natural forests still cover approximately 50–100% of various federal ownerships, with 0–30 year-old plantations dominating much of the remainder (Lehmkuhl *et al.* 1991; Ripple *et al.* 1991).

The avifaunas of these two regions were selected for study because: data on life-history traits of most species had been compiled for both locations; historic and present landscape dynamics differ substantially between the biomes and thus the life histories of the avifaunas are expected to differ; and we were familiar with each system.

We tallied several life-history traits for each species in the two bird communities (Appendices I and II). These traits involved reproductive strategy, feeding strategy, habitat use, and use of space. Most of the data for the EDF community are from Whitcomb *et al.* (1981) who drew on several previous surveys and their own extensive field studies to compile the species list and the life-history data. We added raptors to Whitcomb's list and derived life history information for them from Ehrlich *et al.* (1988).

The Pacific Northwest (PNW) bird list includes those species identified by Brown (1985) as having primary habitats in low and mid-elevation conifer and conifer-hardwood forests in Oregon and Washington west of the Cascade Mountain crest. Brown derived life-history information from previous studies in the region. We supplemented Brown's life-history accounts with data from the other sources listed in Appendix I. Scientific names of bird species mentioned in the text are listed in Appendices I and II.

The quality of data in these Appendices is probably variable. Some bird species in each community are poorly studied. The data for the EDF are probably, in general, more reliable than those for the PNW due to a longer history of avian research. Some traits have received more attention in the

Table 1. Number of species and percent of total species (in parentheses) represented in various life-history guilds for Pacific Northwest and Eastern Deciduous forest avifaunas. The guilds are not necessarily mutually exclusive. See Appendices I and II for lists of species included in the analysis.

Guild	Number of species	
	PNW	EDF
Edge specialist or small forest patch associate	4 (5.3%)	27 (36.0%)
Patch interior or large forest patch associate	14 (18.7%)	27 (36.0%)
Large tree, snag or fallen tree associate	24 (32.0%)	20 (26.7%)
Neotropical migrant, closed-forest specialist, open nests near ground (0–3 m) and low reproductive effort (< = 6 eggs/yr)	0 (0.0%)	8 (10.7%)
Carnivorous, closed-forest specialist and large territory size (> 40 ha)	5 (6.7%)	3 (4.0%)

EDF (*i.e.* response to edge and patch size), whereas others are better known in the PNW (association with seral stage and certain microhabitat elements such as dead trees). Despite these limitations, these data sets are among the best available and are useful for comparison.

The data were used to determine the number of species in each avifauna that was represented in five life-history guilds (Table 1). The guilds were defined by combinations of life-history traits thought to be related to species responses to landscape dynamics. Some involved only a few life-history traits such as response to patch size and edge. Others include a more complex array of attributes such as those identified by Whitcomb *et al.* (1981) as characteristics of species sensitive to forest fragmentation in the EDF. In cases where data were not available to judge a life-history trait for a species, we assumed the species was a generalist relative to the trait.

The potential responsiveness of the avifaunas to landscape change was assessed via a 'sensitivity' index. The index was based on eight of the life-history traits listed in the Appendices. Each species was rated from 1 (least sensitive) to 3 (most sensitive) for

each of the eight traits. A total score for a species was derived by summing the scores across traits. The mean and frequency distribution among all species were used to characterize the sensitivity of the community. One set of criteria was used to assess sensitivity to forest fragmentation (Table 2) and only species associated with closed-canopy forest were included in this analysis. [Open-canopy stands are defined here as the shrub/forb seral stage where canopy closure is less than about 70%. Closed-canopy stands are defined as all older seral stages where canopy closure usually exceeds 70%.] Another set of criteria applied to landscape change in general (Table 3). In this case, all species were included. The rationale for the criteria follow the findings of Whitcomb *et al.* (1981) who conducted a detailed analysis of the life-history traits of EDF bird species sensitive to forest fragmentation.

To examine the validity of the landscape sensitivity index, we evaluated the correlation between the sensitivity scores for species and their recent population trends. We did this only for the PNW community because the required data were readily available only for this area. The demographic data were obtained from Sharp (1990) who used results of the U.S. Fish and Wildlife Service Breeding Bird Survey to describe population trends over the last 20 years for neotropical migrants breeding in Oregon. We used the Kendall's tau-b Correlation Coefficient to examine the relationship between scores for sensitivity to landscape change and the probability of significant species population changes. Landscape changes have been dramatic in the PNW during this time period (*e.g.* Ripple *et al.* 1991) and species sensitive to these changes are likely to show population responses. Without a detailed analysis of the types of changes relative to bird species life histories, it is not possible to predict the direction of change for each species. Thus, both positive and negative population changes were lumped in the analysis. Four probability classes were used in the analysis: $P < 0.1$; $0.1 \leq P < 0.05$; $0.05 \leq P < 0.01$; $P \leq 0.01$.

Table 2. Life-history criteria used to rate the sensitivity (1 – least sensitive, 3 – most sensitive) of closed-canopy bird species to forest fragmentation.

Variable	Sensitivity index		
	1	2	3
Reproductive effort (eggs/yr)	> 10	6–10	0–5
Nest form	Hole		Open
Nest height (m)	> 3	1–3	0–1
Territory size (ha)	< 4	4–40	> 40
or			
Territory density (males/km ²)	> 100	15–100	< 15
Migration	Resident	Short	Long
Edge	Generalist, edge, no data		Interior
Area	Generalist, edge, no data		Positive

Table 3. Life-history criteria used to rate the sensitivity (1 – least sensitive, 3 – most sensitive) of bird species to landscape change.

Variable	Sensitivity index		
	1	2	3
Reproductive effort (eggs/yr)	> 10	6–10	0–5
Nest form	Hole		Open
Nest height (m)	> 3	1–3	0–1
Territory size (ha)	< 4	4–40	> 40
or			
Territory density (males/km ²)	> 100	15–100	< 15
Seral stage	Generalist	Open-canopy, closed-canopy	Old growth
Migration	Resident	Short	Long
Edge	Generalist, no data		Interior, edge
Area	Generalist, no data		Positive, negative

3. Results

The PNW and EDF avifaunas each included 75 species. The communities were generally similar in the life-history traits, nest type, microhabitat association, and feeding strategy (Table 4). They differed relative to seral stage association, migration strategy, and response to edge and patch size. The PNW community had a higher proportion of seral-stage

Table 4. Representation of various life-history strategies among the Pacific Northwest (PNW) and Eastern Deciduous (EDF) forest avifaunas. Data are means (and standard deviations) or frequencies. See Appendices I and II for species and data sources.

Life-history trait	Avifauna	
	PNW	EDF
Nest type		
open	79%	79%
hole	21%	20%
brood parasite	0%	1%
Territory density (males/km ²)	89.5 (86.9)	49.7 (44.9)
Seral stage association		
generalist	33%	45%
open canopy	28%	24%
young and mature	33%	29%
old growth	5%	0%
no data	0%	1%
Microhabitat association		
generalist	68%	73%
logs	5%	4%
snags	23%	23%
large trees	3%	0%
no data	1%	0%
Feeding strategy		
carnivore	16%	13%
herbivore	8%	3%
insectivore	55%	55%
omnivore	21%	29%
Response to edge		
generalist	24%	32%
edge specialist	5%	32%
interior specialist	12%	20%
no data	59%	16%
Response to patch size		
generalist	19%	29%
negative association	0%	9%
positive association	9%	33%
no data	72%	28%
Migratory strategy		
neotropical migrant	28%	41%
short-distance migrant	16%	23%
resident	56%	36%

specialists, non-migratory species, and edge and patch size generalists.

The distribution of species among the five life-history guilds differed significantly between the two communities (G-Test, $n = 132$, $G = 24.19$, $P < .001$). The EDF community had more species in the edge/small patch guild and in the interior/large

Table 5. Number of species in the Eastern Deciduous (EDF) and Pacific Northwest (PNW) avifaunas meeting each life-history criterion (and all criteria listed above it) for the guild of forest birds described by Whitcomb *et al.* (1981) as being sensitive to forest fragmentation in the EDF. Data are from Appendices I and II.

Guild criteria	EDF	PNW
Neotropical migrant	31	22
Closed-canopy specialist	15	8
Open nest	14	7
Reproductive effort ≤ 6 eggs/yr	10	7
Nest height ≤ 3 m	8	0

patch guild (Table 1). Data on response to edge and patch size were not available for several species in the PNW community. Even so, considering only those species for which data were available, PNW birds were more generalist relative to edge and patch size than EDF species.

A few more species were associated with large trees, snags and downed trees in the PNW than in the EDF. Larger differences between the communities occurred for the guild described by Whitcomb *et al.* (1981) as especially sensitive to forest fragmentation. This guild included eight species in the EDF but no species in the PNW. Analyzing the number of species successively meeting each of the life-history criteria that defined the guild, the PNW had about 30% fewer neotropical migrants than the EDF (Table 5). About a half to a third of these migrants were closed-canopy specialists. The relative proportions of this group meeting the nest type and reproductive effort constraints did not differ between the communities. Nest height was an important determinant of guild membership: none of the PNW species otherwise meeting the criteria for guild membership nested within 3 m of the ground, whereas 8 of the EDF birds did so (4 of these nested on the ground).

The final guild, closed-forest, predatory birds with large territories, included slightly more PNW than EDF species (Table 1). Moreover, two of the EDF species (sharp-shinned hawk and Cooper's hawk) had very low abundances in the Maryland study area (Whitcomb *et al.* 1981).

The index of sensitivity to forest fragmentation

was significantly higher for the EDF avifauna than for the PNW community (Wilcoxon 2-Sample Test; $n = 22,29$; $Z = 4.61$; $P < .0001$) (Fig. 1). EDF species with the highest sensitivity scores were, as expected, those identified by Whitcomb *et al.* (1981) as absent from small forest patches. Among the most sensitive PNW birds were spotted owl, varied thrush, winter wren, western wood-pewee, sharp-shinned hawk, solitary vireo, Hammond's flycatcher, and marbled murrelet.

The sensitivity score for landscape change also was significantly higher for the EDF community than for the PNW community (Wilcoxon 2-Sample Test; $n = 75,75$; $Z = 3.99$, $P < .0001$) (Fig. 2). Among the list of sensitive species in the PNW were some birds associated with open canopies (Table 6).

The scores for sensitivity to landscape change for neotropical migrants breeding in Oregon were significantly correlated with the probability of significant population trends (either positive or negative) ($n = 28$, $R = .40$, $P < .015$).

4. Discussion

4.1. Life-history traits

This comparison of life-history traits and guilds revealed some important similarities and differences between the PNW and EDF avifaunas. Species nesting in cavities and otherwise associated with snags and fallen trees were represented nearly equally in each community. This is somewhat surprising given that PNW forests are characterized by an abundance of large snags and fallen logs (Franklin 1988). Perhaps these features were also common in the EDF during pre-settlement times and species associated with them have been able to persist, likely at lower abundance, in modern EDF forests.

The relative similarity in feeding strategy between communities is also unexpected. Most primary productivity in the PNW is fixed as wood and relatively unpalatable conifer leaves. Hence, carnivorous and insectivorous species of mammals, amphibians, and reptiles are substantially more numerous than herbivorous species (Harris 1984). The relatively more abundant and palatable leaves,

SENSITIVITY TO FOREST FRAGMENTATION

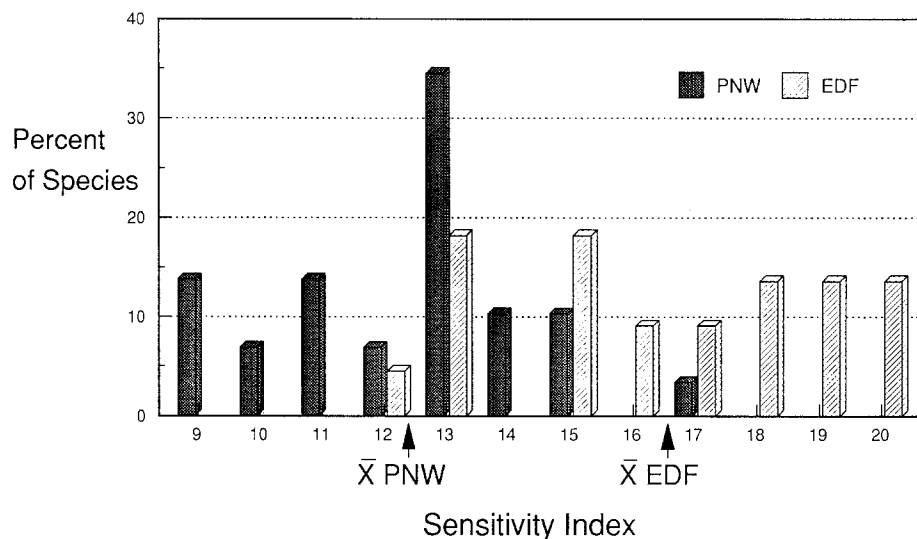


Fig. 1. Frequency distributions of scores for sensitivity to forest fragmentation of forest-dwelling bird species from the Pacific Northwest (PNW) and Eastern Deciduous (EDF) avifaunas. The rating system is depicted in Table 2.

SENSITIVITY TO LANDSCAPE CHANGE

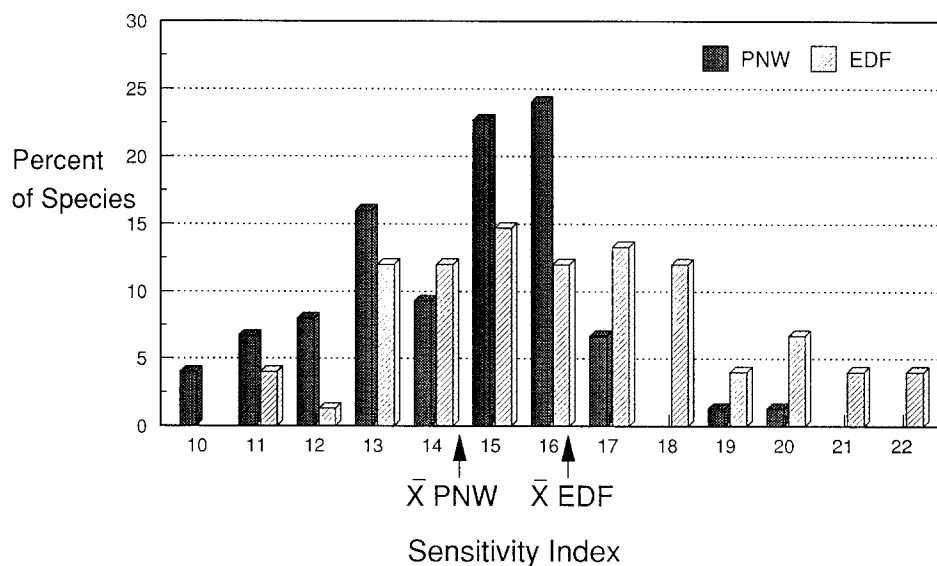


Fig. 2. Frequency distributions of scores for sensitivity to landscape change for bird species from the Pacific Northwest (PNW) and Eastern Deciduous (EDF) avifaunas. The rating system is depicted in Table 3.

seeds, fruits in the EDF could be expected to support relatively more herbivorous species. Yet, there are only a few more carnivorous birds in the PNW and both communities have equal numbers of in-

sectivores.

The communities did differ substantially in response to patch size and edge. Although fewer studies on this topic have been completed in the

Table 6. Species from the Pacific Northwest avifauna with relatively high scores for sensitivity to landscape change. Population trends are from Sharp (1990). An asterisk denotes that the trend is statistically significant at the $P \leq .10$ level. ND denotes no data.

Species	Sensitivity index	Seral stage	Population trend
Spotted owl	19	CC	- ?
Orange-crowned warbler	20	OC	- 1.4%*
Black-headed grosbeak	16	OC	- 1.2%*
Olive-sided flycatcher	17	CC	- 4.3%*
Varied thrush	17	CC	ND
Wilson's warbler	17	G	+ 2.7%*
Winter wren	17	CC	ND
Western wood-peewee	16	CC	- 4.1%*
Yellow warbler	16	OC	- 1.6%*
White-crowned sparrow	16	OC	- 3.8%*
Western tanager	16	G	- 3.1%*

PNW, those that have suggest that both forest patch size and distance from forest edge are much less important forces structuring bird communities in the PNW than in the EDF. Rosenburg and Raphael (1986), for example, found many fewer species in northwestern California associated either positively or negatively with forest size than did Robbins *et al.* (1989) working in Maryland. Similarly, Hansen *et al.* (in preparation) found no bird species in western Oregon that specialized on forest/clearcut boundaries and only three species associated with forest interiors. Much stronger edge responses have been documented in the EDF by Kroodsmas (1982), Chasko and Gates (1982), and Noss (1991). The rather weak response to these landscape features in the PNW may be due to the fact that the landscapes studied thus far are much less fragmented (forest cover exceeding 50%) than many of those studied in the EDF. Patch size and edge effects may become more obvious as fragmentation thresholds (Franklin and Forman 1987) are exceeded. Alternatively, there may be fundamental differences between the two avifaunas in response to patch size and edge.

The lack of membership of PNW birds in the 'fragmentation-sensitive' guild identified by Whitcomb *et al.* (1981) suggests that the communities do indeed have basic differences. Migration strategy

may be among the most important of these differences. Whitcomb *et al.* (1981, pg. 172) argued that neotropical migration is 'a powerful organizing force, perhaps the most important of all the life history features'. They found that migration strategy correlated with habitat use, nest type, reproductive effort, and body weight. Furthermore, they suggested that neotropical migration constrains dispersal on the breeding grounds and, in total, decreases tolerance to habitat fragmentation. The greater number of resident and short-migration species in the PNW may confer less sensitivity to fragmentation.

Nest height is the other important life-history trait that explains the lack of PNW species in the fragmentation guild. Of the seven PNW species that meet all other criteria defining this guild, none nest within three meters of the ground. The abundance of ground-based predators has increased dramatically with fragmentation in the EDF (Terborgh 1989) and nests near forest edges are especially vulnerable to predation (Gates and Gysel 1978; Wilcove 1985; Small and Hunter 1988). Increased predation is likely the primary reason that members of this guild are absent in small forest tracts in the EDF, and it may partially explain declines in their regional populations (Terborgh 1989). The relatively higher nest placement among the closed-forest neotropical migrants in the PNW may make these species less susceptible to ground predators than their EDF counterparts.

Brood parasitism by brown-headed cowbirds also constrains reproduction near forest edges for several EDF species (Gates and Gysel 1978; Brittingham and Temple 1983). The low abundance of cowbirds in the conifer forests of western Oregon and Washington may further reduce the impacts of fragmentation in the region. This could change, of course, if cowbirds become more numerous as favorable agricultural habitats are created, as has happened in the EDF.

Of particular concern in the PNW are closed-forest predators with large territories. The spotted owl, in particular, is suffering dramatic population declines and is likely to go extinct if present land-use trends continue (Dawson 1986). The reduction of suitable habitat, increasing edge effects, and in-

creasing habitat isolation are likely responsible (Thomas *et al.* 1990). This guild is better represented in the PNW than the EDF in terms of numbers of species and perhaps density and it may be particularly vulnerable to forest fragmentation.

These similarities and differences in life histories between the PNW and EDF communities have obvious consequences for the ways the communities are likely to respond to landscape change. The removal of snags and downed logs is likely to have strong negative consequences in both systems, given the numbers of species associated with these features. Passerine species are likely less sensitive to forest fragmentation in the PNW than in the EDF for the reasons described above. Even so, this should not minimize concern over the three PNW passerines that appear to be associated with forest interiors (varied thrush, Swainson's thrush, winter wren) (Hansen *et al.* in preparation). Finally, forest predators appear to be declining in both regions in association with current land-use patterns.

4.2. Sensitivity to landscape change

The comparison of mean sensitivity scores for the two communities further supports the notion that the PNW avifauna in total is less vulnerable to forest fragmentation and to landscape change in general. It is important to bear in mind, however, that the criteria used in these indices are largely derived from studies in the EDF. Factors operating in the PNW that are yet undiscovered could alter this conclusion.

Among the PNW species with the highest indices of sensitivity to forest fragmentation are some that have received little attention thus far from conservationists and land managers. These include varied thrush, sharp-shinned hawk, solitary vireo, and Hammond's flycatcher. Further study of these species is suggested.

Similarly, open-canopy species have been virtually ignored by ecologists and conservationists, under the assumption that they are r-selected 'weedy' species that thrive in anthropogenic landscapes (Noss 1983). This is not universally true. Some open-canopy specialists were among the most sensitive to

landscape change in our life-history analysis (PNW: orange-crowned warbler, black-headed grosbeak, yellow warbler, white-crowned warbler; EDF: blue-winged warbler, blue grosbeak, orchard oriole, eastern kingbird). Also, Hansen *et al.* (in preparation) found that some of these species avoid the edges of forest openings, suggesting that patch size can be an important constraint for open-canopy species just as it is for some forest interior specialists. Most importantly, Breeding Bird Survey data show that some of these open-canopy species are declining significantly in abundance in the PNW (Sharp 1990) (Table 6).

The validity of using life histories to predict species response to landscape change is supported by the fact that our sensitivity scores correlated significantly with independent data on species population trends. We would expect that the species most sensitive to landscape change would be undergoing population increases or decreases during this period of dramatic landscape change in the PNW.

5. Conclusion

This analysis provides initial evidence for the hypotheses that life-history traits are likely to differ among communities and that these differences can cause communities from distinct geographic locations to respond uniquely to a given landscape trajectory. Our comparison of the EDF and PNW avifaunas were limited in that they were: not replicated; did not consider species abundances; and did not analyze the relationships between life-history traits and population responses for all species in both communities. Nonetheless, these initial results indicate that more rigorous analyses of these hypotheses are merited.

An implication of the findings is that conservation strategies should be uniquely tailored to a region based on the types of life-history attributes represented in the community. While this implication is intuitively obvious, we are not aware of cases where community life-history traits are explicitly used to guide management strategies. Our results suggest, for example, that the challenge in parts of the EDF is to expand the abundance of forest inte-

rior habitats to benefit the large groups of forest-dwelling neotropical migrants while also maintaining sufficient habitats for the large guild of edge specialists. The focus in the PNW should be on maintaining natural microhabitats, large tracts of forest for forest predators, and sufficiently large openings for open-canopy specialists.

More generally, these results and those of Hansen *et al.* (1992) suggest that avian community dynamics are strongly influenced by species' life histories and local landscape dynamics. Knowledge of both factors is critical to effective conservation. Approaches are needed that evaluate past, present, and possible future landscape dynamics in an area and their ecological consequences. It also is important to examine the life-history characteristics of the local community and examine the responses of not just species thought to be sensitive, but a broad range of guilds and species. Landscape change is sufficiently rapid in some regions that the types of species experiencing rarity are in a state of flux. It is not widely appreciated yet, for example, that portions of the EDF reached maximum deforestation in the 1800's and that afforestation may now be jeopardizing species associated with open habitats. Similarly, conservation strategies in the Pacific Northwest that advocate only the retention of old-growth habitats and late successional species probably err in assuming that open-canopy species are 'weedy' and will always do well in disturbed landscapes. Some of these species are presently declining in abundance, possibly because the microhabitats or patch sizes they require are not being created at sufficient levels.

Attention to a paradigm linking disturbance, landscape dynamics, and plant and animal communities can provide a basis for regional biodiversity plans and knowledge for designing landscapes to optimize conservation of biodiversity and other natural resources.

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Appendix I. Life history traits of bird species with primary habitats in low to mid elevation conifer and conifer-hardwood forests in western Oregon and Washington. Migration strategy is from Ehrlich *et al.* (1988) and Love (1990). All other data are from Brown (1985) unless otherwise noted. ‘.’ denotes missing data. Character variables are coded – for all variables: Generalist – G; No data available – ND; Nest type: Open – O, Hole – H, Parasite – P; Seral stage association: Open-canopy – OC, Closed-canopy – CC, Old-growth – OG; Microhabitat association: Fallen-tree – L, Snag – S, Large tree – T; Food type: Carnivorous – C, Herbivorous – H, Insectivorous – I, Omnivorous – O; Response to edge: Edge specialist – E, Interior specialist – I; Response to area: Negative – N, Positive – P.

Species	Repro- ductive effort	Nest type (1)	Nest height (m) (1)	Territory size (ha)	Territory density	Seral stage assoc. (2)	Micro- habitat assoc.	Feeding strategy (1)	Response to edge (3, 4)	Response to patch size (3)
Neotropical migrants										
HERMIT WARBLER <i>Dendroica occidentalis</i>	4	O	17.7	.	353.2	CC	G	I	G	ND
SOLITARY VIREO <i>Vireo Solitarius</i>	4	O	11.3	1.7	54.3	CC	G	I	ND	ND
HAMMOND'S FLYCATCHER <i>Empidonax hammondii</i>	4	O	7.6	1.2	29.6	CC	G	I	G	G
WESTERN WOOD-PEWEE <i>Contopus sordidulus</i>	3	O	7.6	1.6	12.4	CC	G	I	ND	ND
WESTERN FLYCATCHER <i>Empidonax difficilis</i>	6	O	4.6	.	42.0	CC	G	I	G	G
OLIVE-SIDED FLYCATCHER <i>Contopus borealis</i>	4	O	12.2	1.6	.	CC	G	I	E	G
TOWNSEND'S WARBLER <i>Dendroica townsendi</i>	4	O	3.7	.	353.2	CC	G	I	G	ND
VIOLET-GREEN SWALLOW <i>Tachycineta thalassina</i>	6	H	3.1	.	49.4	OC	S	I	G	ND
ORANGE-CROWNED WARBLER <i>Vermivora celata</i>	5	O	0.6	2.0	103.7	OC	G	I	I	ND
RED-EYED VIREO <i>Vireo violaceus</i>	4	O	12.2	0.4	98.8	OC	G	I	ND	ND
BLACK-HEADED GROSBEAK <i>Pheucticus melanocephalus</i>	4	O	2.4	.	163.0	OC	G	I	ND	ND
YELLOW WARBLER <i>Dendroica petechia</i>	4	O	2.1	.	247.0	OC	G	I	ND	ND
WARBLING VIREO <i>Vireo gilvus</i>	4	O	18.3	.	103.7	OC	G	I	ND	ND
VAUX'S SWIFT <i>Chaetura vauxi</i>	5	H	1.2	2.0	.	OG	S	I	ND	ND
WILSON'S WARBLER <i>Wilsonia pusilla</i>	5	O	0.6	0.8	42.0	G	G	I	G	ND
YELLOW-RUMPED WARBLER <i>Dendroica coronata</i>	8	O	8.3	.	98.8	G	G	I	ND	ND
BLACK-THROATED GRAY WARBLER <i>Dendroica nigrescens</i>	4	O	7.0	.	37.1	G	G	I	ND	ND
WESTERN Tanager <i>Piranga ludoviciana</i>	4	O	11.0	.	113.6	G	G	I	E	ND
TREE SWALLOW <i>Tachycineta bicolor</i>	5	H	3.1	0.2	54.3	G	S	I	G	ND
BAND-TAILED PIGEON <i>Columba fasciata</i>	4	O	5.5	8.0	.	G	G	H	ND	ND
SWAINSON'S THRUSH <i>Catharus ustulatus</i>	8	O	3.7	.	98.8	G	G	I	I	ND

Species	Repro- ductive effort	Nest type (1)	Nest height (m) (1)	Territory size (ha)	Territory density	Seral stage assoc. (2)	Micro- habitat assoc. (2)	Feeding strategy (1)	Response to edge (3, 4)	Response to patch size (3)
Short-distance migrants										
BROWN-HEADED COWBIRD <i>Molothrus ater</i>	11	P	6.1	2.0	.	OC	G	O	E	ND
TURKEY VULTURE <i>Cathartes aura</i>	2	O	3.1	40.0	.	OC	S	X	ND	ND
AMERICAN GOLDFINCH <i>Carduelis tristis</i>	5	O	4.6	0.1	.	OC	G	H	I	ND
ANNA'S HUMMINGBIRD <i>Calypte anna</i>	4	O	4.6	4.0	.	OC	G	O	ND	ND
AMERICAN ROBIN <i>Turdus migratorius</i>	8	O	4.6	.	64.2	OC	G	O	G	P
CHIPPING SPARROW <i>Spizella passerina</i>	8	O	1.8	2.8	76.6	OC	G	O	ND	ND
WESTERN BLUEBIRD <i>Sialia mexicana</i>	5	H	7.6	.	37.1	OC	S	I	G	ND
MARbled MURRELET <i>Brachyramphus marmoratus</i>	2	O	22.9	8.0	.	OG	T	C	ND	ND
HERMIT THRUSH <i>Catharus guttatus</i>	5	O	1.2	0.8	24.7	G	G	I	G	G
RUFous HUMMINGBIRD <i>Selasphorus rufus</i>	4	O	2.4	0.1	.	G	G	O	G	ND
CEDAR WAXWING <i>Bombycilla cedrorum</i>	10	O	7.0	1.6	.	G	G	H	ND	ND
TOWNSEND'S SOLITAIRE <i>Myadestes townsendi</i>	4	O	1.5	4.0	7.4	G	L	I	ND	G
Residents										
BROWN CREEPER <i>Certhia americana</i>	6	H	8.0	.	32.1	CC	S	I	G	G
NORTHERN GOSHAWK <i>Accipiter gentilis</i>	3	O	12.2	3000.0	.	CC	G	C	ND	ND
WINTER WREN <i>Troglodytes troglodytes</i>	6	H	0.9	0.8	34.6	CC	L	I	I	P
DOWNY WOODPECKER <i>Picoides pubescens</i>	5	H	8.3	2.8	.	CC	S	I	ND	G
HAIry WOODPECKER <i>Picoides villosus</i>	4	H	9.8	2.8	.	CC	S	I	G	G
COOPER'S HAWK <i>Accipiter cooperi</i>	4	O	12.2	280.0	.	CC	G	C	ND	ND
BLUE GROUSE <i>Dendragapus obscurus</i>	9	O	0.0	4.4	.	CC	G	O	ND	G
CHESTNUT-BACKED CHICKADEE <i>Parus rufescens</i>	7	H	2.1	1.3	61.8	CC	S	I	G	P
SHARP-SHINNED HAWK <i>Accipiter striatus</i>	6	O	10.7	100.0	.	CC	G	C	ND	P
VARIED THRUSH <i>Ixoreus naevius</i>	4	O	8.3	.	7.4	CC	G	I	I	ND
GOLDEN-CROWNED KINGLET <i>Regulus satrapa</i>	16	O	9.8	.	148.2	CC	G	I	G	G
PILEATED WOODPECKER	4	H	13.8	184.0	.	CC	S	I	ND	P

Species	Repro- ductive effort	Nest type (1)	Nest height (m) (1)	Territory size (ha)	Territory density	Seral stage assoc. (2)	Micro- habitat assoc. (2)	Feeding strategy (1)	Response to edge (3, 4)	Response to patch size (3)
Neotropical migrants										
PINE SISKIN <i>Carduelis pinus</i>	8	O	8.6	.	34.6	G	G	O	ND	ND
PURPLE FINCH <i>Carpodacus purpureus</i>	5	O	7.0	.	54.3	G	G	O	G	ND
COMMON RAVEN <i>Corvus corax</i>	5	O	6.1	12.0	.	G	G	O	ND	ND
DARK-EYED JUNCO <i>Junco hyemalis</i>	10	O	3.1	1.0	133.4	G	G	O	G	ND
EVENING GROSBEAK <i>Coccothraustes vespertinus</i>	4	O	18.3	.	130.9	G	G	O	ND	ND
Mean or frequency (5)	5.6 (2.6)	O-79% H-21% P- 0%	6.8 (5.1)	119.9 (472.7)	89.5 (86.9)	G-33% OC-28% CC-33% OG- 5%	G-68% L- 5% S-23% T- 3%	C-16% H- 8% I-55% O-21%	G-24% E- 5% I-12% ND-59%	G-19% N- 0% P- 9% ND-72%

(1) From Ehrlich *et al.* (1988).

(2) Serving as primary habitat as defined by Brown (1985).

(3) From Rosenburg and Raphael (1986).

(4) From Hansen *et al.* in prep.

(5) Standard deviation of the mean is in parentheses.

Appendix II. Life-history traits of bird species within a three-county area in central Maryland. Data are from Whitcomb *et al.* (1981) and Ehrlich *et al.* (1988) unless otherwise noted. Character variables are coded as in Appendix I.

Species	Repro- ductive effort	Nest type	Nest height	Territory density (males/km ²)	Seral stage assoc.	Micro- habitat assoc.	Food type	Response to edge	Response to patch size (1)
Neotropical migrants									
WORM-EATING WARBLER <i>Helmitheros vermivorus</i>	4	O	0.0	26.0	CC	G	I	I	P
KENTUCKY WARBLER <i>Oporornis formosus</i>	8	O	0.0	36.0	CC	G	I	I	P
BLACK/WHITE WARBLER <i>Mniotilta varia</i>	6	O	0.0	27.0	CC	G	I	I	P
HOODED WARBLER <i>Wilsonia eitrinia</i>	3	O	0.9	63.0	CC	G	I	I	G
AMERICAN REDSTART <i>Setophaga ruticilla</i>	4	O	6.1	71.0	CC	G	I	I	G
EASTERN WOOD PEWEE <i>Contopus virens</i>	3	O	6.1	24.0	CC	G	I	G	P
OVENBIRD <i>Seiurus aurocapillus</i>	5	O	0.0	114.0	CC	G	I	I	P
VEERY <i>Catharus fuscescens</i>	3	O	1.0	42.0	CC	G	O	I	P
RED-EYED VIREO <i>Vireo violaceus</i>	6	O	2.8	138.0	CC	G	I	G	P

Species	Reproductive effort	Nest type	Nest height	Territory density (males/km ²)	Seral stage assoc.	Micro-habitat assoc.	Food type	Response to edge	Response to patch size (1)
ACADIAN FLYCATCHER <i>empidonax virescens</i>	6	O	2.8	68.0	CC	G	I	I	P
PROTHONOTARY WARBLER <i>Protonotaria citrea</i>	8	H	1.6	40.0	CC	G	I	G	G
LOUISIANA WATERTHRUSH <i>Seiurus motacilla</i>	5	O	0.0	16.0	CC	G	I	I	P
WOOD THRUSH <i>Hylocichla mustelina</i>	8	O	2.6	125.0	CC	G	O	G	P
SCARLET TANAGER <i>Piranga divacea</i>	6	O	6.4	27.0	CC	G	O	I	P
CERULEAN WARBLER <i>Dendroica cerulea</i>	3	O	10.7	83.0	CC	G	I	I	P
ORCHARD ORIOLE <i>Icterus spurius</i>	4	O	4.7	29.0	OC	G	I	E	ND
EASTERN KINGBIRD <i>Tyrannus tyrannus</i>	3	O	8.5	17.0	OC	G	I	E	ND
BLUE GROSBEAK <i>Guiraca caerulea</i>	6	O	1.3	4.0	OC	G	O	E	ND
BLUE-WINGED WARBLER <i>Vermivora pinus</i>	4	O	0.0	47.0	OC	G	I	E	ND
NORTHERN PARULA <i>Parula americana</i>	3	O	5.1	47.0	G	G	I	G	P
PRAIRIE WARBLER <i>Dendroica discolor</i>	8	O	1.0	85.0	G	G	I	E	G
RUBY-THROATED HUMMINGBIRD <i>Archilochus colubris</i>	4	O	4.0	15.0	G	G	O	G	P
YELLOW-BILLED CUCKOO <i>Coccyzus americanus</i>	3	O	4.0	17.0	G	G	I	G	P
YELLOWTHROATED VIREO <i>Vireo flavifrons</i>	6	O	8.8	25.0	G	G	I	G	G
YELLOW-BREASTED CHAT <i>Icteria virens</i>	4	O	1.1	36.0	G	G	I	E	G
YELLOW WARBLER <i>Dendroica petechia</i>	4	O	1.2	63.0	G	G	I	E	ND
BLUEGRAY GNATCATCHER <i>Polioptila caerulea</i>	10	O	8.8	28.0	G	G	I	G	P
WHIP-POOR-WILL <i>Caprimulgus vociferus</i>	4	O	0.0	13.0	G	G	I	G	G
INDIGO BUNTING <i>Passerina cyanea</i>	6	O	0.9	52.0	G	G	O	E	N
GREAT CRESTED FLYCATCHER <i>Myiarchus crinitus</i>	5	H	2.3	17.0	G	G	I	G	P
PINE WARBLER <i>Dendroica pinus</i>	4	O	10.4	76.0	CC	G	I	I	P
EASTERN BLUEBIRD <i>Sialia sialis</i>	8	H	2.0	151.0	OC	S	I	E	ND
COMMON GRACKLE <i>Quiscalus quiscula</i>	4	O	5.5	151.0	OC	G	O	E	G
WHITE-EYED VIREO <i>Vireo griseus</i>	6	O	1.0	40.0	OC	G	I	G	G
TURKEY VULTURE	2	O	3.3	7.0	OC	S	C	ND	ND

Species	Reproductive effort	Nest type	Nest height	Territory density (males/km ²)	Seral stage assoc.	Micro-habitat assoc.	Food type	Response to edge	Response to patch size (1)
<i>Cathartes aura</i> BROWN THRASHER	8	O	1.3	34.0	OC	G	O	E	ND
<i>Toxostoma rufum</i> COMMON YELLOWTHROAT	8	O	0.2	111.0	OC	G	I	G	G
<i>Geothlypis trichas</i> BLACK VULTURE	2	O	2.0	7.0	OC	S	C	ND	ND
<i>Coragyps atratus</i> AMERICAN GOLDFINCH	10	O	3.0	21.0	OC	G	H	E	G
<i>Carduelis tristis</i> HOUSE WREN	12	H	2.3	100.0	G	L	I	E	N
<i>Troglodytes aedon</i> MOURNING DOVE	8	O	2.4	151.0	G	G	H	E	G
<i>Zenaida macroura</i> AMERICAN ROBIN	12	O	6.1	122.0	G	G	O	E	N
<i>Turdus migratorius</i> RUFIOUS-SIDED TOWHEE	8	O	0.4	68.0	G	L	O	G	G
<i>Pipilo erythrophthalmus</i> GRAY CATBIRD	12	O	2.3	198.0	G	G	O	G	N
<i>Dumetella carolinensis</i> BROWN-HEADED COWBIRD	10	P	1.6	42.0	G	G	O	E	G
<i>Molothrus ater</i> NORTHERN FLICKER	6	H	5.8	27.0	G	S	I	G	G
<i>Colaptes auratus</i> EASTERN PHOEBE	10	O	2.3	15.0	ND	S	I	G	ND
<i>Sayornis phoebe</i>									
Residents									
BARRED OWL <i>Strix varia</i>	3	O	10.0	7.0	CC	S	C	ND	G
COOPER'S HAWK <i>Accipiter cooperii</i>	4	O	12.0	7.0	CC	G	C	ND	ND
SHARPEL-SHINNED HAWK <i>Accipiter striatus</i>	5	O	10.0	7.0	CC	G	C	ND	ND
WHITE-BREADED NUTHATCH <i>Sitta carolinensis</i>	6	H	6.1	20.0	CC	S	I	I	P
HAIRY WOODPECKER <i>Picoides villosus</i>	4	H	8.8	11.0	CC	S	I	I	P
PILEATED WOODPECKER <i>Dryocopus pileatus</i>	2	H	10.4	1.0	CC	S	I	I	P
AMERICAN KESTREL <i>Falco sparverius</i>	5	H	21.0	30.0	OC	S	I	ND	ND
EASTERN SCREECH OWL <i>Otus asio</i>	5	H	20.0	30.0	OC	S	I	ND	N
CHIPPING SPARROW <i>Spizella passerina</i>	6	O	2.2	90.0	OC	G	O	E	ND
BARN OWL <i>Tyto alba</i>	6	O	20.0	30.0	OC	S	C	ND	ND
SONG SPARROW <i>Melospiza melodia</i>	12	O	1.0	109.0	OC	G	O	E	ND
FIELD SPARROW <i>Spizella pusilla</i>	12	O	0.4	80.0	OC	G	O	E	ND

Species	Reproductive effort	Nest type	Nest height	Territory density (males/km ²)	Seral stage assoc.	Micro-habitat assoc.	Food type	Response to edge	Response to patch size (1)
CAROLINA CHICKADEE <i>Parus crolinensis</i>	6	H	1.5	39.0	G	S	I	G	N
TUFTED TITMOUSE <i>Parus bicolor</i>	5	H	3.4	56.0	G	S	I	G	P
CAROLINA WREN <i>Thryothorus ludovicianus</i>	10	O	1.5	59.0	G	L	I	G	G
DOWNY WOODPECKER <i>Picoides pubescens</i>	4	H	9.1	21.0	G	S	I	G	G
NORTHERN CARDINAL <i>Cardinalis cardinalis</i>	9	O	2.0	96.0	G	G	O	G	G
GREAT HORNED OWL <i>Bubo virginianus</i>	4	O	18.0	7.0	G	G	C	ND	G
BROAD WINGED HAWK <i>Buteo platypterus</i>	3	O	12.0	7.0	G	G	C	ND	ND
NORTHERN BOBWHITE <i>Colinus virginianus</i>	30	O	0.0	5.0	G	G	O	E	G
BLUE JAY <i>Cyanocitta cristata</i>	5	O	7.0	40.0	G	G	O	G	P
NORTHERN MOCKINGBIRD <i>Mimus polyglottos</i>	12	O	1.7	28.0	G	G	O	E	ND
EUROPEAN STARLING <i>Sturnus vulgaris</i>	15	H	4.0	151.0	G	S	O	E	N
RED-TAILED HAWK <i>Buteo jamaicensis</i>	3	O	18.0	7.0	G	G	C	ND	ND
RED-BELLIED WOODPECK <i>Melanerpes carolinus</i>	5	H	8.8	29.0	G	S	O	G	P
RED-SHOULDERED HAWK <i>Buteo lineatus</i>	3	O	12.0	7.0	G	G	C	ND	ND
AMERICAN CROW <i>Corvus brachyrhynchos</i>	10	O	10.4	30.0	G	G	O	E	P
Mean or frequency (2)	6.4 (4.1)	O-79% H-20% P- 1%	5.1 (5.3)	49.7 (44.9)	G-45% OC-24% CC-29% ND- 1%	G-73% L- 4% S-23%	C-13% H- 3% I-55% O-29%	G-32% E-32% I-20% ND-16%	G-29% N- 9% P-33% ND-28%

(1) From Robbins *et al.* (1989).

(2) Standard deviation of the mean is in parentheses.