

rived largely by applying a growing body of theory in behavioral ecology to the excellent and extensive data on the Alcidae assembled in the above books.

Gaston (1998) is suspicious about the model's "good fit with empirical observations." The history of science teaches us, however, that the other part of Gaston's opening statement—that the observations "otherwise are difficult to explain"—is as important to scientists in evaluating a model. Although perhaps a fluke, these models at least have the virtue that they provide possible explanations where previously there were none, and as yet there seems to be no strong competing model.

Nonetheless, I would not wish to defend this particular model too vigorously. In the longer run it will have to be evaluated empirically. I disagree, however, with the implication made in the closing sentence of Gaston's (1998) commentary that elaborations of the model and its predictions should not be made before a better evaluation of the current model is completed. To me, this is as unjustified and shortsighted as would be a charge to cease data collection until a model is perfected. If anything, there would seem to be a greater role for modeling in seabird studies than has been the case in the past. Both data and ideas are needed for progress in our discipline, and often we need to struggle to understand new ideas, as well as new data. As the interplay between them often is less-than-straightforward (e.g. Fagerstrom 1987, Ydenberg and Bertram 1989), seldom is a clear prescription possible for what step should be next. In seeking to understand something as complicated as alcid departure strategies, we should explore every avenue of inquiry.

## LITERATURE CITED

- FAGERSTROM, T. 1987. On theory, data and mathematics in ecology. *Oikos* 50:258–261.
- GASTON, A. J. 1998. Modeling departure strategies in auks. *Auk* 115:798–800.
- GASTON, A. J., AND D. N. NETTLESHIP. 1981. The Thick-billed Murres of Prince Leopold Island: A study of the breeding ecology of a colonial high arctic seabird. Canadian Wildlife Service, Ottawa, Ontario.
- HARRIS, M. P. 1984. *The Puffin*. T. & A. D. Poyser, Calton, United Kingdom.
- NETTLESHIP, D. N., AND T. R. BIRKHEAD. 1985. *The Atlantic Alcidae: The evolution, distribution and biology of auks inhabiting the Atlantic Ocean and adjacent water areas*. Academic Press, London.
- YDENBERG, R. C. 1989. Growth and mortality trade-offs and the evolution of juvenile life histories in the Alcidae. *Ecology* 70:1496–1508.
- YDENBERG, R. C., AND D. F. BERTRAM. 1989. Lack's clutch size hypothesis and brood enlargement studies on colonial seabirds. *Colonial Waterbirds* 12:134–137.
- YDENBERG, R. C., C. W. CLARK, AND A. HARFENIST. 1995. Intraspecific fledging mass variation in the Alcidae, with special reference to the seasonal fledging mass decline. *American Naturalist* 145: 412–433.

Received 24 October 1997, accepted 7 January 1998.  
Associate Editor: J. M. Eadie

*The Auk* 115(3):801–805, 1998

### On Forest-interior Species, Edge Avoidance, Area Sensitivity, and Dogmas in Avian Conservation

MARC-ANDRÉ VILLARD<sup>1</sup>

*Département de biologie, Université de Moncton, Moncton, New Brunswick E1A 3E9, Canada*

In their search for generality, ecologists often classify species sharing certain life-history characteristics into groups or guilds. Some ecological classifications aim to reflect the influence of landscape structure or habitat fragmentation on species distribution and abundance. For example, species have been classified according to their response to habitat

edges. The preference of certain species for ecotones or edges has long been recognized (reviewed in Robinson 1988). However, the notion that some species strongly prefer the habitat interior is recent. The concept of habitat-interior preference or specialization has mainly been used when investigating potential effects of habitat fragmentation on: (1) the distribution and abundance of plant and animal species (e.g. Whitcomb et al. 1981, Fraver 1994); (2) microclimate (Chen et al. 1993, Young and Mitchell 1994); and (3)

<sup>1</sup> E-mail: villarm@bosoleil.ci.umoncton.ca

interactions among microclimate, vegetation and animals (e.g. Burgess and Sharpe 1981). This concept has been applied to a wide variety of taxa, including lichens (Sillett 1994), vascular plants (Fraver 1994, de Casenave et al. 1995), crustaceans (Peterson and Turner 1994), birds (Whitcomb et al. 1981), and mammals (Heske 1995).

In avian ecology, the concept of habitat-interior preference was applied through the development of a classification of forest bird species among four categories: (1) forest-interior specialists, (2) interior-edge generalists, (3) edge species, and (4) field-edge species (Whitcomb et al. 1981). Whitcomb et al. (1981:139) defined forest-interior specialists as species that "nest only within the interior of the forest and tend to avoid edge habitats." This classification was quickly adopted by avian ecologists (Butcher et al. 1981, Lynch and Whigham 1984, Freemark and Merriam 1986, Askins et al. 1987), and the term "forest-interior species" entered the vocabulary of researchers, managers, and amateur birdwatchers alike. More recently, a classification of forest bird species was proposed to reflect their response to the area of forest fragments. Area-sensitive species are defined as species that occur more frequently, or increase in density, as fragment area increases (Freemark and Collins 1992:446).

In this paper, I review the empirical evidence for edge avoidance among species currently considered to be forest-interior specialists, examine the degree of correspondence between species classified as forest-interior specialists and area-sensitive species, and reevaluate these concepts and their application in ecology and conservation.

*Edge avoidance.*—Following Whitcomb et al.'s (1981) definition, the empirical data required to reliably classify forest-interior species should include nest and territory locations relative to forest edges. The original classification was "largely based on spot-mapping data" (Whitcomb et al. 1981:139) and reflected patterns observed in territory placement relative to forest-field or forest-urban edges. To support their classification, Whitcomb et al. (1981) provided maps showing territory locations for a typical forest-interior species (Hooded Warbler [*Wilsonia citrina*]), a typical interior-edge generalist (Northern Cardinal [*Cardinalis cardinalis*]), and an edge specialist (Indigo Bunting [*Passerina cyanea*]). The most recent classification (Freemark and Collins 1992) includes 91 species typically nesting in the eastern deciduous forest. This updated classification is based on five studies, three of which used the point-count method. This represents a serious problem, given the definition of a forest-interior specialist, because the point-count method is neither designed for nor efficient in providing evidence of nesting.

Only a few studies have directly tested the occurrence of edge avoidance in forest birds. In these studies, the number of territories or proportion of regis-

trations was compared among arbitrarily defined distance classes. Results from these studies are compiled in Table 1. Eight species showed significant edge avoidance in at least one of the four studies considered; six of these are classified as forest-interior species. Except for Noss (1991), significant edge avoidance was found in less than half of the forest-interior species considered. Ironically, the species exhibiting the most consistent pattern of edge avoidance, Red-eyed Vireo (*Vireo olivaceus*), is classified as an interior-edge species (Whitcomb et al. 1981, Freemark and Collins 1992).

Two major caveats must be pointed out: (1) census methods and distance classes (from the forest edge) varied among the studies included in Table 1, which makes cross-study comparisons problematic; and (2) because none of these studies included nest searches, species showing no significant avoidance of edges in certain studies may have been represented by floaters or unpaired territorial males near edges (Van Horn et al. 1995, R. F. Whitcomb pers. comm.). Nonetheless, these results raise important issues. First, few species appear to be "true" forest-interior species relative to the number of species considered in these studies. Second, even in species that exhibit significant edge avoidance, the distribution of territories relative to the forest edge may not differ significantly from that of randomly placed simulated territories (see King et al. 1997). Third, given the fact that unpaired males may defend territories during most of the breeding season (Villard et al. 1993, Holmes et al. 1996), few studies have reported the reproductive data required to demonstrate the existence of forest-interior species sensu Whitcomb et al. (1981) (but see Van Horn et al. 1995, King et al. 1996).

*Forest-interior versus area-sensitive species.*—In Freemark and Collins' (1992) classification, the vast majority of forest-interior species also are considered to be area-sensitive (91% of 22 species classified for area sensitivity). This may be interpreted as a direct consequence of the fact that smaller patches tend to have a higher proportion of their area near edges. However, as we have seen above, few studies have actually tested for edge avoidance, and when this was done, it was observed in only a few species. In contrast, the tendency for some species to be absent, or present at low abundance in small forest fragments, is well supported empirically for a large number of species (e.g. Robbins et al. 1989, Blake 1991).

*Discussion.*—To many researchers, forest-interior habitat use and area sensitivity have become synonymous to the point that these terms are sometimes used interchangeably. Part of the confusion surrounding these terms may stem from the documentation of negative edge effects on reproductive performance (see Paton 1994). However, edge-related decreases in reproductive success, edge avoidance, and area sensitivity are distinct phenomena that may result from very different biological mechanisms.

TABLE 1. Species exhibiting significant (\*,  $P < 0.10$ ) edge avoidance in four different studies.

	Kroodsmas (1984)	Noss (1991)	King et al. (1997)	Germaine et al. (1997)
Location	Tennessee	Florida	New Hampshire	Vermont
No. species considered	22	27	7	25
No. forest-interior species <sup>a</sup>	8	7 <sup>b</sup>	6	12 <sup>b</sup>
Acadian Flycatcher <sup>c</sup> ( <i>Empidonax virescens</i> )	*	*	— <sup>d</sup>	—
Wood Thrush ( <i>Hylocichla mustelina</i> )	ns	*	—	ns <sup>e</sup>
Hermit Thrush <sup>c</sup> ( <i>Catharus guttatus</i> )	—	ns	*	*
Solitary Vireo <sup>c</sup> ( <i>Vireo solitarius</i> )	—	—	—	*
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	ns	*	*	*
Black-throated Green Warbler <sup>c</sup> ( <i>Dendroica virens</i> )	—	—	ns	*
Hooded Warbler <sup>c</sup> ( <i>Wilsonia citrina</i> )	ns	*	—	—
Ovenbird <sup>c</sup> ( <i>Seiurus aurocapillus</i> )	*	ns	ns	*

<sup>a</sup> Based on Whitcomb et al. (1981) and Freemark and Collins (1992).

<sup>b</sup> One species could not be classified using references in (a).

<sup>c</sup> Forest-interior species, according to references in (a).

<sup>d</sup> Species not included in study.

<sup>e</sup> Significant difference in abundance among distance classes, but no edge avoidance.

Low reproductive success near edges may promote dispersal (Darley et al. 1977, Nolan 1978, Harvey et al. 1979, Shields 1984, Weatherhead and Boak 1986, Gavin and Bollinger 1988, Pärt and Gustafsson 1989). However, active avoidance of habitat edges (and, thus, of small fragments) by unsuccessful nesters searching for a future breeding territory has yet to be documented.

Significant edge avoidance by birds could also reflect edge effects on microclimate, vegetation structure, prey abundance, and their interactions. Studies have shown edge-to-interior gradients in microclimate (e.g. wind velocity, soil and air moisture; Chen et al. 1993), vegetation structure (Ranney et al. 1981, Chen et al. 1992), and plant species composition (Fraver 1994), which in turn could influence the abundance and species composition of arthropods (Shure and Phillips 1991). True forest-interior species might feed mainly on moisture-dependent arthropods, as suggested by Gibbs and Faaborg (1990) for Ovenbirds (*Seiurus aurocapillus*).

Ecological classifications can have great heuristic value. However, their uncritical use can also lead to simplistic perspectives on nature. Classification of species according to their preference for forest-interior habitat or avoidance of small fragments tends to focus attention on the local (i.e. fragment) scale, whereas processes underlying these phenomena may take place over landscape (Villard et al. 1995, Wiens 1995) or even continental scales (Maurer and

Villard 1994). For example, Donovan et al. (1997) have shown that the probability of predation of artificial nests and the abundance of Brown-headed Cowbirds (*Molothrus ater*) vary not only with the proximity to forest edges, but also with the degree of forest fragmentation (landscape type) and the interaction between these two variables. Fragment occupancy by birds also is influenced by landscape context (proximity to other local populations), rather than strictly by local characteristics (Fritz 1979, Villard et al. 1995). Consequently, forest-interior preference and area sensitivity should be considered in a landscape context.

Landscape-scale analyses also can lead to oversimplifications. Considering only the core area (sensu Temple 1986) of habitat when analyzing a landscape may give the impression that edge habitat or small fragments serve no function for habitat-interior species. Even though birds defending territories close to an edge or in a small fragment may experience low pairing success (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995), this habitat is still valuable for the metapopulation as a whole in that it provides resources to support individuals that may enter the breeding population later (Howe et al. 1991). Therefore, small fragments should not be disregarded when planning the ecological restoration or rehabilitation of a landscape. However, their value is indeed limited in landscapes that completely lack

extensive tracts of habitat (Whitcomb et al. 1976, 1981).

The fact that certain species gradually disappear from smaller fragments (Whitcomb et al. 1981, Robbins et al. 1989, Blake 1991) indicates that area sensitivity and forest-interior preference have major conservation implications. However, blindly applying classifications and confusing forest-interior preference with area sensitivity might focus the attention of conservationists: (1) on the wrong species, or (2) on the right species in the wrong landscapes. This attitude, and the mistakes that result, will slow down our progress toward an understanding of the subtleties of spatiotemporal dynamics in avian populations.

*Acknowledgments.*—I sincerely thank Robert Whitcomb for his thorough review of the manuscript. Pierre Drapeau, Kathy Martin, Peter Paton, Kurtis Trzcinski, and Jeffrey Walters also made stimulating comments on the manuscript. This study was supported by a research grant from the Natural Sciences and Engineering Research Council of Canada (NSERC).

#### LITERATURE CITED

- ASKINS, R. A., M. J. PHILBRICK, AND D. S. SUGENO. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* 39: 129–152.
- BLAKE, J. G. 1991. Nested subsets and the distribution of birds on isolated woodlots. *Conservation Biology* 5:58–66.
- BURGESS, R. L., AND D. M. SHARPE (Eds.). 1981. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- BUTCHER, G. S., W. A. NIERING, W. J. BARRY, AND R. H. GOODWIN. 1981. Equilibrium biogeography and the size of nature reserves: An avian case study. *Oecologia* 49:29–37.
- CHEN, J., J. F. FRANKLIN, AND T. A. SPIES. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2:387–396.
- CHEN, J., J. F. FRANKLIN, AND T. A. SPIES. 1993. Contrasting microclimates among clearcut, edge, and interior old growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219–237.
- DARLEY, J. A., D. M. SCOTT, AND N. K. TAYLOR. 1977. Effects of age, sex, and breeding success on site fidelity of Gray Catbirds. *Bird-Banding* 48:145–151.
- DE CASENAVE, J. L., J. P. PELOTTO, AND J. PROTOMASTRO. 1995. Edge-interior differences in vegetation structure and composition in a Chaco semi-arid forest, Argentina. *Forest Ecology and Management* 72:61–69.
- DONOVAN, T. M., P. W. JONES, E. M. ANNAND, AND F. R. THOMPSON III. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. *Ecology* 78:2064–2075.
- FRAVER, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. *Conservation Biology* 8:822–832.
- FREEMARK, K. E., AND B. COLLINS. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pages 443–454 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- FREEMARK, K. E., AND H. G. MERRIAM. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biological Conservation* 36:115–141.
- FRITZ, R. S. 1979. Consequences of insular population structure: Distribution and extinction of Spruce Grouse populations. *Oecologia* 42:57–65.
- GAVIN, T. A., AND E. K. BOLLINGER. 1988. Reproductive correlates of breeding-site fidelity in Bobolinks (*Dolichonyx oryzivorus*). *Ecology* 69:96–103.
- 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.
- GIBBS, J. P., AND J. FAABORG. 1990. Estimating the viability of Ovenbird and Kentucky warbler populations in forest fragments. *Conservation Biology* 4:193–196.
- HARVEY, P. H., P. J. GREENWOOD, AND C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). *Journal of Animal Ecology* 48:305–313.
- HESKE, E. J. 1995. Mammalian abundances on forest-farm edges versus forest interiors in southern Illinois: Is there an edge effect? *Journal of Mammalogy* 76:562–568.
- HOLMES, R. T., P. P. MARRA, AND T. W. SHERRY. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): Implications for population dynamics. *Journal of Animal Ecology* 65:183–195.
- HOWE, R. W., G. J. DAVIS, AND V. MOSCA. 1991. The demographic significance of “sink” populations. *Biological Conservation* 53:239–255.
- KING, D. I., C. R. GRIFFIN, AND R. M. DEGRAAF. 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in forested landscapes. *Conservation Biology* 10:1380–1386.
- 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.
- KROODSMA, R. L. 1984. Effect of edge on breeding forest bird species. *Wilson Bulletin* 96:426–436.
- LYNCH, J. F., AND D. F. WHIGHAM. 1984. Effects of forest fragmentation on breeding bird communities

- in Maryland, USA. *Biological Conservation* 28: 287–324.
- MAURER, B. A., AND M.-A. VILLARD. 1994. Population density: Geographic variation in abundance of North American birds. *National Geographic Research and Exploration* 10:306–317.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithological Monographs* No. 26.
- NOSS, R. F. 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth Florida hammock. *Natural Areas Journal* 11:34–47.
- PÄRT, T., AND L. GUSTAFSSON. 1989. Breeding dispersal in the Collared Flycatcher (*Ficedula albicollis*): Possible causes and reproductive consequences. *Journal of Animal Ecology* 58:305–320.
- PATON, P.W.C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8:17–26.
- PETERSON, G. W., AND R. E. TURNER. 1994. The value of salt marsh edge vs. interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* 17:235–262.
- RANNEY, J. W., M. C. BRUNER, AND J. B. LEVENSON. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67–95 in *Forest island dynamics in man-dominated landscapes* (R. L. Burgess, and D. M. Sharpe, Eds.). Springer-Verlag, New York.
- ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic states. *Wildlife Monographs* No. 103.
- ROBINSON, S. K. 1988. Reappraisal of the costs and benefits of habitat heterogeneity for nongame wildlife. *Transactions of the North American Wildlife and Natural Resources Conference* 53: 145–155.
- SHIELDS, W. M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *Auk* 101:780–789.
- SHURE, D. J., AND D. L. PHILLIPS. 1991. Patch size of forest openings and arthropod populations. *Oecologia* 86:325–334.
- SILLETT, S. C. 1994. Growth rates of two epiphytic cyanolichen species at the edge and in the interior of a 700-year-old Douglas fir forest in the western Cascades of Oregon. *Bryologist* 97:321–324.
- TEMPLE, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: A comparison of two models. Pages 301–304 in *Wildlife 2000* (J. Verner, C. J. Ralph, and M. L. Morrison, Eds.). University of Wisconsin Press, Madison.
- VAN HORN, M. A., R. M. GENTRY, AND J. FAABORG. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracks. *Auk* 112:98–106.
- VILLARD, M.-A., P. R. MARTIN, AND C. G. DRUMMOND. 1993. Habitat fragmentation and pairing success in the Ovenbird (*Seiurus aurocapillus*). *Auk* 110:759–768.
- VILLARD, M.-A., G. MERRIAM, AND B. A. MAURER. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a fragmented temperate forest. *Ecology* 76:27–40.
- WEATHERHEAD, P. J., AND K. A. BOAK. 1986. Site infidelity in Song Sparrows. *Animal Behaviour* 34: 1299–1310.
- WHITCOMB, R. F., J. F. LYNCH, M. K. KLIMKIEWICZ, C. S. ROBBINS, B. L. WHITCOMB, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125–205 in *Forest island dynamics in man-dominated landscapes* (R. L. Burgess and D. M. Sharpe, Eds.). Springer-Verlag, New York.
- WHITCOMB, R. F., J. F. LYNCH, P. A. OPLER, AND C. S. ROBBINS. 1976. Island biogeography and conservation: Strategy and limitations. *Science* 193: 1030–1032.
- WIENS, J. A. 1995. Habitat fragmentation: Island vs. landscape perspectives on bird conservation. *Ibis* 137:597–610.
- YOUNG, A., AND N. MITCHELL. 1994. Microclimate and vegetation edge effects in a podocarp-broadleaf forest in New Zealand. *Biological Conservation* 67:63–72.

Received 13 May 1997, accepted 30 January 1998.  
Associate Editor: K. Martin