

Avian habitat evaluation: should counting birds count?

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There are times when birds reproduce at higher rates in places where they are less abundant, limiting the generally accepted value of bird counts as environmental indicators. But how often, and under what circumstances, does this happen? In 109 published cases involving 67 species across North America and Europe, higher density sites displayed greater recruitment per capita and per unit of land area in 72% and 85% of cases, respectively. The frequency of negative relationships between abundance and reproductive success did not differ between different kinds of birds or habitats. However, density was negatively related to reproductive success more often in areas of human disturbance than in relatively natural areas. Although further study is needed to confirm the generality of this pattern, especially in areas such as the tropics, results suggest that birds can fail to recognize ecological traps or opportunities in landscapes that differ from those in which they evolved.

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Density is a fundamental property of all populations that can vary spatially and temporally in response to habitat change (Holmes and Sherry 2001; Morris 2003). However, over 20 years ago, Van Horne (1983) warned that density could be a misleading indicator of habitat quality if it were negatively correlated with other critical population attributes, especially reproductive success and survival. Although Van Horne felt at the time that she was “just pointing out the obvious”, her paper has had an enduring impact on animal ecology and conservation biology.

Based on citation frequency, the response to Van Horne’s warning started slowly, grew quickly through the 1990s, and may only have peaked in the new millennium (Figure 1). Her paper has been cited more than 500 times, mostly by ornithologists and conservation biologists, who were understandably concerned that disconnects between abundance and the ability of birds to reproduce and survive in a specific area would

decrease the value of bird numbers (and a variety of long-term datasets) as indicators of environmental conditions (O’Connor 1991; Vickery *et al.* 1992; Gibbons *et al.* 1993; Price *et al.* 1995; Brawn and Robinson 1996). But how often, and under what circumstances, have avian biologists actually found negative correlations between the results of their bird counts (Figure 2) and measures of reproductive success or survival?

Van Horne suggested that density was most likely to fail to predict habitat quality under two conditions: first, when population size has been determined at a time or place other than that in which it is being measured (eg migratory birds, whose populations may be limited outside the breeding season; Webster *et al.* 2002), and second, when dominant individuals secure space in prime habitats, forcing subordinate individuals to aggregate in large numbers in marginal areas (Fretwell and Lucas 1970; Van Horne 1982; Pulliam 1988).

A third set of conditions, not explicitly considered by Van Horne, might occur when anthropogenic disturbances impair the animals’ ability to correctly recognize and select optimum habitats. This circumstance could arise, for example, when disturbances reshape relationships between predators or competitors and aspects of habitat or landscape structure that birds have evolved to use when choosing places to settle (Martin 1995; Misenhelter and Rotenberry 2000; Pidgeon *et al.* 2003). Given the frequent application of bird count results in the assessment of human environmental impacts (Koskimies 1989; Peakall 2000), this sort of disconnect could be particularly serious.

The purpose of our study was to learn just how frequently, and under what circumstances, bird densities actually have failed to predict either recruitment or sur-

In a nutshell:

- Studies indicate that birds are usually more abundant in habitats where reproduction is highest, confirming the legitimacy of using bird counts as indicators of breeding habitat quality and as a basis for management decisions
- Disconnects between abundance and reproduction may occur more often in disturbed areas
- More studies are needed outside the northern hemisphere, especially in the tropics, to confirm that this pattern exists there too
- Relatively few data are available comparing abundance with survival, another key demographic variable

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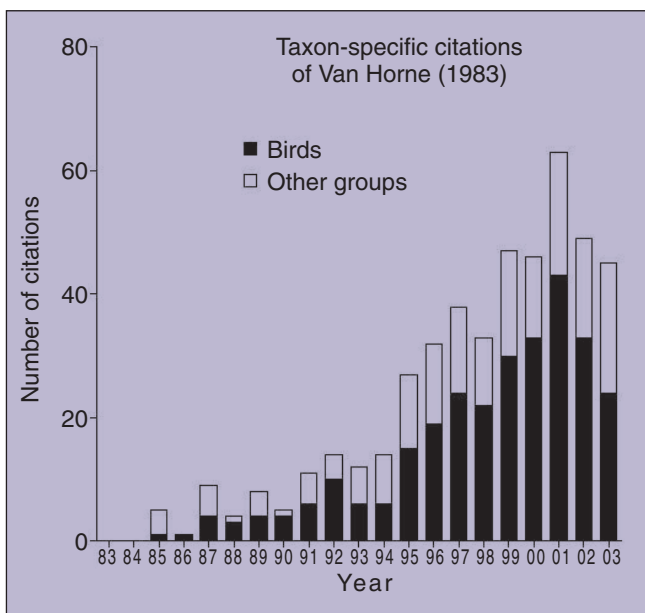


Figure 1. Yearly frequency of citations of Van Horne (1983) in the Web of Science database that dealt with specific groups of plants or animals, and the frequency with which these involved birds. Results are the numbers of citations listed in the database through January 15, 2004.

vival. Our method was to review and synthesize the results of studies published over the past 20 years, most of which have cited Van Horne’s 1983 paper.

■ Finding and selecting the studies to analyze

The survey was limited to published studies about birds reported in the Web of Science database (www.isiknowledge.com), that were available to us electronically or in our library, and that either cited Van Horne (1983) or used the key words “abundance”, “reproduction”, and/or “survival”. Species from a wide variety of terrestrial and freshwater habitats were included, but none from marine ecosystems, in part because of the inherent difficulty in obtaining density estimates for species that forage widely over the open

sea. We excluded all studies that involved the use of artificial nest boxes, as these can result in densities, predation rates, and competitive effects unrelated to overall habitat quality (Both 1998; Poysa and Poysa 2002; Mitrus 2003). Only studies that monitored at least five nests or territories in each of the areas being compared were included. Data were obtained from 114 cases that reported the requisite information about abundance versus reproduction or survival across two or more study sites, but only five of these occurred outside Europe or North America. We were therefore not comfortable extrapolating our results to other parts of the world. The final database consisted of 109 cases from Europe or North America, involving 67 species, reported in 58 publications (see WebTable 1).

■ Building and analyzing the dataset

The ideal study for a test of Van Horne’s predictions would be one in which study sites were replicated in sufficient numbers to correlate density with reproduction or survival. However, most publications presented data as two-group comparisons (eg the means of fragmented versus unfragmented areas), precluding this approach. In order to include results of all these studies in one common sample, each case was reduced to such a bivariate comparison, pooling data into two landscape or habitat categories whenever possible. In those cases where this was not possible (eg a number of different study areas that did not sort themselves logically into two categories), we determined the two areas with the highest and lowest densities and compared their demographics.

Avian population variables have been calculated in numerous ways (Ralph *et al.* 1993). Our approach was to divide each variable from the high-density area by its equivalent in the low-density area, to obtain unitless ratios that could be compared across all studies, regardless of their methods. First, we calculated a density ratio (D_{high}/D_{low}). We next calculated ratios of per capita reproduction (R_c) and survival (S) in the higher density versus lower density study areas ($R_c \cdot D_{high}/R_c \cdot D_{low}$; $S \cdot D_{high}/S \cdot D_{low}$). These



Figure 2. Counting birds in an Arizona grassland.

ratios were then correlated with one another across all studies (using logs to reduce the effects of outliers), to determine if density predicted per capita reproduction or survival (Figure 3). The density ratios had a minimum value of 1.0 by definition, while the reproductive and survival ratios were less than 1.0 if the relationship to density was negative.

Density itself is a major contributor to reproduction when it is calculated per unit land area. Per capita reproduction should drive the habitat selection decisions of individual birds, but reproduction per unit area could influence conservation decisions, if the goal is to protect habitats that produce the most young. We therefore multiplied density by per capita reproduction to generate a third variable for each study – the ratio of reproduction per unit land area (R_a) in the high- versus the low-density area ($R_a\text{-Dhigh}/R_a\text{-Dlow}$) – and correlated this variable with the density ratio. Each case was categorized where the reproductive or survival ratio was >1.0 as positive, and all cases where the reproductive or survival ratio was <1.0 as negative (Table 1).

Cases were also categorized by habitat and species attributes in order to test predictions about the circumstances where density and reproduction or survival might be uncoupled. Information was taken from the studies themselves, as well as from general references about avian natural history (Poole and Gill 1992–2002, see reference; Snow and Perrins 1998). These attributes were categorized as follows (see Web Table 1 and Table 1): (a) type of bird (to Order); (b) habitat type; (c) location of the study (Europe, eastern North America, or western North America); (d) migratory versus resident status; (e) degree of territoriality, ranging from species that defend the entire home range (type A; Nice 1941; Maher and Lott 1995) to those that defend only part of their range (type B) or none except the nest or mating site (type C); and (f) whether the study involved higher versus lower amounts of anthropogenic disturbance, based on our comparative evaluation of the entire dataset. Cases where disturbance was relatively minor (eg removal of $<10\%$ of a forest canopy) were placed in the “lower” category.

We computed product–moment correlation coefficients (r -values) between density and reproductive ratios (Figure 3), and compared the frequencies of positive versus negative associations between density and reproduction against a null expectation of 50:50, using the chi-square goodness of fit statistic. Two approaches were used to test for effects of various study attributes such as type of bird, amount of habitat disturbance, and degree of territoriality on the probability of density and per capita reproduction being positively versus negatively related. First, we examined the effects of each variable separately, using Fisher’s exact tests or chi-square contingency statistics (Table 1). Next, we included each variable in a multiple logistic regression, and tested for the independent contribution each variable made to the whole model, as well as effects on the model of removing each variable (Table 2). The probabilities of spurious (chance) associations are shown as P -values, and, according to tradition, any P -value equal to or less than 0.05 was con-

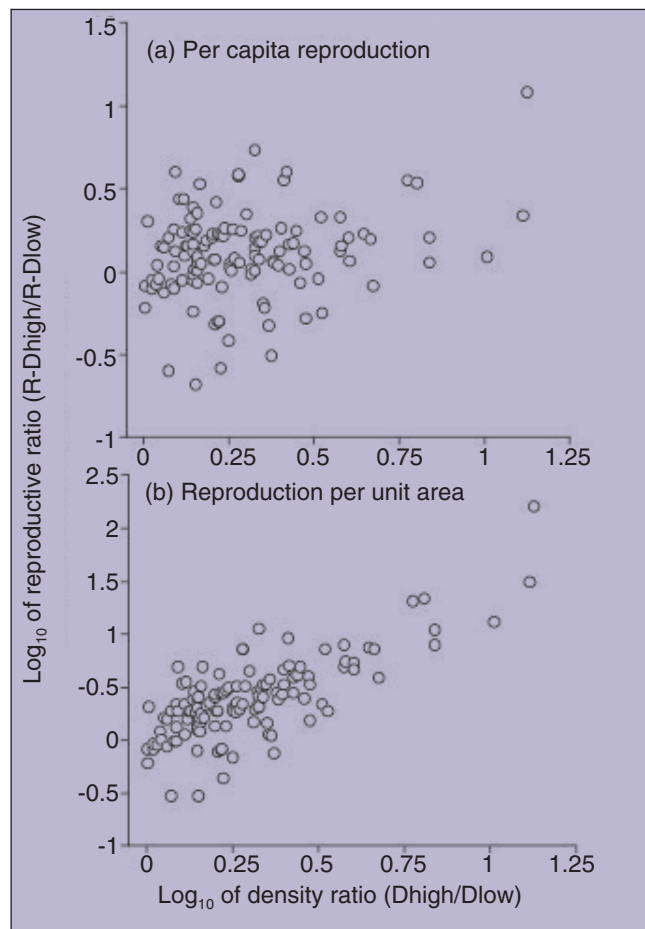


Figure 3. Does density difference predict reproductive difference between two areas? Log of the ratio of higher versus lower density between two areas (D_{high}/D_{low}), plotted against the logs of ratios of two measures of reproduction (R) in the high versus low density areas: (a) per capita reproduction, and (b) reproduction per unit land area; $n = 109$ cases, for 67 species.

sidered statistically significant. All analyses were performed using StatView (SAS Publishing 1999).

■ How often was abundance negatively related to survival or reproduction?

In only seven cases was it possible to compare abundance and survivorship between two areas, and the relationship was negative in three of them. Given the small sample size, all we can conclude regarding density as an indicator of survival among birds is that many more studies are needed.

Abundance and per capita reproduction were positively associated in 78 of 109 cases (72%), far more than would be expected by chance (chi-square = 20.3, $P < 0.0001$). The magnitude of density difference between two areas was only weakly positively correlated with the per capita reproductive difference (Figure 3a; $r = 0.267$, $P = 0.005$). However, this may be a case where the boundary of a distribution of points is more interesting and useful than the scatter (Cade and Noon 2003), because the magnitude of

Table 1. Number of cases (and percentages) where density and per capita reproduction were positively versus negatively associated, in paired comparisons between plots, habitats, or landscapes with higher versus lower densities (n = 109)

Comparison type	Positive	Negative	Statistical comparison
(a) Type of bird			
Songbird	60 (69.8)	26 (30.2)	Fisher's exact P = 0.60
Other	18 (78.3)	5 (21.7)	
(b) Habitat			
Forest/shrub	39 (63.9)	22 (36.1)	chi-square = 4.13 (P = 0.13)
Grassland/agricultural	25 (83.3)	5 (16.7)	
Aquatic/wetland	14 (77.8)	4 (22.2)	
(c) Migratory species			
Yes	60 (70.6)	25 (29.4)	Fisher's exact P = 0.80
No	18 (75.0)	6 (25.0)	
(d) Degree of territoriality			
High (A)	47 (68.1)	22 (31.9)	chi-square = 1.81 (P = 0.40)
Medium (B)	19 (73.1)	7 (26.9)	
Low (C)	12 (85.7)	2 (14.3)	
(e) Level of overall anthropogenic disturbance			
Higher	54 (65.9)	28 (34.1)	Fisher's exact P = 0.03
Lower	24 (88.9)	3 (11.1)	
(f) Area of study, disturbed sites only			
Europe	14 (82.4)	3 (17.6)	chi-square = 9.50 (P = 0.01)
Eastern North America	35 (70.0)	15 (30.0)	
Western North America	5 (33.3)	10 (66.7)	

the density ratio corresponded closely with the lower limit of the reproductive ratio (Figure 3a). The per capita reproductive ratio was likely to be negative (lower density area having higher per capita reproduction) only if the magnitude of the density ratio was less than about 3.5 ($\log_{10} = 0.54$).

Abundance and reproduction per unit land area were positively associated in 93 of 109 cases (85%; chi-square = 54.4, $P < 0.0001$), and these variables were strongly positively correlated (Figure 3b; $r = 0.754$, $P < 0.0001$). These results make it clear that adult density was usually a major contributor to number of young produced per area, and that per capita reproductive differences rarely trumped density effects to the point where density alone failed to accurately predict the more productive breeding habitat.

■ When has abundance failed to predict reproductive success?

The data as a whole suggest that ornithologists and ecologists in Europe and North America have good reason for using bird count results as indicators of environmental condition – at least in terms of breeding habitat quality. But has this link been stronger for some kinds of birds or environments than for others?

A major complication in teasing apart differences

between birds and habitats is that they are not always independent. For example, waterfowl are more often associated with wetlands than are songbirds. Therefore, if we found that density and reproductive success were more likely to be uncoupled in ducks than in warblers, we would have difficulty attributing this to something about the birds as opposed to something about their habitats. One approach would be to break down the dataset into many small categories (for example, songbirds found only in wetlands), but this inevitably leads to problems of small sample sizes in each category, and the increased likelihood of some statistical tests being significant just by chance. Our approach was therefore to conduct a relatively small number of tests on a few key factors, in most cases involving the whole dataset (Table 1). Each of these variables was then included in one multiple logistic regression model, to test for its effect on the likelihood of positive versus negative relationships between density and per capita reproduction, independent of the possible confounding effects of other variables.

Two obvious factors of interest are the different types of birds and habitats. Eighty-six of the 109 studies involved songbirds (Order Passeriformes), while studies of the other orders of birds were too few to meaningfully analyze, except as a group. There was a slightly higher frequency of negative associations between abundance and reproductive output among

songbirds as compared to other species, but this difference did not approach statistical significance (Table 1a). There were no significant differences between the three major habitat types (Table 1b), although negative results appeared somewhat more likely in forest/shrublands than in aquatic/wetlands, while grassland/agricultural areas gave intermediate results. Two of Van Horne's (1983) principal concerns were that disconnects between abundance and reproductive success would be more likely to occur in migratory and/or highly territorial species. In separate contingency tests, neither attribute was significantly related to the frequency of disconnects between abundance and reproductive success (Tables 1c and 1d).

The value of bird counts as environmental indicators would be especially high in areas being impacted by human activity (Koskimies 1989; Peakall 2000). Our results here are cautionary, because the chance of a negative association between abundance and reproductive success was significantly higher in disturbed than in relatively undisturbed areas (Table 1e). Most importantly, level of anthropogenic disturbance was the only variable that significantly affected the multiple logistic regression, in terms of contributing to the power of the overall model (Table 2a), or affecting the model upon its removal from the dataset (Table 2b).

The data strongly suggest that human disturbance ham-

pers the ability of many birds to recognize and occupy the places best suited for their reproduction, and that this relationship is independent of type of bird or habitat. An illustrative example involves two studies of the blackcap (*Sylvia atricapilla*) in the Czech Republic (Figure 4). In a comparison between two native habitats, blackcaps were both more abundant and more reproductively successful in mixed conifer forests than in deciduous riparian woodlands (Weidinger 2000). By contrast, Remes (2003) found that blackcaps were over 1.5 times more abundant in a plantation of non-native trees than in a native floodplain forest, but per capita reproductive success was nearly four times higher in the native forest. Remes (2003) concluded that the exotic plantation was an “ecological trap” – defined as a poor-quality area or habitat that nevertheless attracts large numbers of individuals (Schlaepfer *et al.* 2002).

Another example of a possible ecological trap involves the black-throated sparrow (*Amphispiza bilineata*; Figure 5) in southern New Mexico (Pidgeon *et al.* 2003). Among a variety of desert grass–shrub habitats, the breeding sparrows aggregated in the highest densities in mesquite (*Prosopis* spp) savannas, despite very low reproductive success; the authors attributed this to an historic loss of grassy understory caused by livestock grazing.

In many cases, abundance and per capita reproductive success have remained positively associated, even in human-altered landscapes, because birds appropriately chose the relatively natural areas. For example, forest-dwelling songbirds in the northeastern US have usually proven both more productive and more abundant in forest interiors than at edges or in small fragments. Examples include the ovenbird (*Seiurus aurocapillus*; Ortega and Capen 1999; Porneluzi and Faaborg 1999; Figure 6), scarlet tanager (*Piranga olivacea*; Roberts and Norment 1999; Figure 7), and wood thrush (*Hylocichla mustelina*; Weinberg and Roth 1998).

In some cases, an anthropogenically altered environment may provide good breeding habitat that birds fail to recognize as such. For example, sage sparrows (*Amphispiza belli*) avoided disturbed habitat patches in an urbanizing southern California landscape, despite the fact that a scarcity of predators rendered such areas superior for breeding (Misenhelter and Rotenberry 2000). In other cases, birds have apparently been able to take advantage of human habitat alteration. For example, Eurasian eagle owls (*Bubo bubo*; Figure 8) were both more abundant and more productive in

Table 2. Results of multiple logistic regression, with positive versus negative relationships between density and per capita reproduction as the two-state dependent variable, and five study attributes as independent variables (as shown in Table 1): type of bird, habitat, migratory status, degree of territoriality, and level of habitat disturbance

(a) Whole model coefficients and partial correlations			
Variable	Beta coefficient (standard error)	Wald chi-square (P)	Partial correlation
Type of bird	0.71 (1.01)	0.50 (0.48)	<0.001
Habitat type			
• forest/shrub vs grassland/agricultural	-0.91 (0.62)	2.17 (0.14)	-0.036
• forest/shrub vs. aquatic/wetland	-0.05 (0.95)	<0.01 (0.96)	<0.001
Migratory status	0.02 (0.66)	<0.01 (0.98)	<0.001
Degree of territoriality			
• A vs B	-0.27 (0.54)	0.25 (0.62)	<0.001
• B vs C	-0.75 (0.98)	0.58 (0.45)	<0.001
Level of habitat disturbance	-1.63 (0.82)	3.90 (0.05)	-0.121
Constant	-0.40 (0.32)	1.58 (0.21)	<0.001
(b) Effect on model if a variable removed			
Variable	df	chi-square (P)	
Type of bird	1	0.51 (0.48)	
Habitat	2	2.43 (0.30)	
Migratory status	1	<0.01 (0.98)	
Degree of territoriality	2	0.79 (0.68)	
Level of habitat disturbance	1	4.99 (0.03)	

parts of southern France where long-term human activity maintained a relatively open habitat mosaic and a greater variety of prey (Penteriani *et al.* 2002).

One intriguing pattern in the dataset suggests that birds might be able to adapt to human disturbance given suffi-



Figure 4. A nesting Blackcap (*Sylvia atricapilla*)



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Figure 5. Black-throated sparrow (*Amphispiza bilineata*).

cient time, in terms of both avoiding ecological traps and seizing ecological opportunities. Among the 82 studies involving relatively disturbed sites, negative relationships between abundance and per capita reproduction were most common in western North America, intermediate in eastern North America, and least common in Europe (Table 1f), which ranks inversely with time since humans first imposed their agricultural, industrial, and urban impacts on the environment. At least in our dataset, the American West is the only place where negative relationships between density and reproduction have outnumbered the positive (Tables 1f).

■ Conclusions and recommendations for further research

The results of our survey suggest that European and North American birds are usually able to aggregate in the higher quality breeding locations, regardless of the



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Figure 6. Ovenbird (*Seiurus aurocapillus*).

type of bird or habitat. In most cases, density will be a reliable indicator of habitat quality, and bird-count data will be an appropriate basis from which to make land-management and conservation decisions. However, this generally rosy assessment is only a statistical one, and need not apply to any particular case. We have identified a number of areas that require more careful study, and to which avian ecologists and conservation biologists could profitably turn their attention. The first and most obvious of these is geographic; more studies are needed outside Europe and North America, to determine whether the patterns we found in this review apply to other areas, most particularly to the tropics.

Our data strongly suggest that human habitat disturbance can impair the ability of birds to recognize and occupy the best places. However, more data are needed to confirm this relationship. Especially important will be additional studies of birds in recently disturbed areas, where they may not have had the time to learn (evolutionarily or otherwise) to recognize the difference between ecological traps and opportunities (Misenhelter and Rotenberry 2000; Pidgeon *et al.* 2003).

Van Horne's (1983) major concern was that density would be a negative indicator of habitat quality because a smaller number of dominant, reproductively successful individuals could displace a larger number of young and other subordinate individuals into marginal areas. While our analysis failed to support this assertion statistically, we are not ready to rule out its importance, because the data clearly point in that direction. A negative association between density and per capita reproduction occurred in the most highly territorial species more than twice as often as in the least territorial species (Table 1d). Older, more experienced birds frequently do push younger, less experienced individuals into marginal areas (Graves 1997; Bayne and Hobson 2002). What remains to be resolved is how frequently this results in higher densities in those marginal places, so that we end up being misled about habitat quality.

Finally, it must be asked whether birds are the best subjects for testing Van Horne's fundamental concerns. The emphasis on birds is understandable and justified (Figure 1), given their popularity as environmental indicators and the relative ease of determining both bird numbers and reproductive output compared to most other sorts of organisms. However, survivorship is at least as important as reproduction in determining population

growth. Here, birds fall far short of ideal, because their extraordinary mobility makes it very difficult to follow the long-term fate of individuals. All too rarely have ornithologists been able to link density and reproduction with survival of adults or young (Misenhelter and Rotenberry 2000; Monrós *et al.* 2002). A number of studies involving other sorts of animals, mammals in particular, have successfully compared density with reproduction and/or survival (eg Ecke *et al.* 2002; Wheatley *et al.* 2002). However, the mobility and elusiveness of most mammals make them little, if any, better than birds as subjects for testing Van Horne's hypotheses.

The ideal organisms for examining Van Horne's ideas would have at least four attributes. First, they should be stationary, so that counting them is easy. Second, they should produce offspring that are associated with their parents long enough to be assigned to them. Third, dispersal distances must be short, so that the fate of both young and adults can be measured in, and attributed to, a particular place. Fourth, the effects of competitive interactions between individuals on both survival and reproduction should be relatively easy to measure. The most likely candidate organisms are therefore not any sorts of animals, but rooted plants in terrestrial ecosystems. While plant population demography is rich in studies that could be used to address Van Horne's questions (eg White 1985; Toft and Fraizer 2003), plant biologists rarely cite her study (but see Mandak and Pysek 1999; and Blossey 2003). Critical new tests of Van Horne's concerns and predictions about relationships



Figure 7. Scarlet tanager (*Piranga olivacea*).



Figure 8. Eurasian eagle owl (*Bubo bubo*).

between density and habitat quality will probably come from studies of plants.

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