

Putting Density Back into the Habitat-Quality Equation: Case Study of an Open-Nesting Forest Bird

AURORE PÉROT* AND MARC-ANDRÉ VILLARD*†

*Chaire de recherche du Canada en conservation des paysages, Département de biologie, Université de Moncton, Moncton, Nouveau-Brunswick, E1A 3E9, Canada

Abstract: Ecological traps and other cases of apparently maladaptive habitat selection cast doubt on the relevance of density as an indicator of habitat quality. Nevertheless, the prevalence of these phenomena remains poorly known, and density may still reflect habitat quality in most systems. We examined the relationship between density and two other parameters of habitat quality in an open-nesting passerine species: the Ovenbird (*Seiurus aurocapilla*). We hypothesized that the average individual bird makes a good decision when selecting its breeding territory and that territory spacing reflects site productivity or predation risk. Therefore, we predicted that density would be positively correlated with productivity (number of young fledged per unit area). Because individual performance is sensitive to events partly determined by chance, such as nest predation, we further predicted density would be weakly correlated or uncorrelated with the proportion of territories fledging young. We collected data in 23 study sites (25 ha each), 16 of which were located in untreated mature northern hardwood forest and seven in stands partially harvested (treated) 1–7 years prior to the survey. Density explained most of the variability in productivity ($R^2 = 0.73$), and there was no apparent decoupling between density and productivity in treated plots. In contrast, there was no significant relationship between density and the proportion of territories fledging ≥ 1 young over the entire breeding season. These results suggest that density reflects habitat quality at the plot scale in this study system. To our knowledge this is one of the few studies testing the value of territory density as an indicator of habitat quality in an open-nesting bird species on the basis of a relatively large number of sizeable study plots.

Keywords: density-productivity relationship, ecological traps, habitat selection, managed forest landscapes, Neotropical migrant bird conservation, Ovenbird, *Seiurus aurocapilla*

Regresando la Densidad a la Ecuación de Calidad del Hábitat: Caso de Estudio de una Ave Forestal de Nidos Abiertos

Resumen: Las trampas ecológicas y otros casos de selección de hábitat aparentemente no adaptativos generan dudas sobre la relevancia de la densidad como un indicador de la calidad del hábitat. Sin embargo, la prevalencia de esos fenómenos es poco conocida, y la densidad aun puede reflejar la calidad del hábitat en la mayoría de los sistemas. Examinamos la relación entre la densidad y otros dos parámetros de la calidad del hábitat en una especie de ave paserina que hace nidos abiertos: *Seiurus aurocapilla*. Probamos la hipótesis de que el ave individual promedio toma una buena decisión cuando selecciona su territorio de nidación y que espacio entre territorios refleja la productividad del sitio o el riesgo de depredación. Por lo tanto, pronosticamos que la densidad estaría correlacionada positivamente con la productividad (número de volantones por unidad de área). Debido a que el funcionamiento individual es sensible a eventos determinados parcialmente por el azar, como la depredación de nidos, pronosticamos que la densidad estaría correlacionada débilmente o no correlacionada con la proporción de territorios con volantones. Recolectamos datos en 23 sitios (25 ha cada uno), 16 de los cuales estaban localizados en bosque maduro no tratado y siete en bosques parcialmente cosechados (tratados) entre 1 y 7 años antes del muestreo. La densidad explicó la mayor parte de la variabilidad en la productividad ($R^2 = 0.73$), mientras que no hubo separación aparente entre la densidad y la productividad en las parcelas tratadas. En contraste, no hubo relación significativa

†Address correspondence to M.-A. Villard, email marc-andre.villard@umoncton.ca
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entre la densidad y la proporción de territorios con ≥ 1 volantes a lo largo de la época reproductiva. Estos resultados sugieren que la densidad refleja la calidad del hábitat en las parcelas de este sistema en estudio. Hasta donde sabemos, este es uno de los pocos estudios que prueban el valor de la densidad de territorios como un indicador de la calidad del hábitat en una especie de ave que hace nidos abiertos con base en un número relativamente grande de parcelas de tamaño considerable.

Palabras Clave: conservación de aves migratorias neotropicales, paisajes forestales bajo manejo, relación densidad-productividad, *Seiurus aurocapilla*, selección de hábitat, trampas ecológicas

Introduction

Assessing habitat quality can be challenging, not only for ecologists but also for the organisms they study. Departures from an ideal free distribution of individuals among available habitat types have been attributed to strong social interactions (Van Horne 1983; Lanyon & Thompson 1986), temporally unpredictable habitats (Van Horne 1983), postdisturbance crowding effects (Schmiegelow et al. 1997), or ecological traps (Remés 2003; Weldon & Haddad 2005; Lengyel 2006). Van Horne (1983) warns against the use of density as the sole parameter of habitat quality, advocating instead that habitat quality be defined as “the product of density, mean individual survival probability, and mean expectation of future offspring” (1983: 896). Thus, ultimately, habitat quality should reflect the suitability of local conditions for population growth. Although Van Horne’s warning is based on a review of various circumstances under which density and habitat quality may be decoupled, she includes density in her definition of habitat quality.

Since the publication of Van Horne’s seminal paper, ecologists and especially ornithologists have increasingly collected data on per capita reproductive success or plot-level productivity when modeling species-habitat relationships (Bock & Jones 2004). Measuring survival rate, however, remains a daunting task, especially for highly mobile organisms such as migratory birds. Reproductive success also can be challenging to quantify at spatial scales relevant to population management and, for this purpose, researchers have developed indirect methods such as indexes of reproductive activity (Vickery et al. 1992; Bonifait et al. 2006) or artificial nests. Nevertheless, both approaches have been criticized for their failure to provide an absolute measure of productivity (Zanette 2002; Burke et al. 2004; Thompson & Burhans 2004). The ability of artificial nests to provide reliable data on actual or even relative predation risk in different sites and habitat types has also been called into question (Faaborg 2004; but see Villard & Pärt 2004).

Several authors use per capita reproductive success to compare habitat quality among sites or habitat types (e.g., King et al. 1996; DeCecco et al. 2000; Purcell 2006) or against a population growth rate (λ) calculated on the basis of published estimates of survival rates (e.g., Trine

1998; Burke & Nol 2000; Knutson et al. 2006). In conservation planning the rationale for focusing on the reproductive performance of individuals is to ensure that priority is given to sites contributing positively to population growth so as to avoid population sinks or ecological traps. Nevertheless, per capita reproductive success is sensitive to density-dependent effects (Rodenhouse et al. 2003; Sillett & Holmes 2005; Sutherland 2006), and λ values based on a rough estimation of juvenile survival rate may not be reliable. Moreover, by itself, per capita reproductive success mainly provides information on the quality of habitat-selection decisions made by individuals. From a conservation perspective, it would seem most relevant to protect sites or habitat types that are more productive (i.e., those consistently producing the most offspring per unit area) (Van Horne 1983; Pidgeon et al. 2006). Hence, protecting high-quality breeding sites while ensuring that a relatively small proportion of a regional population occupies marginal-quality habitat is a major challenge for conservation planners.

Bock and Jones (2004) reviewed 109 studies to determine whether positive density-productivity relationships are the rule or the exception in bird populations. At least for Europe and North America, their results suggest that positive relationships are the rule. Nevertheless, their data also indicate that human disturbance is the main factor causing a departure from a positive density-productivity relationship, irrespective of habitat type.

We examined the relationship between density and two potential indicators of habitat quality measured at the level of study plots to assess the value of density as an indicator of habitat quality. For this purpose we sampled a relatively large number of sizeable (25-ha) plots. By comparison, studies included in Bock and Jones’ (2004) meta-analysis could be based on as few as two study sites. Plot size also is an important consideration because one expects the accuracy of density and, possibly, productivity estimates to increase with plot area. Large plot size improves density estimation because a larger proportion of mapped territories are fully encompassed within plot boundaries. The same argument would be expected to apply to productivity estimation: young fledged outside a study plot should be less likely to wander into a large, compact plot than into a small, elongated one.

As a case study, we focused on the Ovenbird (*Seiurus aurocapilla*) in a managed forest landscape of New Brunswick Canada. Reproductive success in this species reflects forest productivity and macroinvertebrate biomass (Seagle & Sturtevant 2005). Thus, the status of Ovenbird populations may provide a snapshot of overall ecosystem status. Moreover, this species is one of the most sensitive to alterations of its habitat, even at moderate intensity (Vanderwel et al. 2007). Hence, it is important to determine the reliability of indirect parameters of habitat quality so that the status of the Ovenbird and other focal species can be assessed appropriately for research and monitoring purposes.

Throughout its range, the Ovenbird's habitat is altered by forestry, urbanization, or, in some regions, agricultural intensification. In New Brunswick northern hardwood forests have been managed under various partial harvest systems since the 1980s (S. Makepeace, personal communication). Hence, individual birds increasingly face a variety of postharvest stand structures, many of which represent habitat of marginal quality for reproduction (Bourque & Villard 2001; S. Haché & M.-A. Villard, unpublished data). Our data set includes plots subjected to a variety of silvicultural treatments 1–7 years prior to the survey as well as untreated plots. This provides an ideal setting to test whether recent human disturbance alters the ability of birds to detect and occupy the best habitat for reproduction, as suggested by the meta-analysis of Bock and Jones (2004).

We assessed habitat quality either through the number of fledglings produced per unit area (hereafter productivity) or the proportion of mapped territories fledging young. We hypothesized that Ovenbirds would generally recognize cues linked to habitat quality. Although this species is fairly tolerant of variations in floristic composition of the forests it inhabits, it is tightly associated with the presence of patches of open understory (Van Horn & Donovan 1994) or perhaps more directly with the presence of a deep litter of dead leaves and an abundance of invertebrates (Burke & Nol 1998; Matsson & Niemi 2006). Smith and Shugart (1987) provide evidence that suggests Ovenbirds can assess local habitat quality as a function of forest stand structure. We extended this relationship to the plot scale in our hypothesis: Ovenbirds settle preferentially in sites exhibiting structural or other cues associated with a high likelihood of successful reproduction. In addition to vegetation structure, Ovenbirds may respond to perceived predation risk through the density of potential nest predators (Morton 2005; Fontaine & Martin 2006). Experimental evidence further suggests that conspecific attraction may override habitat cues in the process of site selection (Betts et al. 2008). Therefore, we predicted a strong positive correlation between density and productivity at the scale of forest plots, itself reflecting an adaptive response to a variety of habitat cues. When comparing the proportion of successful territories

within plots, however, we expected the density-quality relationship to be weak or not significant because mean reproductive success per territory is subject to negative density-dependent effects and some Ovenbird pairs apparently can find suitable habitat patches within sites of marginal overall quality (S. Haché & M.-A. Villard, unpublished data).

Methods

Study Area

Black Brook and West Tobique districts are located in northwestern New Brunswick, Canada (47°N; 67°W). These forest districts are privately owned by J.D. Irving Ltd. and Acadian Timber Income Fund, respectively. The data set comprises 23, 25-ha plots surveyed at least once between 1997 and 2006 (Table 1). We randomly selected one survey-year per plot for statistical analyses.

All plots consisted of 500 × 500 m (25 ha) grids, except for four plots in 2005 and six plots in 2006, where variations in grid shape were required to fit a 25-ha grid within untreated mature deciduous forest. Plots were 1.3–62 km apart (mean [SD] = 25.4 km [13.9]). All plots were characterized by mature northern hardwood forest dominated by shade-tolerant deciduous species (sugar maple [*Acer saccharum*], American beech [*Fagus grandifolia*], yellow birch [*Betula alleghaniensis*]). Coniferous species (balsam fir [*Abies balsamea*], spruces [*Picea glauca*, *P. rubens*]) were present as scattered trees and saplings in most plots.

Of the 23 plots selected, 16 were in mature stands that showed no sign of recent harvesting and seven were in treated stands (single-tree selection harvesting, patch, or strip cutting) (Table 1). Single-tree selection removes approximately 30% of the basal area on a 15- to 25-year

Table 1. Characteristics of the 23 study plots surveyed.

Plot	Year of survey	Harvest treatment	Time since treatment (years)
IH-UC*	1997	uncut	-
MH-UC*	1998	uncut	-
MH-SC*	1999	Selection cut	6
IH-SC1*	1999	Selection cut	5
1	2001	Uncut	-
2	2002	Uncut	-
3	2002	Patch cut	4
4	2002	Strip cut	1
5	2003	Uncut	-
6	2003	Selection cut	1
7	2004	Selection cut	1
8	2004	Patch cut	7
9 to 13	2005	Uncut	-
14 to 19	2006	Uncut	-

*Data from Bourque and Villard (2001).

rotation. Patch cutting consists of small, circular clearcuts (20-m radius) separated by 60 m along parallel trails. Strip cutting is characterized by 7-m-wide clearcut strips 60 m apart. Plots were embedded in a mosaic of managed forest composed of spruce plantations (1–50 years old) and deciduous stands subjected to a variety of treatments (see Guénette & Villard 2005 for details).

Focal Species

The Ovenbird is relatively common in the study area (Bourque & Villard 2001; Guénette & Villard 2005). Its density varies as a function of at least some of the harvest treatments considered (e.g., Bourque & Villard 2001; Gram et al. 2003; Jobes et al. 2004). The fact that it nests on the ground facilitates monitoring the fate of nesting attempts. This species is typically associated with closed-canopy forest stands with a relatively sparse ground cover (Van Horn & Donovan 1994). In northern hardwood forests these conditions are found in mature and old, untreated stands. Nevertheless, the species still occupies partially harvested stands where patches of open understory subsist (Bourque & Villard 2001; Guénette & Villard 2005; S. Haché & M-A. Villard, unpublished data).

Density Estimation

Ovenbird males return to the study area in early May and try to establish their territory almost immediately. From the second half of May to early July each year, we made eight visits to each plot and used the spot-mapping method to locate the territories of all males (Bibby et al. 2000). We conducted spot mapping between 05:30 and 10:00, when weather conditions (rain, wind) did not interfere with bird detection. We delineated territories based on clusters of detections, countering males, and a maximum distance of 140 m among locations within a putative territory, which would correspond to a 1.5-ha circular territory. Finally, we estimated density (number of territories/25 ha) by counting the number of territories within each plot and estimating fractions of territories (0.25, 0.33, 0.50, etc.) partially overlapping the plot.

Productivity Estimation

We searched for nests approximately from the last week of May until the end of July each year. We surveyed each plot 13–21 times for a mean of 6.6 h/visit (SD 0.8), which included the time spent spot mapping. We separated each visit by 2–6 days. Observers monitored territories closely to detect any sign of reproductive activity such as the presence of a pair and adults carrying nest material or food. We used these data, combined with territory maps updated after every visit, to focus nest searching and territory monitoring in specific portions of each plot. Time spent in a territory was approximately proportional to the area overlapping the plot. To monitor nests we followed

the protocol developed by Bourque and Villard (2001). When no nest could be found, we pursued monitoring to detect family groups, if present (see Porneluzi et al. 1993; Bourque & Villard 2001). A family group was considered to belong to the territory being monitored when fledglings were incapable of sustained flight or were fed by color-banded adults. As part of a separate project, we color banded 104 males and three females.

Because Ovenbird pairs normally split parental duties once young have fledged, it is difficult to confirm the number of fledglings belonging to a given pair. Because the mean number of young fledged per successful nest did not vary significantly among years ($F_{3,20}, p = 0.879$), we considered the number of fledglings per family group was equal to the mean value for all sites and years (3.62 [SD 0.86]; $n = 25$). Hence, we calculated productivity as the number of successful territories times the mean number of fledglings per nest. We never recorded a case of double brooding, but re-nesting was frequent when nesting attempts failed early in the breeding season (Bourque & Villard 2001; A.P. and M.A.V., personal observation). The mean number of young fledged per brood is similar to that reported by Podolski et al. (2007) (3.79 [SD 0.19]; $n = 43$) in the southern Appalachians.

Statistical Analyses

We first tested for spatial autocorrelation in density and productivity with Moran's I and found no significant relationship. For this reason, and because plots surveyed over multiple years were represented only once in the data set, we considered each plot as an independent observation. Density, productivity per plot, and the proportion of territories fledging ≥ 1 young were normally distributed and, therefore, we only applied an arcsine transformation on the proportion of successful territories.

Results

From a total of 265 territories monitored (including territories overlapping study plots by >0.25), we found 62 Ovenbird nests, 27 (43.5%) of which fledged ≥ 1 young. We detected recently fledged young in 98 territories where we did not find a nest (Table 2). Not a single case of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) was recorded.

As expected, density was a good predictor of productivity across plots ($R^2 = 0.73$), but it failed to predict the proportion of successful territories (Fig. 1). Recent silvicultural treatment did not correspond to increased scatter around the linear trend (Fig. 1a). Ovenbird density and productivity varied among plots and years, but they were both significantly higher in untreated (mean density: 11.9 [SD 3.9]; mean productivity: 17.4 [SD 7.0]) than in treated plots (mean density: 5.7 [SD 2.6]; mean

Table 2. Ovenbird density and productivity in treated^a and untreated study plots (25 ha each)^b.

	Year and study plot																		
	2001		2002		2003		2004		2005			2006							
	1	2	3 ^a	4 ^a	5	6 ^a	7 ^a	8 ^a	9	10	11	12	13	14	15	16	17	18	19
Number of territories	9.7	9.3	7.3	10.0	4.5	5.0	5.0	6.0	10.0	14.3	13.0	8.0	15.0	14.7	10.8	8.5	9.8	14.4	14.7
Number of nests found	5	3	4	2	0	0	1	2	1	3	1	2	4	2	3	0	0	7	8
Nests fledging ≥ 1 young (%)	80.0	33.3	25.0	0.0	-	-	100.0	0.0	100.0	100.0	0.0	100.0	75.0	50.0	33.3	-	-	14.3	0.0
Territories fledging ≥ 1 young (%)	52.6	39.7	13.8	29.9	53.8	45.0	40.0	50.0	40.0	38.6	38.5	56.3	33.3	45.5	51.2	15.6	38.1	39.3	25.0
Productivity (number of fledglings /25 ha)	18.0	12.9	3.0	10.8	8.7	8.1	7.6	11.2	14.7	18.9	18.1	17.1	18.9	24.5	19.9	4.8	13.6	17.9	13.3

^aTreated plots. Harvest treatments were selection, patch, or strip cutting (see Table 1 and Methods for details).

^bData for the four remaining plots can be found in Bourque and Villard (2001).

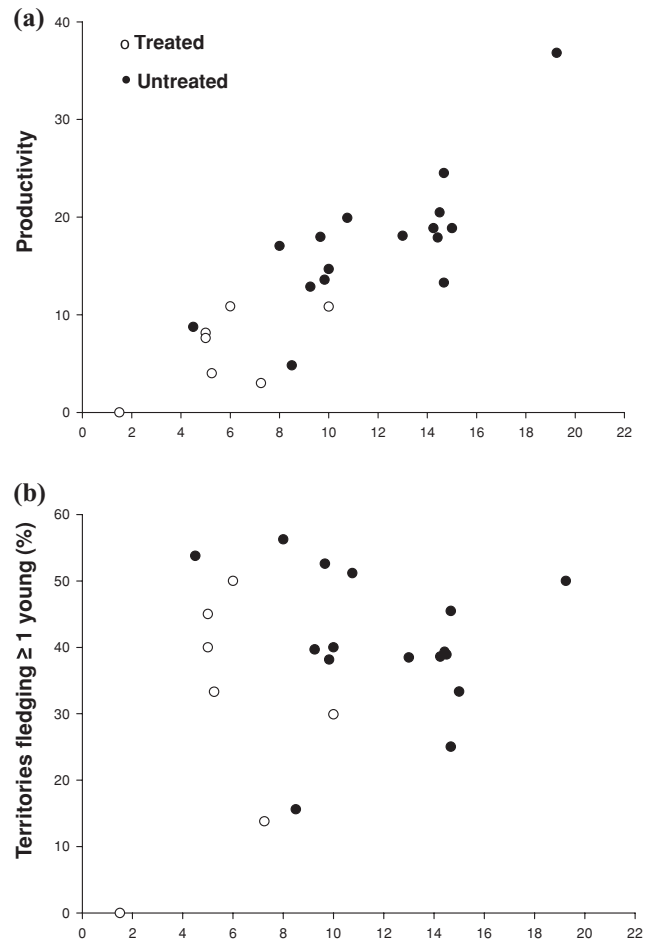


Figure 1. Relationship between Ovenbird density and (a) productivity (number of fledglings / 25 ha) and (b) proportion of successful territories in seven treated and 16 untreated plots (see Table 1 and Methods for details on harvest treatments).

productivity: 6.3 [SD 4.1]; *t* tests, *df* = 21, *p* < 0.01) (Fig. 1a). Data points corresponding to the study sites where we could not fit a square grid (see Methods) did not depart from the general trend and, hence, they were kept in the final analysis.

Discussion

Density was strongly, positively correlated with productivity per unit area but not with the proportion of successful territories. We found no tendency for a decoupling of density and productivity in recently treated plots. Such a decoupling might be expected in intensively managed landscapes (Donovan & Thompson 2001) and in recently disturbed habitat (Bock & Jones 2004; Arlt & Pärt 2007). This suggests Ovenbirds could correctly detect cues linked to habitat quality in our study area even though some harvest treatments were applied recently

(1 year prior to the survey). Moreover, the proportion of territories fledging young was not negatively related to local density, which suggests there were no ecological traps in this system (Fig. 1). Harvested plots supported lower densities and produced fewer young per unit area.

Review papers have renewed the interest in ecological traps (Battin 2004; Robertson & Hutto 2006), but studies documenting the various habitat cues used by individuals when selecting their breeding sites suggest that many species may be adapted to avoid traps. Among other factors, past reproductive performance (Haas 1998; Citta & Lindberg 2007), social cues (Doligez et al. 2004; Fletcher 2007; Seppänen et al. 2007), and the assessment of predation risk (Poysä et al. 1999; Morton 2005; Fontaine & Martin 2006) may play major roles when individuals select their breeding territory. Compared with other portions of their range, Ovenbird populations in our study region may face fewer confounding factors when assessing habitat quality. Brood parasites and alien predators on nests or adults were absent. In addition, potential effects of habitat fragmentation on Ovenbird pairing success (e.g., Gibbs & Faaborg 1990) would not be expected to apply to the managed forest landscapes we surveyed.

Bock and Jones' (2004) review was instrumental in bringing back the focus on density as an index of habitat quality. Our results are consistent with their conclusion that "in most cases" density is a reliable indicator of habitat quality. According to their results, populations occupying recently disturbed study sites should have been especially likely to show either no relationship or a negative density-productivity relationship, but this was not the case here. Surprisingly Bock and Jones (2004) used *abundance* and *density* interchangeably in their article. In ornithological studies *density* normally refers to estimates obtained through the mapping of territories. It is also noteworthy that Van Horne (1983) strictly uses the term *density* when defining habitat quality as "mean individual fitness per unit area." The distinction between density and abundance indexes is not trivial: measuring numbers of individuals per unit area requires intensive survey methods.

Well-replicated studies based on accurate density estimates should be conducted on other species and in different systems to verify the generality of our findings. For example, population densities in forest fragments in suburban landscapes may be less likely to indicate habitat quality owing to the greater potential for ecological traps (e.g., predation risk associated with domestic cats may be difficult to assess relative to that of native predators). Future studies should actually include survival data, if at all possible, to apply Van Horne's (1983) strict definition of habitat quality (see Introduction).

In a study on the Black-throated Sparrow (*Amphispiza bilineata*), Pidgeon et al. (2006) report that the product of density of reproductive pairs and individual reproductive success (i.e., productivity per unit area) was the best

indicator of population-level habitat quality. Precise density estimates combined with various indirect methods of productivity estimation, may provide a reasonable surrogate for intensive nest searching and monitoring as long as these indirect methods are properly calibrated (Villard & Pärt 2004). Spot mapping requires moderately intensive surveys (Bibby et al. 2000) that are compatible with an estimation of reproductive activity (Vickery et al. 1992; Buford et al. 1996).

Van Horne's seminal article has been interpreted as a warning against the use of density as an indicator of habitat quality. This warning has spread so effectively that the focus of avian conservation biologists quickly moved to productivity measures and, more recently, fitness metrics. Nevertheless, obtaining accurate estimates of fitness can be problematic when assessing habitat quality for species with cryptic reproductive habits, for entire landscape mosaics, or for species assemblages. The debate surrounding the use of density as an indicator of habitat quality will only be resolved when the causes of non-ideal habitat selection, including ecological trap phenomena, are elucidated (Arlt & Pärt 2007). Concordance between spatial scale and fitness metrics used seems critical (Chalfoun & Martin 2007). Until then, we agree with Bock and Jones (2004) that density (*sensu stricto*) should be considered as a reasonable indicator of habitat quality under most circumstances or at the very least that it should be used in combination with measures of individual fitness. Then, the estimation of survival rate will remain the ultimate challenge for the measurement of habitat quality, as defined by Van Horne (1983).

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