An index of reproductive activity provides an accurate estimate of the reproductive success of Palm Warblers

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ABSTRACT. Various indices of reproductive activity (IRA) have been used to estimate the reproductive success of songbirds. However, the performance of IRAs varies among systems examined, and this approach still requires more effort than standard surveys. We tested the accuracy of an IRA in a survey of birds nesting in bogs in eastern New Brunswick, Canada. We compared an IRA obtained through point counts with playbacks ("extensive" IRA) to another IRA obtained through intensive searches for evidence of breeding ("intensive" IRA) by Palm Warblers (*Dendroica palmarum*). Both the extensive IRA and associated abundance index were correlated with the intensive IRA, the former correlation being stronger. However, the extensive IRA tended to underestimate the status of breeding birds and overestimate the status of nonreproducing individuals that behaved more conspicuously. Nonetheless, the extensive IRA obtained using song playbacks represents a time-efficient alternative to intensive nest monitoring when estimating habitat quality at the scale of small (0.78 ha) study plots.

SINOPSIS. Un índice de actividad reproductiva que provee de un estimado más preciso de éxito reproductivo: un caso de estudios con Dendroica palmarum

Se han utilizado varios índices de actividad reproductiva (IAR) para determinar el éxito reproductivo de aves canoras. Sin embargo, el desenpeño de las IAR varía entre los sistemas examinados y este tipo de acercamiento aún requiere más esfuerzo que una encuesta estandar. Se puso a pruebas la exactitud de un IAR en una encuesta de aves que anidan en pantanos. Comparamos la IAR obtenida por conteo de puntos con la ayuda de grabaciones (IAR extensiva) con otra IAR obtenida mediante la búsqueda intensiva de evidencia reproductiva (IAR intensiva) en una población de *Dendroica palmarum*. La IAR extensiva y un indice de abundancia de conteo de puntos, fueron correlacionados con la IAR intensiva resultando la primera en una correlación más fuerte. Sin embargo la IAR extensiva tiende a subestimar el estatus de las aves que se reproducen y sobre estima el estatus de individuos noreproductivos que se comportan de forma conspicua. No obstante, la IAR que se determina usando grabaciones representa una alternativa eficiente para monitorear intensivamente el anidamiento, cuando se trata de determinar la calidad del habitat en predios pequeños (0.78 ha).

Key words: bogs, Dendroica palmarum, index of reproductive activity, playbacks, point counts, reproductive success

Bird occurrence or abundance is not necessarily linked with productivity and, therefore, habitat quality (Vickery et al. 1992a, Rangen et al. 2000, Betts et al. 2005). Discrepancies between bird distribution and the relative quality of available habitat may reflect a despotic distribution of individuals (Van Horne 1983), conspecific attraction (Muller et al. 1997), or the possible influence of anthropogenic activities (Remeš 2003).

Recognizing the limitations of occurrence or abundance data when assessing habitat quality, avian ecologists have increasingly focused on quantifying productivity (see Bock and Jones 2004). However, nest searching and monitoring

are time-consuming and sometimes increase predation risk (Major 1990). Hence, time-efficient alternatives to nest searching and monitoring are desirable in many situations. Indirect methods have been developed to estimate the productivity of bird populations, such as the index of reproductive activity (IRA) of Vickery et al. (1992b).

IRAs may be especially useful when surveying species whose nests are highly cryptic, but signs of reproductive activity (including fledged young) can be readily observed. An efficient IRA must be representative of the actual breeding status of local individuals, or should at least reflect the productivity of populations being surveyed (Vickery et al. 1992b, Gunn et al. 2000, Christoferson and Morrison 2001). Relationships between habitat quality and IRAs have been tested in grassland (Vickery et al. 1992b) and forest (Rangen et al. 2000) birds. IRAs

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have been quantified as part of spot-mapping (Vickery et al. 1992b, Rangen et al. 2000, Rivers et al. 2003), line transects (Christoferson and Morrison 2001), and point count surveys (Gunn et al. 2000, Betts et al. 2005). Although IRAs are time-efficient compared to nest searching and monitoring, their quantification still requires substantial effort. In all but one of the studies mentioned above, study sites were visited at least four or five times.

IRAs seem to be useful in studies of grassland birds, providing an accurate but conservative estimate of reproductive success, as well as identification of optimal habitat (Vickery et al. 1992b). Although an IRA failed to provide accurate estimates of productivity in a study of Dickcissels (Spiza americana; Rivers et al. 2003), features of this study system, including high levels of brood parasitism, might explain the difficulties encountered. When comparing density, productivity, and an IRA among forest stands at different seral stages, Rangen et al. (2000) reported that their IRA was correlated with productivity for only 40–45% of species. Moreover, it failed to discriminate between treatments because of low statistical power and biases in visibility (closed habitats). Hence, additional research is required to test the accuracy of IRAs as estimates of reproductive success in a variety of situations. In particular, differences among target species, dominant habitat type, and survey methods can lead to variable results. Careful calibration of IRAs is therefore needed to validate the method for each specific case (Rivers et al. 2003, Villard and Pärt 2004).

In this study, we tested the performance of an IRA as part of a point count survey of bog songbirds. To our knowledge, IRAs have never been used in this habitat type, but we wanted to obtain an estimate of habitat quality beyond abundance indices. Because signs of reproductive activity are rarely detected during short, silent counts, we used playbacks to increase the probability of visual detection and the likelihood of observing such signs (Johnson et al. 1981, Gunn et al. 2000, Betts et al. 2005, Doran et al. 2005). We recorded all songbird species present with special attention to three species associated with bogs: Palm Warbler (*Dendroica palmarum*), Savannah Sparrow (Passerculus sandwichensis), and Lincoln's Sparrow (*Melospiza lincolnii*). For each of these species, we broadcast conspecific vocalizations as part of the playbacks. To test the accuracy

of our IRA, we conducted intensive searches for nests and other signs of reproductive activity of Palm Warblers, the species most strongly associated with bogs (Calmé and Desrochers 2000, Delage et al. 2000, Carignan 2001, Calmé et al. 2002). Moreover, compared to other bog songbirds, Palm Warblers are relatively conspicuous and their reproductive behaviors (e.g., provisioning) are relatively easy to detect. Then, we compared reproductive status as determined by this intensive approach (hereafter, the "intensive IRA") to IRA values obtained through a point count survey ("extensive IRA").

METHODS

We surveyed peatland birds at 130 point count stations (50-m radius circular plots) in the Escuminac Peninsula, New Brunswick, Canada (47°N; 65°W). Each station was located in ombrotrophic habitat, including lagg areas (with sometimes a weak minerotrophic influence), but excluding forested bogs. Palm Warblers were detected at 71 stations. Because we focused on the reproductive status of Palm Warblers, we excluded plots with microhabitat clearly unsuitable for nesting (open areas with sparse trees; Welsh 1971, Ibarzabal and Morrier 1995, Wilson 1996). Individuals detected in such habitat were assumed to be nonterritorial and possibly performing off-territory explorations (Nolan 1978). Therefore, we restricted intensive searches to 36 stations characterized by intermediate cover (10–85%) of trees primarily <1.5 m in height, but including 5–20% stems taller than 1.5 m, and dominated by *Sphagnum* mosses and shrubs (*Ericaceae*). Dominant tree species were black spruce (Picea mariana), tamarack (Larix *laricina*) and, to a lesser extent, jack pine (*Pinus* banksiana) and white pine (P. strobus). Each study plot was delimited with pin flags.

Study species. Palm Warblers are specialists of peatlands (Ibarzabal and Morrier 1995, Wilson 1996, Carignan 2001), typically nesting in relatively open bogs with shrubs and scattered trees (mainly black spruce, tamarack, or pines) and open coniferous boggy forests. Territories are usually at the periphery of bogs or in areas dominated by conifers (Welsh 1971, Wilson et al. 1998, Delage et al. 2000). Nests are typically located on the ground, either at the base or in the lower branches of a small

tree (Welsh 1971, Ibarzabal and Morrier 1995, Wilson 1996). Nests we located (N = 6) were at the base of jack pines or black spruce, or on the lower branches of black spruce trees growing in hollows, so that nest cups were at ground level.

Index of reproductive activity. We indexed the reproductive activity of Palm Warblers during intensive searches for nests and fledged young (hereafter the "intensive method") and during point counts (hereafter the "extensive method"). We ranked reproductive status as (1) bird present but showing no indication of territorial activity, (2) singing male, (3) pair (simultaneous observation of two birds within ca. 5 m of each other and showing no agonistic interactions), (4) female carrying nest material or a nest present with or without eggs, (5) bird carrying food, or nest containing nestlings, and (6) presence of fledglings (incapable of sustained flight). Only birds observed within the 50-m radius plots were recorded. Hence, the IRAs provide estimates of Palm Warbler reproductive status at the scale of study plots.

Extensive method. Extensive bird surveys were conducted using a modified point count method. During each count, we broadcast recordings to enhance the probability of detecting the target species (Johnson et al. 1981) and to validate absences. In previous studies featuring an IRA, playbacks of the mobbing calls of Black-capped Chickadees (*Poecile atricapillus*) were used to obtain a multispecific response (Gunn et al. 2000, Betts et al. 2005). Because few songbird species are specific to bogs, we used playback of the conspecific songs of three bog-associated species (Palm Warbler, Savannah Sparrow, and Lincoln's Sparrow), with a brief recording of chickadee mobbing calls at the end of the playback tape. Two surveys were conducted between sunrise and 10:00 during the territory establishment and breeding periods (first visit: 30 May–14 June 2005; second visit: 15-29 June 2005). Surveys were interrupted when weather conditions interfered with bird detection (heavy rain or strong wind). During each survey, we observed silently for 5 min, followed by 5 min of playback (Palm Warbler songs for 1 min 20 s, followed by the songs of Savannah and Lincoln's Sparrows and chickadee mobbing calls), and then a second 5-min period of silent observation. IRA rank 2 (singing male) was only assigned when the individual was heard before playback (spontaneous behavior). Singing males

heard after playback were assigned rank 1. We recorded the maximum number of individuals (abundance index) and maximum IRA rank for each species in each study plot, but the method was specifically designed for songbirds with special attention to bog-associated species.

Intensive method. In addition to the two point counts, we performed two intensive searches for Palm Warbler nests or signs of reproduction in each plot (N = 36). Each search lasted 45 min. First, we attempted to locate the birds present in the plot or in the immediate vicinity and follow them to detect reproductive behaviors. If no bird was detected, we systematically searched apparently favorable nesting microhabitats. Because the habitat is open to semiopen, the study plots are relatively small, and Palm Warbler reproductive behaviors are relatively conspicuous, we were confident in the precision of IRA ranks assigned. The same two observers (SB and DP) conducted both extensive and intensive surveys. This could potentially lead to biases, but during extensive surveys, observers remained at the center of the plots and no nests were found. Furthermore, during intensive surveys, all suitable nest microhabitats could be searched relatively easily. Thus, we do not believe that prior suspicion about the location of nests (based on observations made during extensive surveys) biased our results.

The breeding phenology of Palm Warblers could be estimated based on observations in and outside study plots. The first survey coincided with the incubation and nestling stages (16–29 June 2005), and the second took place after young had fledged from most nests (30 June–8 July 2005). Both surveys were conducted between sunrise and 12:00. During intensive searches, we also recorded the time elapsed until reproductive behaviors associated with IRA ranks were first observed.

Statistical analyses. We compared maximum IRAs obtained using intensive and extensive methods using Spearman rank correlation. We also computed the proportion of correct predictions for each rank, assuming that the extensive method yielded an equal or inferior rank than that obtained through the intensive method. For each rank, we calculated the proportions of correct predictions for the lower and higher indices of the rank considered, and their median. Because the total duration of point counts was 30 min, we compared the cumulative

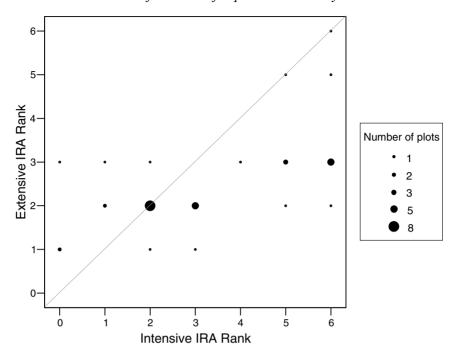


Fig. 1(A). Relationship between IRA obtained from intensive searches for nests or fledglings and an extensive method (point counts with conspecific playbacks).

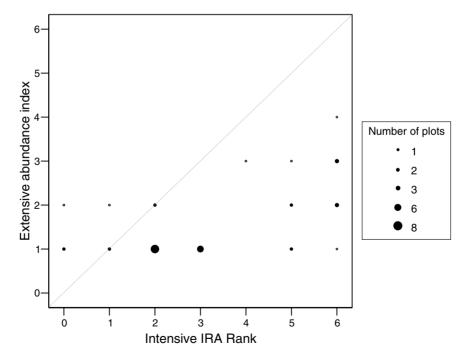


Fig. 1(B). Abundance index obtained from extensive survey and IRA values from the intensive method. The extensive IRA provides a better estimate of Palm Warbler reproductive status than the abundance index (extensive IRA: $r_i = 0.59$, P < 0.001; abundance index: $r_i = 0.51$, P = 0.001). The diagonal line, representing a perfect correspondence between IRAs, is shown as a reference. See Methods for definition of IRA ranks.

proportion of each IRA rank detected during intensive plot searches (N=72) after 30 min of intensive searches using a G-test and a Student-Newman-Keuls-type multiple comparisons test (Zar 1999).

RESULTS

Both Palm Warbler abundance index and IRA values from the extensive method were positively correlated with the intensive IRA (Fig. 1). However, the correlation was stronger for the extensive IRA ($r_s = 0.59$; P < 0.001) than for the abundance index ($r_s = 0.51$; P =0.001). When the intensive method revealed a high reproductive status in a given plot (IRA ranks >3), it generally corresponded to lower extensive IRAs, and vice versa. Therefore, the extensive index seemed to underestimate Palm Warbler reproductive status when intensive IRA values were high and overestimate it when they were low. Singing males (rank 2), representing a large proportion of overall detections, might have unduly influenced the correlation. When removing plots with low IRA ranks (<3), the correlation between extensive and intensive IRAs was indeed weaker, but still significant ($r_s =$ 0.43; P = 0.043; N = 23). The extensive IRA provided an accurate prediction of the intensive IRA in 80.6% of the 36 study plots. When calculated for each rank, the global rate of correct predictions increased with IRA rank (Fig. 2), showing a greater accuracy for nesting birds. Indeed, the proportion of correct predictions reached a plateau at rank 4.

After 30 min of observation time, the cumulative proportion of detections exhibited wide variation among different ranks (Fig. 3; G = 20.98; P = 0.002). Multiple comparison tests showed that indices of low reproductive status (rank 1 [93.1% of total IRA rank 1 detections at 30 min and 2 [85.2%]) were detected more rapidly than indices indicating a higher status (4 [20%], 6 [50%], and 5 [58.8%]). The rank corresponding to the presence of pairs (3) had an intermediate percentage (80%). Changes in IRA values over time, and between extensive and intensive methods (Fig. 4), underline natural changes in reproductive activity over the course of the breeding season, but also differences in the intensity of these methods.

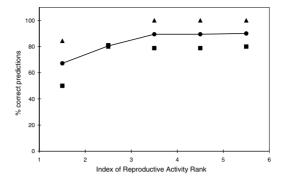


Fig. 2. Proportion of stations correctly predicted from the extensive IRA. We distinguished extensive IRA values that were inferior (squares) or superior (triangles) to IRAs obtained from the intensive method. Dots indicate the median. Extensive IRA values ≥ 4 provide a good prediction of IRAs from the intensive method.

DISCUSSION

The breeding and nesting status of Palm Warblers determined using intensive searches for nests could be estimated at the scale of study plots from a time-efficient IRA (extensive method) and, to a lesser extent, from a point count abundance index. These results support the contention that, in habitat evaluation studies, extensive methods such as point counts and, especially, point counts modified to collect an IRA, may represent a valuable alternative

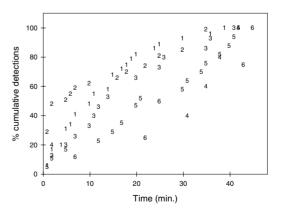


Fig. 3. Proportion of low reproductive status indices detected after 30 min (intensive method) is greater than for high reproductive status indices (G = 20.98; P = 0.002). Numbers correspond to IRA ranks.

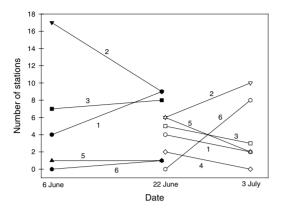


Fig. 4. Change in maximum IRA (rank next to each segment) per sample plot from extensive to intensive method (extensive survey: closed symbols; intensive survey: open symbols).

to more intensive methods. Point counts are more time-efficient and allow data collection for many species simultaneously. Intensive searches for nests and fledglings must focus exclusively on one or a few species to correctly assess their reproductive status (Martin and Geupel 1993). Even though our extensive surveys were three times shorter (30 min) than intensive ones (90 min) at the scale of a study plot, the significant correlation between extensive and intensive IRAs suggests that the former provide a valid estimate of reproductive success, at least for Palm Warblers. The time saved would increase with the size of study areas. Another probable advantage of extensive approaches is the reduction in observer-induced effects on reproductive success. Even moderate human disturbance could increase reproductive failure in certain species (Major 1990), at least during critical periods (Bolduc and Guillemette 2003).

The extensive method did not overestimate the reproductive status of Palm Warblers, increasing our confidence in its validity. A slight underestimation of Palm Warbler plot-scale reproductive status was expected because sampling effort (survey duration and multispecific data collection) was lower and extensive surveys took place earlier in the breeding cycle. The departure from the diagonal (Fig. 1) suggests reduced accuracy for stations with nonbreeding individuals and where pairs failed to breed, but could also reflect the greater detectability of unpaired males (Gibbs and Wenny 1993). The relatively low

detection of high-ranking indices (14 cases with ranks \geq 4) compared to lower ones could be explained by the fact that our study plots were smaller than Palm Warbler territories (Welsh 1971). Therefore, some plots may have contained microhabitats less attractive for nesting or may have been located at the periphery of territories. This would account for the presence of territorial males or other signs of reproductive activity, but no confirmation of nesting, even with the intensive IRA.

Based on a plot of the time needed to obtain each intensive IRA rank (Fig. 3), it appears that signs of nesting behavior were more difficult to detect than lower ranking indices. The apparently low detectability of intensive IRA rank 4 was probably due to the fact that we conducted intensive surveys later in the reproductive season (Welsh 1971, Wilson 1996). In standard bird surveys, most individuals detected are singing males (Scott et al. 1981, Schieck 1997). Therefore, procedures to enhance the probability of detection of high status reproductive behaviors are required. Playbacks increase the probability of visual observation of birds, and hence the probability of detecting signs of reproductive activity (Gunn et al. 2000, Doran et al. 2005). Conspecific calls have been used mainly to assess density or distribution of a wide range of species, especially elusive ones (Takats et al. 2001, Conway and Gibbs 2005). Surprisingly, the efficiency of conspecific playbacks for studying the reproductive success of songbirds has rarely been tested. Our study suggests that playbacks represent an efficient tool for determining breeding and nesting status. Birds in our study responded well to playbacks and permitted us to easily assess reproductive status based on behavior.

Changes in the indices recorded (Fig. 4) reflect the normal progress of reproduction. Low scores dominated at the beginning of the season and indices 5 and 6 were more prevalent in late June and early July. One feature of our extensive survey was the low number of visits. Increasing the number of visits may have provided better results, especially later in the season. However, for late surveys, care must be taken not to record fledglings capable of sustained flight, especially when surveying small study plots. When conducting point counts, the probability of detecting recently fledged young (rank 6) is doubtless low, given their typically cryptic behavior. Therefore, we consider it more efficient to focus on

indices 4 and 5, and to plan visits in accordance to these indices, rather than adding extra survey rounds later in the season.

Point counts with playbacks provided an accurate estimate of the reproductive status of Palm Warblers at the scale of study plots, especially for high-ranking observations. As the extensive IRA reflected more precisely the birds' reproductive status estimated by the intensive IRA than an abundance index, it is a useful complement to standard point count protocols. Adding an extensive IRA is time efficient and this method probably has a lower impact on bird reproduction than intensive nest searching and monitoring (Major 1990, Bolduc and Guillemette 2003). This may be an important consideration, particularly for species at risk. Finally, we recommend that, whenever possible, investigators calibrate the extensive IRA for their particular study system.

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LITERATURE CITED

- BETTS, M. G., N. P. P SIMON, AND J. J. NOCERA. 2005. Point count summary statistics differentially predict reproductive activity in bird-habitat relationship studies. Journal of Ornithology 146: 151–159.
- studies. Journal of Ornithology 146: 151–159.

 BOCK, C. E., AND Z. F. JONES. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2: 403–410.
- BOLDUC, F., AND M. GUILLEMETTE. 2003. Human disturbance and nesting success of Common Eiders: interaction between visitors and gulls. Biological Conservation 110: 77–83.
- CALMÉ, S., AND A. DESROCHERS. 2000. Biogeographic aspects of the distribution of bird species breeding in Québec's peatlands. Journal of Biogeography 27: 725–732.
- ——, ——, AND J.-P. L. SAVARD. 2002. Regional significance of peatlands for avifaunal diversity in southern Québec. Biological Conservation 107: 273– 281.

- Carignan, V. 2001. Sélection et suivi d'indicateurs aviaires potentiels de l'intégrité écologique des tourbières et forêts du Grand écosystème de Kouchibouguac. M. S. thesis, Département de Biologie, Université de Moncton, Moncton, Canada.
- CHRISTOFERSON, L. L., AND M. L. MORRISON. 2001. Integrating methods to determine breeding and nesting status of three western songbirds. Wildlife Society Bulletin 29: 688–696.
- CONWAY, C. J., AND J. P. GIBBS. 2005. Effectiveness of call-broadcast surveys for monitoring marsh birds. Auk 122: 26–35.
- Delage, V., M.-J. Fortin, and A. Desrochers. 2000. Effets de lisière et d'isolement des habitats d'oiseaux dans les tourbières exploitées. Écoscience 7: 149– 156.
- DORAN, P. J., P. Z. GULEZIAN, AND M. G. BETTS. 2005. A test of the mobbing playback method for estimating bird reproductive success. Journal of Field Ornithology 76: 227–234.
- GIBBS, J. P., AND D. G. WENNY. 1993. Song output as a population estimator: effect of male pairing status. Journal of Field Ornithology 64: 316–322.
- GUNN, J. S., A. DESROCHERS, M.-A. VILLARD, J. BOURQUE, AND J. IBARZABAL. 2000. Playbacks of mobbing calls of Black-capped Chickadees as a method to estimate reproductive activity of forest birds. Journal of Field Ornithology 71: 472–483.
- IBARZABAL, J., AND A. MORRIER. 1995. Paruline à couronne rousse. In: Les Oiseaux nicheurs du Québec: Atlas des oiseaux nicheurs du Québec méridional (J. Gauthier, et Y. Aubry, eds.), pp. 900–903. Association québecoise des groupes d'ornithologues, Société québécoise de protection des oiseaux, Service canadien de la faune, Environnement Canada, région du Québec, Montréal, Canada.
- JOHNSON, R. R., B. T. BROWN, L. T. HAIGHT, AND J.M. SIMPSON. 1981. Playback recordings as a special avian censusing technique. Studies in Avian Biology 6: 68– 75.
- MAJOR, R. E. 1990. The effect of human observers on the intensity of nest predation. IBIS 132: 608–612.
- MARTIN, T. E., AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64: 507–519.
- MULLER, K. L., J. A. STAMPS, V. V. KRISHNAN, AND N. H. WILLITS. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). American Naturalist 150: 650–661.
- NOLAN, V. 1978. The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). Ornithological Monographs 26: 1–595.
- RANGEN, S. A., K. A. HOBSON, AND R. G. CLARK. 2000. A comparison of density and reproductive indices of songbirds in young and old boreal forest. Wildlife Society Bulletin 28: 110–118.
- REMEŠ, V. 2003. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap (*Sylvia atricapilla*). Conservation Biology 17: 1127–1133.
- RIVERS, J. W., D. P. ALTHOFF, P. S. GIPSON, AND J. S.

- PONTIUS. 2003. Evaluation of a reproductive index to estimate Dickcissel reproductive success. Journal of Wildlife Management 67: 136–143.
- SCHIECK, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. Condor 99: 179–190.
- Scott, J. M., F. L. Ramsey, and C. B. Kepler. 1981. Distance estimation as a variable in estimating bird numbers from vocalizations. Studies in Avian Biology 6: 334–340.
- TAKATS, D. L., C. M. FRANCIS, G. L. HOLROYD, J. R. DUNCAN, K. M. MAZUR, R. J. CANNINGS, W. HARRIS, AND D. HOLT. 2001. Guidelines for nocturnal owl monitoring in North America. Beaverhill Bird Observatory and Bird Studies Canada, Edmonton, Alberta, Canada.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893–901.
- VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992a. Is density an indicator of breeding success? Auk 109: 706–710.

- reproductive index to evaluate relationship between habitat quality and breeding success. Auk 109: 697–705.
- VILLARD, M.-A., AND T. PÄRT. 2004. Don't put all your eggs in real nests: a sequel to Faaborg. Conservation Biology 18: 371–372.
- Welsh, D. A. 1971. Breeding and territoriality of the Palm Warbler in a Nova Scotia bog. Canadian Field-Naturalist 85: 31–37.
- WILSON, W. H., JR. 1996. Palm Warbler (Dendroica palmarum). In: The Birds of North America, No. 238 (A. Poole, and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.
- ———, R. E. ZIERZOW, AND A. R. SAVAGE. 1998. Habitat selection by peatland birds in a central Maine bog: the effects of scale and year. Journal of Field Ornithology 69: 540–548.
- Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, NJ.