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A REVIEW OF THE POPULATION ESTIMATION APPROACH OF THE NORTH AMERICAN LANDBIRD CONSERVATION PLAN

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AS PART OF their development of a continental plan for monitoring landbirds (Rich et al. 2004), Partners in Flight (PIF) applied a new method to make preliminary estimates of population size for 448 species of landbirds present in the continental United States and Canada (Table 1). Estimation of the global population size of North American landbirds was intended to (1) identify the degree of vulnerability of each species, (2) provide estimates of the current population size for each species, and (3) provide a starting point for estimating population sizes in states, provinces, territories, and Bird Conservation Regions (Rich et al. 2004). A method proposed by Rosenberg and Blancher (2005) was used to derive population estimates from available survey data. To enhance the credibility of these estimates, PIF organized a review of the methodology used to estimate North American landbird population sizes. A planning committee selected members from the ornithological and biometrical communities (hereafter "the panel"), with the aim of selecting individuals from academia, state natural-resource agencies, and the U.S. and

Canadian federal governments, including the Canadian Wildlife Service, the U.S. Geological Survey, and the U.S. Department of Agriculture Forest Service.

The panel addressed three questions: (1) Were the methods of population estimation proposed by PIF reasonable? (2) What actions could be taken to improve the data or analyses on which the PIF population estimates were based? and (3) How should the PIF population estimates be interpreted?

VALUE OF POPULATION ESTIMATES IN BIRD CONSERVATION

Collecting reliable, useable information on the status of bird populations is a critical step in developing and updating bird conservation plans. Such efforts often involve setting population goals, using models to predict changes in bird population size as a function of habitat (and other) variables, developing plans to modify habitats through management, and using survey data to monitor progress toward goals. Unfortunately, integrating our present sources of information on bird populations into this system is complicated by the nature of the data

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TABLE 1. Estimates of population size for 10 species of birds in the United States and Canada and globally, as estimated by Rich et al. (2004), rounded to the nearest thousand.

Species	U.S. and Canadian population	Global population
Common Black-Hawk (<i>Buteogallus anthracinus</i>)	63	2,000,000
Great Gray Owl (<i>Strix nebulosa</i>)	31,000	63,000
California Thrasher (<i>Toxostoma redivivum</i>)	195,000	216,000
American Dipper (<i>Cinclus mexicanus</i>)	582,000	626,000
Connecticut Warbler (<i>Oporornis agilis</i>)	1,170,000	1,170,000
Belted Kingfisher (<i>Ceryle alcyon</i>)	2,212,000	2,212,000
Cactus Wren (<i>Campylorhynchus brunneicapillus</i>)	4,142,000	8,284,000
Pacific-slope Flycatcher (<i>Empidonax difficilis</i>)	7,946,000	8,291,000
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	14,092,000	15,153,000
Common Yellowthroat (<i>Geothlypis trichas</i>)	32,389,000	32,389,000

collected by surveys; most large-scale surveys collect indices of population size rather than unbiased estimates of population size.

An index is a statistic (e.g., point count or relative abundance measure) that is assumed to be correlated with the actual quantity of interest (e.g., population size or density). Understanding the relationship between counts and population sizes at sample sites by estimating the proportion of animals counted (detection rate) has been an important focus of wildlife statistics (e.g., Nichols et al. 2000, Buckland et al. 2001). For bird surveys, indices often are not based on probabilistic samples, which introduces an additional source of uncertainty (e.g., count locations may not sample all possible locations representatively). For the North American Breeding Bird Survey (BBS), for example, data from roadside point counts are frequently criticized because they may be poor indices of the number of birds at count locations and may not be representative of bird populations within regions because of the nature of roadside counts (Bibby et al. 1992). Historically, these factors were often ignored in analyses that made strong but unstated assumptions about the consistency of indices and randomness of samples. Modern analyses of BBS indices attempt to limit the influence of inconsistent indices by controlling for site-specific differences in detection (e.g., through observable covariates; Link and Sauer 1998); no analyses presently control for the roadside nature of the sample. Comparisons of indices of abundance among species also may be flawed if species differ in their detectability; and if detection rates also differ among habitats, use of survey data in bird-habitat models used in developing population and habitat objectives

may be invalid. Each of these difficulties in the use of index data can potentially result in inappropriate conservation decisions.

Any analysis of index data thus can be criticized by postulating differences in detection rates among treatments. These concerns have motivated conservationists to avoid direct use of relative abundance indices in conservation planning, and instead to include in their plans estimates of species-specific population sizes that incorporate estimates of detection rates. These population size estimates are then used in models as parts of objective functions for setting goals for the number of birds in relation to available habitat, or used to predict the total amount of habitat that must be conserved or created to support species-specific numerical population goals.

This interest in making estimates of population numbers and density by habitat has previously led to development of several national and continental estimates of bird population sizes. For instance, McAtee (1931) estimated that there were 2.6 billion breeding landbirds in the contiguous United States, and Wing (1956) estimated that 5.6 billion birds were present in the United States in summer and 3.75 billion in winter. The American Ornithologists' Union (1975) once suggested that as many as 10 billion birds were present in the contiguous United States in each breeding season, with a fall population of 20 billion.

Estimates of population size as opposed to indices may be especially useful in conservation because they resonate with the public; they impart meaning not generally found in indices, contributing to impressive statements about the magnitude of conservation problems. For

instance, the National Audubon Society (1997) estimated that 100 million birds per year are killed by free-roaming cats (*Felis catus*); this number alone imparts an importance to the issue not found by suggesting, for instance, that cats kill the equivalent of one bird per highway kilometer per day (Lepczyk et al. 2004). Among the various other sources of bird mortality in North America, total anthropogenic sources of mortality have been estimated to be 400–1,600 million birds killed per year (Table 2).

Conservation plans for various species often include numerical population objectives. For instance, the 1986 North American Waterfowl Management Plan (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986) advocated a goal of a continental breeding population of 62 million ducks during years with average environmental conditions, a number expected to support a fall flight of 100 million birds, and it is these numerical population objectives that have been credited for much of the success of the plan (Donovan et al. 1999). To date, however, the few estimates of total bird populations for any geographic region have been highly speculative and variable.

METHODS FOR ESTIMATING SIZE OF A BIRD POPULATION

Rich et al. (2004, appendix B) and Rosenberg and Blancher (2005) described their method for estimating species-specific population size from survey data (hereafter referred to as the “Rosenberg and Blancher” approach). Two procedures were used, one for birds largely restricted to the United States and Canada south of the Arctic and the other for birds present in the Canadian Arctic. Survey data

available for estimating population sizes for these two areas differ in several important aspects. For the United States and sub-Arctic Canada, North American BBS data were used, whereas for the Canadian Arctic, data from the Breeding Bird Census (BBC) and Northwest Territories–Nunavut Bird Checklist Survey (Checklist) were used. For the BBS data, counts from acceptable routes were averaged for the 1990s for each species recorded on a route. For regions where BBS routes were infrequently run (boreal forest portions of Canada), routes from other decades were included. Numbers of birds by species were averaged for every route in geopolitical regions formed by the intersection of state–province–territory and Bird Conservation Region boundaries. Averages from neighboring regions were assigned if the geopolitical region was not sampled by BBS. Averages from each geopolitical region were divided by the area presumed to be covered by a BBS route (25.1 km²) and multiplied by the area of the region. Bird Conservation Region indices were calculated by summing over all geopolitical regions within a Bird Conservation Region. These Bird Conservation Region-wide indices were converted to population estimates after multiplying the indices by three adjustments (Rosenberg and Blancher’s adjustment factors).

The three adjustments were a “pair” adjustment, a detection-area adjustment, and a time-of-day adjustment. The pair adjustment led to the indices being multiplied by two, with the assumptions that BBS observers typically detect the male of a species and that all birds are paired with a single female. The detection-area adjustment was the square of the ratio between the theoretical detection radius for the BBS (i.e., 400 m) and one of five effective detection

TABLE 2. Estimated sources of annual avian mortality associated with human activity in North America (not limited to landbirds), in order of estimated magnitude.

Mortality source	Number killed annually (in millions)	Study
Collisions with communication towers	4–50	Kerlinger (2000), National Wind Coordinating Committee (2001)
Vehicle collisions	50–100	Banks (1979), National Wind Coordinating Committee (2001)
Pesticides	67	Deinlein (1998)
Domestic cats	100	National Audubon Society (1997)
Legal harvest	120	Banks (1979)
Window collisions	120–1,200	Klem (1990)

distances (80, 125, 200, 400, and 800 m) assigned to each species (Table 3). This adjustment ostensibly accounted for incomplete detection ≤ 400 m or detection at distances >400 m. Breeding Bird Survey protocol precludes including birds beyond 400 m from the survey stop in the stop count, but the 800-m detection distance was presumed to accommodate those species (e.g., soaring birds, such as the vultures) for which movement was possible from one stop to another during the course of the survey. The time-of-day adjustment was the ratio of counts at the peak of detection to the average count over the whole set of BBS routes (Table 4). The form of the calculation incorporating all three adjustment factors is as follows:

$$\text{Population} = \sum_{k=1}^{k=g} \left(\frac{\sum_{j=1}^{j=m} \sum_{i=1990}^{i=1999} Y_{ij}}{n} \times \frac{\text{area}}{25.1} \right) \times 2 \times \left(\frac{400}{d_e} \right)^2 \times \left(\frac{\text{count}_{\text{peak}}}{\sum_{s=1}^{s=50} \sum_{i=1995}^{i=2001} X_{is}} \times \text{rte} * \text{yrs} \right) \quad (1)$$

where Y is a BBS count reported for route j in year i for a particular species, n is the number of years of acceptable route counts during 1990–1999 (≤ 10), m is the number of routes in the geopolitical region, g is the number of geographic strata, $area$ is the area of the geopolitical region, d_e is the effective detection distance,

$\text{count}_{\text{peak}}$ is a smoothed estimate of the maximum count, derived from a sixth-order polynomial fit, X is a BBS count summed over each stop in the mid-1990s through 2001 period, and $\text{rte} * \text{yrs}$ is the number of routes over the period.

For birds occupying three ecozones in Arctic Canada, BBC data provided estimates of total landbird density. Total landbird density was split among three classes of landbirds on the basis of their likely detection distance: near, intermediate, and far. Relative species-specific abundance was calculated from Checklist data. The ratio of BBC total landbird density to Checklist abundance was calculated, and this density conversion factor was applied to the Checklist abundance data to provide species-specific density estimates. These bird densities were averaged within each ecoregion, then multiplied by the area of the region to derive a population estimate. Population estimates were summed across ecoregions to provide a total population estimate for each Arctic landbird species.

The two estimates were summed for those species that occurred in both Arctic and non-Arctic regions to derive continental estimates of population size. Global population sizes were simply the United States–Canada population size multiplied by the ratio of the total breeding range to that in the United States and Canada.

ARE THE METHODS OF POPULATION ESTIMATION PROPOSED BY ROSENBERG AND BLANCHER REASONABLE?

Rosenberg and Blancher (2005) identified four assumptions in their analysis: (1) each habitat type was sampled in approximate

TABLE 3. Examples of detection distances used in deriving population estimates from North American Breeding Bird Survey data.

Species	Detection distance category (m)	Effect on estimate
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	80	25×
Black-capped Chickadee (<i>Poecile atricapillus</i>)	125	10.24×
Broad-winged Hawk (<i>Buteo platypterus</i>)	125	10.24×
Common Grackle (<i>Quiscalus quiscula</i>)	200	4×
Purple Finch (<i>Carpodacus purpureus</i>)	200	4×
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	200	4×
Blue Jay (<i>Cyanocitta cristata</i>)	400	1×
Red-tailed Hawk (<i>B. jamaicensis</i>)	400	1×
Turkey Vulture (<i>Cathartes aura</i>)	800	0.33×
Common Raven (<i>Corvus corax</i>)	800	0.33×

TABLE 4. Examples of time-of-day adjustment factors used in deriving population estimates from North American Breeding Bird Survey data.

Species	Time-of-day adjustment factor ^a
House Finch (<i>Carpodacus mexicanus</i>) ^b	1.04
American Redstart (<i>Setophaga ruticilla</i>)	1.07
Song Sparrow (<i>Melospiza melodia</i>)	1.40
White-crowned Sparrow	1.79
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	2.24
Long-eared Owl (<i>Asio otus</i>)	3.03
Common Nighthawk (<i>Chordeiles minor</i>)	6.73
Great Horned Owl (<i>Bubo virginianus</i>)	11.00
Western Screech-Owl (<i>Megascops kennicottii</i>)	20.77
Whip-poor-will (<i>Caprimulgus vociferus</i>) ^c	22.30

^a The median adjustment factor for all species was 1.32.

^b Species with the smallest adjustment factor.

^c Species with the greatest adjustment factor.

proportion to its occurrence in each region, (2) birds present but not counted during the BBS were accounted for by one or more of the adjustment factors, (3) the Checklist-BBC data for birds in Arctic Canada were comparable to BBS data, and (4) breeding densities in the United States and Canada were comparable to densities outside the United States and Canada (this latter assumption was relevant only to the extrapolation of North American population size to global estimates of population size). The panel focused primarily on evaluating the first two assumptions, because they apparently have the greatest effect on most population size estimates.

Bias related to habitat sampling in the Breeding Bird Survey.—Two issues, placement of routes and roadside effects, are critical in determining the correctness of the assumption that habitat was sampled by the BBS in approximate proportion to its occurrence in the regional landscape. Intensity and placement of BBS routes dictate whether the habitat was properly sampled. Unfortunately, BBS coverage is limited both by routes that are infrequently surveyed and by large roadless areas that are not sampled within the United States and Canada (Peterjohn 1994, O'Connor et al. 2000). These gaps in coverage may lead to over- or undersampling of particular habitats poorly represented along roadsides. For instance, mountaintops, western riparian areas, and large wetlands are often poorly represented in the BBS (Robbins et al. 1986). Unpublished studies by R. J. O'Connor (University of

Maine, Orono) and colleagues, C. Flather (U.S. Department of Agriculture Forest Service), and P. J. Blancher (Canadian Wildlife Service) suggest that the effect of atypical route placement is minor, but no comprehensive test of this effect has been conducted (O'Connor et al. 2000).

Because the BBS is a roadside survey, another consideration is the influence of roads on measures of bird abundance through their effect on the habitat itself or on bird behavior. Forman (2000) indicated that 20% of the United States is affected by roads. Habitat along roadsides may not be representative of roadless habitat (Miller et al. 1996, Trombulak and Frissell 2000) and, thus, may support a different proportion of a species' population than would occur in roadless habitat. Some birds may be attracted to features associated with roads, whereas others may be repelled (Forman and Deblinger 2000). It is unclear how these effects introduce bias in BBS data (Hutto et al. 1995, Keller and Fuller 1995, Rotenberry and Knick 1995).

Bias because of inadequacy in three adjustment factors.—The second assumption of the population estimation approach was that birds present but not counted during the BBS were accounted for by one or more of the adjustment factors. As noted by Link and Sauer (1998:261), "BBS sampling cannot guarantee either a census or a known fixed area of sampling." Any connection of the BBS index to a population size must account for these uncertainties; the most important issue faced by the panel was the credibility of the assumptions implicit in the

modeled corrections proposed by Rosenberg and Blancher (2005). Many uncertainties exist in these correction factors, and we describe a variety of issues that could influence the quality and precision of these corrections. We also identify the importance of estimating precision of both the corrections and resulting population sizes.

The first adjustment factor was a "pair" adjustment factor. Ostensibly, the pair adjustment multiplied the index (average number of birds per route in the 1990s by geopolitical region) by two, on the assumption that only one member of a pair was detected on a BBS route. This adjustment factor does not account for unpaired, and largely uncounted, "floater" birds. Kenwood and Paxton (2001), for instance, suspected that as many as 36% of the Southwestern Willow Flycatchers (*Empidonax traillii extimus*) at their Arizona study site were unpaired floaters. Also, nocturnal and crepuscular species, early- and late-season breeders, quiet species, and temporary immigrants are poorly counted by the BBS (Robbins et al. 1989, O'Connor et al. 2000) and, thus, may not be accounted for by multiplication by two. Although it is a species not well covered by the BBS, estimates for the Great Horned Owl (*Bubo virginianus*), for instance, suggested that as many as 40–50% of the birds in a population were nonterritorial floaters (Rohner 1997). Unfortunately, the relationship of perceptible birds to undetectable birds in BBS results is generally unknown; the pair adjustment may be conservative (i.e., result in an underestimate) for some species, but also may overestimate overly conspicuous species and those species in which individuals of both sexes vocalize.

The second adjustment factor was intended to address species-specific detection probabilities by assigning each species to one of five detection-distance categories (80, 125, 200, 400, and 800 m) and, in doing so, transform the index of relative abundance into a density estimate. The PIF proportionality ratio reflects a species-specific probability of detection based in part on distance between a bird and the observer. The effect of a detection-distance adjustment factor is to reduce or increase the effective area to which the index is applied. Because the BBS collects relative rather than absolute abundance data, a crucial assumption in this approach is that this index is directly proportional to population size. The panel did not evaluate specific detection distances for individual species but

suggested that this adjustment may be the most important and, coincidentally, the most uncertain of the adjustment factors. For instance, a 200-m detection distance, in effect, quadruples the population estimate, compared with a detection distance of 400 m. For species whose detection distance was 800 m (i.e., vultures and some hawks: 1.8% of species), the reverse occurs, and their estimates were reduced to one-quarter by this adjustment factor. For 62% of the species ($n = 243$ species), their population size estimate was increased by 4 \times over the index; 20.4% ($n = 80$) had their estimate increased 10.24 \times , and 4.8% ($n = 19$) of the species had their estimate increased 25 \times . Estimates for 11% ($n = 43$) of the species incurred no change from the species-specific detection-distance adjustments.

Several elements can potentially influence the validity of the detection-distance adjustment. The literature on factors influencing detection distances is extensive (e.g., Buckland et al. 2001). Effective detection distances undoubtedly vary not only by species but also by habitat, time of day, time of year, calling rate, song volume, and observer (O'Connor et al. 2000, Thompson 2002). For the PIF estimates, a single estimate of detection distance for each species was posited; no attempt was made to accommodate variation associated with these variables. The BBS protocol attempts to standardize conditions under which counts are made. Despite this constancy imposed by protocols, detection distances are not likely to be constant (Nichols et al. 2000, Rosenstock et al. 2002, Norvell et al. 2003). Variation in detection distance may lead to over- or underestimating population sizes (Buckland et al. 2001). Unfortunately, few empirical data exist for appropriate estimation of detection distances from BBS data. It would be useful to directly incorporate the uncertainty associated with these distances into the precision of the population estimates.

The third adjustment factor, a time-of-day adjustment, was used to accommodate time-of-day variation in detectability when the route is surveyed. This adjustment factor was estimated for each species by polynomial fits to tallies of stop counts, where the first stop represents the earliest count and the 50th stop represents the latest count. Fitting a polynomial to these stop-specific counts smooths the pattern in counts. One concern, however, in using polynomials is that they may be particularly ill-fitted at their

extremes because of a paucity of data to anchor the ends of the fitted line. Thus, fits for species whose peaks in abundance occur early (e.g., nocturnal birds) or late may not be properly measured. Maxima drawn from these potentially poorly fitted polynomials may therefore be inadequately assessed (Fig. 1). This, in turn,

would influence the maximum count:mean count ratio. Some species ($n = 14$, strigiform and caprimulgiform species) are especially influenced by this time-of-day adjustment factor, having their estimate of abundance inflated by between 3.0× and 22.3× (Table 4). As with other sources of variation in detection, it would

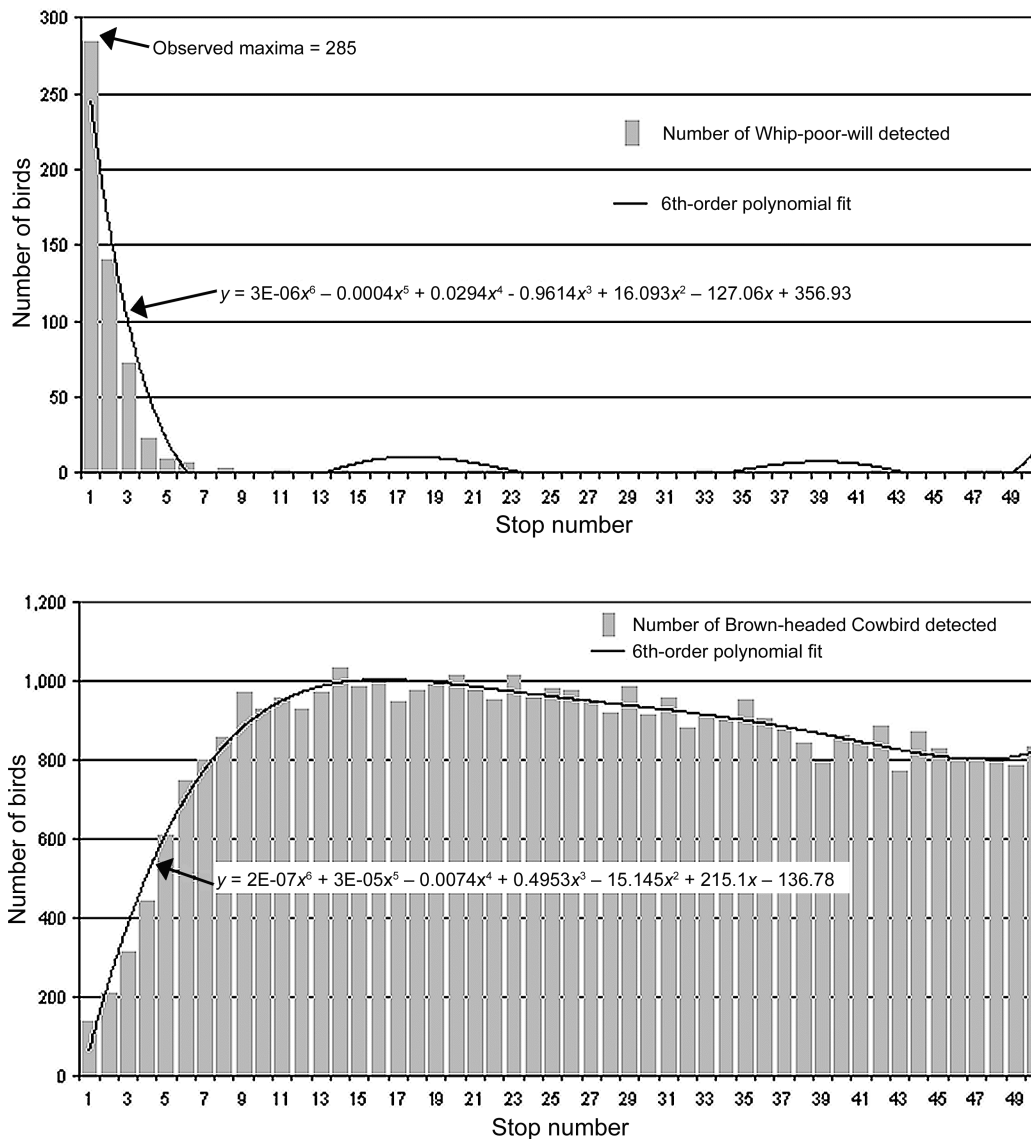


FIG. 1. On the assumption that stop number is a surrogate for time of day, sixth-order polynomials were drawn to mean stop-specific counts across all routes to identify a purported maximum. In the extreme case for Whip-poor-will, the observed maximum count was 285, whereas the predicted maximum from the polynomial fit (at stop 1) was 245. The predicted maximum for Brown-headed Cowbird (*Molothrus ater*) was 1,006. Figures were redrawn from P. J. Blancher and K. V. Rosenberg (unpubl. data).

be useful to directly incorporate uncertainty in estimation of the rates in the population estimate.

Other considerations.—Means for the counts in the 1990s may be based on results from 1 to 10 years. Means derived from only a few years are intrinsically less precise than means based on more years. They may not be representative of the mean conditions within the decade because they may be affected, for instance, by droughts or extremely wet conditions. An additional concern is that baseline observer competence may be changing over time (Link and Sauer 1998), a factor that can be accommodated in more sophisticated analyses (Link and Sauer 2002).

There is also concern regarding the methodology used to extrapolate counts from prior decades for insufficiently sampled areas in boreal Canada. Habitat bias may be important in the boreal zone, given that most BBS routes are located in the southern portion of this large zone.

WHAT ACTIONS CAN BE TAKEN TO IMPROVE THE DATA OR ANALYSES ON WHICH THE PIF POPULATION ESTIMATES WERE BASED?

Recommendations for the short term.—First, because it is unclear how robust the estimates are to the many assumptions implicit in the procedure, we suggest that a simulation exercise be used to document consequences of variation in the assumptions. A sensitivity analysis would identify those parameters of the model (i.e., index values and adjustment factors) that are most influential with respect to error or variability in the assumed input. The adjustment factor for detection distance has the potential for exerting the greatest effect on population size estimates. All estimates should be accompanied by estimates of precision. Sensitivity analysis could identify credible bounds for the population estimates, which to date are expressed only qualitatively.

The Rosenberg and Blancher approach is based on adjustments of mean counts. Alternatively, more sophisticated model-based approaches explicitly incorporating known sources of variability could be used to better incorporate uncertainty in the estimates. For instance, hierarchical modeling approaches allow for direct estimation of route-specific abundances that are adjusted for observer and

population-change effects (e.g., Link and Sauer 2002), spatial effects (Thogmartin et al. 2004), and the detectability adjustments used in the Rosenberg and Blancher (2005) population estimates. For instance, for geopolitical regions not sampled by BBS routes, the model-based solution incorporating spatial correlation in counts may be a useful means of estimating expected counts for areas in which they are unknown.

The present scheme for population estimation from BBS data is limited by uncertainty in the magnitude and precision of the adjustments for detection. Without empirical data on detection rates, estimates will always be subject to criticism. Thus, the panel encourages experimental studies to develop approaches for estimating detectability in the BBS. Until such estimates become available, the panel recommends that ongoing efforts to refine the estimates be initiated, including a comprehensive survey of literature and of current research to identify available information about species-specific detection distances and the effects on detectability of habitat, sex, time of day, time of year, observer, and other factors. Of particular concern is the identification of specific gaps in our knowledge regarding species- and covariate-specific detection-distance categories. The number of species for which detection distances are available is small but growing. Detection distances acquired from the literature, even if they do not account for bias because of roadsides, may be better than the current five-level detection distances. Collecting data on detection is the best way to improve our understanding of species-, space-, and time-specific variation in rates. As noted below, systematic collection of these data in the BBS and other surveys is a long-term strategy for enhancing the quality of the population size estimates.

The validity of the pair adjustment used in the population estimation approach undoubtedly varies among species, reflecting differences in mating strategy, behavior, and habitat. The panel recommends evaluation and study of the pair adjustment factor. Given the paucity of current data, studies based on surveys of marked populations may be the only way to obtain reliable estimates of pair adjustments.

Use of polynomial regression for identifying maximum counts for the time-of-day adjustment should be evaluated against alternative means, such as simple observed maximum, an

average of the top several counts, loess smoothing (Cleveland and Devlin 1988), or more sophisticated approaches such as maximum-likelihood estimation of the maxima.

Additional features that could influence counts should be considered in the analysis. In particular, several authors have suggested that interactions between calling rates and population density can invalidate indices to abundance (e.g., McShea and Rappole 1997, Penteriani 2003). Additional review of literature for cue production studies would be worthwhile. These cue production studies may be particularly relevant to understanding how well polynomial regression predicts peak calling in nocturnal or crepuscular birds.

Because the pair adjustment may not overcome errors in the time-of-day or time-of-year adjustment, we recommend disentangling the pair adjustment from adjustment factors that may be imposed for those species that are nocturnal or crepuscular, early or late breeders, or have an unknown floater population. One obvious adjustment would be to evaluate BBS counts with regard to how they vary seasonally, so as to calibrate the estimates for early- or late-season breeders. Modeling of rangewide progressions of peak song periods and studies of how detectability changes as a function of peak song period would prove informative to these calibrations.

Estimates of population sizes for each of the three terrestrial ecozones in Arctic Canada should be interpreted with caution. Although the methodology used by PIF for estimating population size of landbirds in the Arctic makes use of most of the data that are available for the region, we suggest that the estimates based on those data are particularly prone to bias, because BBC and Checklist sites are not selected randomly and tend to be in areas of high bird densities. The assumption that Checklist-BBC estimates are comparable to BBS estimates likely does not hold. Also, we suggest that the total amount of land useable by birds should be used as the area for which estimates of populations are made, given that large areas in the high Arctic are covered by unsuitable glaciers or are otherwise devoid of vegetation.

Recommendations for the long term.—Much of the uncertainty associated with the approach outlined by Rosenberg and Blancher (2005) is a result of using the data for a purpose for which

they were not intended. The BBS was not originally envisioned to provide continental estimates of population sizes but rather to monitor trends in populations. To fully address these uncertainties, it will be necessary to update the population estimates as new information regarding detection rates and other factors becomes available from experimental studies. Also, concerns about the representativeness of roadside habitats and of data from outside the BBS survey area can be addressed only with additional survey information and continued modeling.

Information on detection of birds along routes.—Statistical procedures such as distance sampling (Buckland et al. 2001), double observer methods (Nichols et al. 2000), and replicate counting methods (Royle and Nichols 2003) permit direct estimation of detection rates from point counts. Direct application of these approaches to the BBS and other surveys would provide data on time-of-day effects, habitat specificity, and effective detection distances, and would allow direct estimation of many of the parameters that are presently unknown or poorly estimated in the Rosenberg and Blancher modeling exercise. The panel suggests that field investigators be encouraged to routinely collect this information. Experimental studies of such approaches along BBS routes would be useful. Additional studies focusing on groups of species of particular interest that have large temporal correction factors, such as strigiforms and caprimulgiforms, are needed.

Development of surveys in northern regions.—Population estimates are most questionable when they are based on extremely limited samples or on detection–nondetection data sources, such as checklists. Given the paucity of data for birds in Arctic Canada and concern that global climate change may be most pronounced at northern latitudes (McCarthy et al. 2001), development of surveys that provide information on bird populations would be useful in documenting both present values and future changes in this important region.

Better integration of survey and habitat data.—Development of statistical models is an essential component of future development of population estimates. Population estimates will be most useful for conservation planning if they are directly related to habitat acquisition and other management goals. Many studies

are using BBS data to develop models associating bird populations with habitat and other environmental features (e.g., Thogmartin et al. 2004), and more use of these models in bird conservation planning may help resolve several of the issues associated with population estimation. For example, nonrepresentativeness of roadside habitats can be addressed either by collection of data in nonroadside habitats or by modeling bird habitat associations using existing data and using the models to predict abundances in off-road habitats. Models can then be used to guide future data-collection efforts, and the additional data (for example, counts made away from roadsides) can be used to improve models. These modeling efforts require appropriate geographic information on habitats, other environmental features that influence bird populations, and BBS data.

Models can allow for controlling of population change in the estimation of abundance. One obvious limitation of species-specific population estimates as they are currently made is that populations are assumed to be static. Sauer et al. (2004), however, indicated that 38% of the Neotropical migrant species surveyed in the BBS during 1980–2003 declined and 18% increased. Because bird populations are not static and, in fact, many are in decline, the panel recommends devising a population estimation scheme that incorporates temporal trends in abundance. Various hierarchical modeling approaches are promising for their ability to estimate population trends (Link and Sauer 2002).

Models also permit a common currency for translating population sizes across spatial scales and for comparing species. The most obvious currency is habitat-specific estimates of density for each species. In the long term, habitat-based models estimating population size for each state–province–territory \times Bird Conservation Region unit would be valuable. These habitat-based models may be able to identify limiting factors and could be used to set habitat-specific numerical population objectives. Further, incorporating habitat-based models with estimates of trend may allow future projections of population size in response to proposed management of habitat.

Extrapolation beyond the United States and Canada.—The fourth assumption of the population estimation approach is that densities of birds are similar in North America and beyond.

This assumption deserves considerable scrutiny, because differences in density for species existing primarily outside the United States and Canada may cause huge errors in the estimated global population size for a species. Much greater investigation into densities of North American species whose ranges overlap boreal Russia and Latin America is needed. The panel suggests that extrapolation to areas outside North America is particularly dangerous and not clearly relevant to PIF goals.

HOW SHOULD THE PIF POPULATION ESTIMATES BE INTERPRETED?

In Rich et al. (2004), current bird populations are estimated using the procedures critiqued in this paper, but goals are often framed in terms of estimation of population trends. At the scale of bird conservation regions, management options are usually defined in terms of acquisition and restoration of habitats, and predicted increases in populations are based on models predicting numbers of birds as a function of added habitat. However, these numbers are not directly comparable to either the estimated trends or the habitat goals defined by bird conservation initiatives. We view this lack of a connection of population estimates, trend, and habitat goals as a flaw in the system. As noted above, opportunities exist to develop models that directly associate management options, trend estimates, and population estimates, and we suggest that these approaches be considered for future analyses.

Uncertainty in population estimates makes comparisons between species, especially for the purposes of prioritization, problematic. Further, this uncertainty in population size adds to uncertainties associated with determining whether species have reached a particular conservation target as outlined in the North American Landbird Conservation Plan. Documenting the extent of variation associated with the population estimates will enhance the value of the estimates, and most of our recommendations reflect our concern that interpretation of the present quantities is complicated by the present lack of variance estimates. Interpretation of the estimates must also be sensitive to temporal variation in bird numbers. Bird populations are dynamic, and successive estimates must reflect the temporal components of population change.

In summary, the panel applauds P. J. Blancher and K. V. Rosenberg for their progress with the difficult task of estimating the population sizes of North American landbirds. As they noted, significant uncertainties still exist with the estimates, and interpretations of the estimates should involve a careful consideration of their limitations. The panel recommends a program of evaluation of the present uncertainties, combined with experimental and theoretical work, to better integrate population estimates with bird conservation and management.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1975. Report of the *ad hoc* committee on scientific and educational use of wild birds. *Auk* 92 (3, Supplement):1A–27A.
- BANKS, R. C. 1979. Human-related mortality of birds in the United States. U.S. Department of Interior, Fish and Wildlife Service, Special Scientific Report—Wildlife, no. 215, Washington, D.C.
- BIBBY, C. J., N. D. BURGESS, AND D. A. HILL. 1992. *Bird Census Techniques*. Academic Press, London.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. *Introduction to Distance Sampling*. Oxford University Press, Oxford.
- CANADIAN WILDLIFE SERVICE AND U.S. FISH AND WILDLIFE SERVICE. 1986. North American Waterfowl Management Plan (NAWMP). A Strategy for Cooperation. U.S. Department of Interior, Fish and Wildlife Service, Washington D.C., and Environment Canada, Canadian Wildlife Service, Ottawa.
- CLEVELAND, W. S., AND S. J. DEVLIN. 1988. Locally weighted regression: An approach to regression analysis by local fitting. *Journal of the American Statistical Association* 83: 596–610.
- DEINLEIN, M. 1998. When it comes to pesticides, birds are sitting ducks. *Smithsonian Migratory Bird Center Fact Sheet*, no. 8. Smithsonian Institution, Washington, D.C.
- DONOVAN, T. M., K. E. FREEMARK, B. A. MAURER, L. PETIT, S. K. ROBINSON, AND V. SAAB. 1999. Setting local and regional objectives for the persistence of bird populations. *In* *Strategies for Bird Conservation: The Partners in Flight Planning Process* (R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, Eds.). U.S. Department of Agriculture Forest Service, Proceedings RMRS-P-16. [Online.] Available at www.birds.cornell.edu/pifcapemay/donovan.htm
- FORMAN, R. T. T. 2000. Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology* 14: 31–35.
- FORMAN, R. T. T., AND R. D. DEBLINGER. 2000. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. *Conservation Biology* 14:36–46.
- HUTTO, R. L., S. J. HEJL, J. F. KELLY, AND S. M. PLETSCHE. 1995. A comparison of bird detection rates derived from on-road vs. off-road point counts in northern Montana. Pages 103–110 *in* *Monitoring Bird Populations by Point Counts* (C. J. Ralph, J. R. Sauer, and S. Droege, Eds.). U.S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-149.
- KELLER, C. M. E., AND M. R. FULLER. 1995. Comparison of birds detected from roadside and off-road point counts in the Shenandoah National Park. Pages 111–115 *in* *Monitoring Bird Populations by Point Counts* (C. J. Ralph, J. R. Sauer, and S. Droege, Eds.). U.S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-149.
- KENWOOD, K. E., AND E. H. PAXTON. 2001. Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt

- Lake, Arizona—2001. U.S. Geological Survey Forest and Rangeland Ecosystem Science Center, Flagstaff, Arizona, and U.S. Bureau of Reclamation, Phoenix, Arizona.
- KERLINGER, P. 2000. Avian mortality at communication towers: A review of recent literature, research, and methodology. U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Washington, D.C. [Online.] Available at migratorybirds.fws.gov/issues/towers/review.pdf.
- KLEM, D., JR. 1990. Collisions between birds and windows: Mortality and prevention. *Journal of Field Ornithology* 61:120–128.
- LEPCZYK, C. A., A. G. MERTIG, AND J. LIU. 2004. Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation* 115:191–201.
- LINK, W. A., AND J. R. SAUER. 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. *Ecological Applications* 8: 258–268.
- LINK, W. A., AND J. R. SAUER. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology* 83: 2832–2840.
- MCATEE, W. L. 1931. Local bird refuges. U.S. Department of Agriculture Farmer's Bulletin, no. 1644.
- MCCARTHY, J. J., O. F. CANZIANI, N. A. LEARY, D. J. DOKKEN, AND K. S. WHITE, Eds. 2001. *Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, United Kingdom.
- MCSHEA, W. J., AND J. H. RAPPOLE. 1997. Variable song rates in three species of passerines and implications for estimating bird populations. *Journal of Field Ornithology* 68: 367–375.
- MILLER, J. R., L. A. JOYCE, R. L. KNIGHT, AND R. M. KING. 1996. Forest roads and landscape structure in the southern Rocky Mountains. *Landscape Ecology* 11:115–127.
- NATIONAL AUDUBON SOCIETY. 1997. Resolution approved by the Board of Directors on Dec. 7, 1997, regarding control and management of feral and free-ranging domestic cats. [Online.] Available at www.audubon.org/local/cn/98march/nasr.html.
- NATIONAL WIND COORDINATING COMMITTEE. 2001. Avian collisions with wind turbines: A summary of existing studies and comparisons of avian collision mortality in the United States. National Wind Coordinating Committee, Washington D.C. [Online.] Available at www.nationalwind.org/publications/wildlife/avian_collisions.pdf.
- NICHOLS, J. D., J. E. HINES, J. R. SAUER, F. W. FALLON, J. E. FALLON, AND P. J. HEGLUND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117:393–408.
- NORVELL, R. E., F. P. HOWE, AND J. R. PARRISH. 2003. A seven-year comparison of relative-abundance and distance-sampling methods. *Auk* 120:1013–1028.
- O'CONNOR, R. J., E. DUNN, D. H. JOHNSON, S. L. JONES, D. PETIT, K. POLLOCK, C. R. SMITH, J. L. TRAPP, AND E. WELLING. 2000. A programmatic review of the North American Breeding Bird Survey: Report of a peer review panel. [Online.] Available at www.pwrc.usgs.gov/bbs/bbsreview/bbsfinal.pdf.
- PENTERIANI, V. 2003. Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality. *Ibis* 145: E127–E135.
- PETERJOHN, B. G. 1994. The North American Breeding Bird Survey. *Birding* 26:386–398.
- RICH, T. D., C. J. BEARDMORE, H. BERLANGA, P. J. BLANCHER, M. S. W. BRADSTREET, G. S. BUTCHER, D. W. DEMAREST, E. H. DUNN, W. C. HUNTER, E. E. IÑIGO-ELIAS, AND OTHERS. 2004. *Partners in Flight North American land-bird conservation plan.* Cornell Lab of Ornithology, Ithaca, New York.
- ROBBINS, C. S., D. BYSTRAK, AND P. H. GEISSLER. 1986. *The Breeding Bird Survey: Its first fifteen years, 1965–1979.* Resource Publication no. 157, U.S. Fish and Wildlife Service, Washington, D.C.
- ROBBINS, C. S., S. DROEGE, AND J. R. SAUER. 1989. Monitoring bird populations with Breeding Bird Survey and atlas data. *Annales Zoologici Fennici* 26:297–304.
- ROHNER, C. 1997. Non-territorial floaters in Great Horned Owls (*Bubo virginianus*). Pages 347–362 in *Biology and Conservation of Owls of the Northern Hemisphere* (J. R. Duncan, D. H. Johnson, and T. H. Nicholls, Eds.). U.S. Department of Agriculture Forest Service, General Technical Report NC-190.

- ROSENBERG, K. V., AND P. J. BLANCHER. 2005. Setting numerical population objectives for priority landbird species. Pages 57–67 *in* Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference (C. J. Ralph and T. D. Rich, Eds.). U.S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-191.
- ROSENSTOCK, S. S., D. R. ANDERSON, K. M. GIESEN, T. LEUKERING, AND M. F. CARTER. 2002. Landbird counting techniques: Current practices and an alternative. *Auk* 119:46–53.
- ROTEBERRY, J. T., AND S. T. KNICK. 1995. Evaluation of bias in roadside point count surveys of passerines in shrubsteppe and grassland habitats in southwestern Idaho. Pages 99–101 *in* Monitoring Bird Populations by Point Counts (C. J. Ralph, J. R. Sauer, and S. Droege, Eds.). U.S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-149.
- ROYLE, J. A., AND J. D. NICHOLS. 2003. Estimating abundance from repeated presence–absence data or point counts. *Ecology* 84:777–790.
- SAUER, J. R., J. E. HINES, AND J. FALLON. 2004. The North American Breeding Bird Survey, results and analysis 1966–2003, version 2004.1. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland.
- THOGMARTIN, W. E., J. R. SAUER, AND M. G. KNUTSON. 2004. A hierarchical spatial model of avian abundance with application to Cerulean Warblers. *Ecological Applications* 14:1766–1779.
- THOMPSON, W. L. 2002. Towards reliable bird surveys: Accounting for individuals present but not detected. *Auk* 119:18–25.
- TROMBULAK, S. C., AND C. A. FRISSELL. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- WING, L. W. 1956. *Natural History of Birds*. Ronald Press, New York.

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