COMPARATIVE DEMOGRAPHY OF NEW WORLD POPULATIONS OF THRUSHES (TURDUS *SSP.*): REPLY

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Conn, Doherty, and Nichols (2005), hereafter CD&N, question the wisdom of using age ratios obtained from museum collections to estimate adult survival rates in populations of birds. Ricklefs (1997), Rohwer (2004), and other studies that have used this approach have been careful to recognize and evaluate potential problems, to the extent possible. The basic assumptions of the method are that adult and first-year birds can be distinguished reliably and that their survival rates do not differ at the time during the annual cycle when the age ratio is estimated. Additional issues discussed by Ricklefs (1997) were potential biases arising from nonstable (growing or declining) populations, varying population size, collecting biases favoring adults or immatures, aseasonal breeding, senescent de-

cline in survival rate, and delayed plumage maturation. To some extent, these biases can be evaluated from museum data, for example by seasonal differences in the ratios of adult to first year birds; species with marked delays in plumage and behavioral maturation that would influence collecting can be avoided. Ricklefs (1997) considered that these potential biases individually were unlikely to be strong, but it was not possible to estimate most of them directly. Nonetheless, age ratios have been useful in comparative studies for estimating average adult survival in populations sampled broadly in time and space. For this purpose, collection-based methods will often outperform local banding studies, which are sensitive to individual dispersal movements. The latter are better suited to addressing more detailed, localized issues such as variation in survival over time or with age.

Perhaps the most fundamental difference between our approach and that of CD&N is our faith in the quality of the data. To be sure, the recapture of a banded bird conveys a certainty about the survival of an individual over a specified period that can be used to build a model of the survival of individuals in a population. The presence of a specimen in a museum collection is a unique observation lacking any direct reference to an earlier point in its life. Although such samples are not suited to longitudinal analyses based on models incorporating probabilities of survival and resighting of individual birds, our statistical methods do provide an estimate of survival for populations where banding approaches are not possible. Many studies in comparative demography will be practical and economical only with the unique resources of museum collections. The data from these collections are better than CD&N claim. Geographically wide-ranging sam-

ples collected over decades, as in Ricklefs' analysis of thrushes and Rohwer's study of warblers, circumvent problems of local dispersal and short-term variation in demography that might otherwise introduce biases. Ornithologists should recognize that band-return approaches also require considerable (often unjustified) faith in unbiased net capture, in emigration being a negligible factor, and in the global applicability of locally estimated parameters. Moreover, the power of mark–recapture methods often greatly exceeds the quality of the data used to feed them.

Additional concerns about the use of age ratios expressed by CD&N derive from biases related to aging error, immigration and emigration, and the uncertainty associated with assumptions about these variables. We comment on these issues in turn. Estimating survival from age ratios requires an accurate age criterion. Because plumage characters most commonly provide these criteria, this depends on careful evaluation of molt cycles. In many cases, suitable plumage markers of age class are not available and age ratios cannot be used. Certainly many of the aging criteria described in banding manuals, such as Jenni and Winkler (1994) and Pyle (1997a, b), are only approximate and do not reliably allow all individuals to be assigned to age class (see, for example, Green [2004]). For many parts of the world, details of feather markings that change with plumage cycles and the limits of incomplete molts, and that allow individuals to be assigned to age classes, are poorly known. However, for Townsend's and Hermit Warblers (Dendroica townsendi and D. occidentalis), plumage characters reliably distinguish first-year and adult males (Jackson et al. 1992, Rohwer 2004). One of the reasons for working with New World species of the genus Turdus was a reliable plumage marker that separates immature birds through most of their first year from birds that are at least one year old (Ricklefs 1997). The marker works less well with some Old World species of Turdus that retain elements of immature-like plumages as adults (e.g., Song Thrush Turdus philomelos; Jenni and Winkler 1994). As CD&N rightly imply, the age ratio technique for museum specimens is not for every species, and probably not for most; further, it may not work for both sexes of a species, because age-related characters are frequently more difficult to assess in females than in males.

The purported bias from immigration and emigration puzzles us. When museum collections sample populations broadly across the range of a species, movement of individuals from one place to another is not an issue. Even for local populations, CD&N's analysis of immigration and emigration seems misleading. It should be evident that if adults and immatures were to move with equal probability, their proportion would not be altered by immigration or emigration, provided that their relative numbers were homogeneous across the metapopulation. CD&N argue otherwise. They define the proportion of individuals with adult plumage in a population after one year of survival and emigration/immigration as $v_{i+1} = \phi_i[F_i + \pi_i(1 - F_i)]$. In this relationship, ϕ_i is the annual survival rate at time i; F_i is a fidelity parameter, i.e., the proportion of individuals that stay at home; and π_i is the rate of immigration relative to that of emigration. Accordingly, the proportion of adult-plumage individuals equals the annual adult survival rate only when there is no movement ($F_i = 1$) or when immigration equals emigration ($\pi_i = 1$). However, CD&N derived this equation supposing that population size is constant, i.e., growth rate $\lambda = 1$, and they therefore calculated the age ratio $v_{i+1} = N_{i+1}^A/(N_i^A + N_i^I)$, where N^A and N^I are the numbers of adult and immature individuals. This is the ratio of adults in one year to the sum of adults and immature individuals in the previous year. In practice, the age ratio is calculated from specimens obtained at the same time and $v_{i+1} = N_{i+1}^A/(N_{i+1}^A + N_{i+1}^I)$. Thus, CD&N confound population change with immigration and emigration. For populations in which births and deaths balance, there is no bias when $\pi_i = 1$; when $\pi_i \neq 1$, population size is not constant.

Of course, adults and immatures in some populations move with different probabilities from one region, or habitat, to another. Thus, Graves (1997) and Rohwer (2004) were careful to argue that changes in age ratios along habitat or density gradients across small distances were likely to represent despotic breeding distributions (Fretwell 1972), rather than differences in survival. In this case, only banding studies can assess differential movement by adults and immatures, but one would have to distinguish immature (1-year-old) and adult ($\geq$2-year-old) individuals because despotic habitat distribution models assume that first-year birds will be prevented from settling in high-quality habitat. Thus, adults replace adults in such habitats, resulting in a net immigration of adults (Rohwer 2004). Plot-based banding studies on mechanisms of habitat distribution therefore would require an assessment of age, which can be determined only by plumage markers where young disperse from their natal area. Moreover, for species that are rarely recovered or resighted outside of study plots, such studies would be easier to justify if the appropriate geographic scale and habitat gradient were first obtained from museum data. CD&N cite the study of Cilimburg et al. (2002) on Yellow Warblers (Dendroica petechia), in which the investigators searched over widely distributed banding plots to increase the probability of resighting dispersed individuals, thus raising the survival estimate. Nonetheless, their estimate was not high enough for the Bitterroot Valley population to be stable, even though the

investigators could have detected location shifts up to 45 km (but could not possibly have searched the entire area) (Cilimburg et al. 2002). An estimate of annual survival based on a regional sample of age ratios would have provided a proper context for evaluating emigration and the source vs. sink status of the Bitterroot population.

CD&N's uncertainty analysis emphasizes sources of variation in estimates of annual survival from age ratios, which is appropriate, but it overstates the problem. Variation in fidelity (F_i) and the immigration/emigration ratio (π_i) do not contribute to variation in the estimate of local adult survival, except through their effect on population growth rate, and not at all on global estimates of survival. CD&N's pencil-and-paper example incorporated a range in variation in λ of up to ± 0.24, certainly beyond typical values in natural populations. Ricklefs (1997) also discussed biases in estimated adult survival resulting from variation in population growth and collecting bias, although his estimates of standard errors did not incorporate these effects. CD&N cite the example of the growth rate of a local Canadian population of the Cerulean Warbler (*Dendroica cerulea*), claimed to be rapidly declining (λ = 0.73) by Jones et al. (2004). This study highlights the challenge of estimating adult survival from band-return analyses. The estimated adult survival (ϕ = 0.49 ± 0.05) was based on 74 resightings of banded males over a six-year study concentrated on 30 ha of forest, with annual variation in estimated ϕ_i ranging between ~0.35 and 0.80. In another cited study, in this case of the Ciril Finch (*Serinus citrinella*), based on 1383 recaptures over nine years in two study populations, Senar et al. (2002: Table 2) found that the 95% confidence limits for adult survival in one set of models extended beyond 0 and 1. Thus, uncertainty is a problem with the estimation of survival, regardless of the approach. We agree with CD&N that sources of uncertainty beyond binomial sampling should be addressed to the extent possible in any study of population processes.

In spite of advances in mark–recapture methodology, including the incorporation of permanent emigration into these models, the realities of survival estimation are that recapture approaches are nonetheless plagued by lack of access to most populations for banding studies, uncertainties about emigration in most cases, and localization in both time and space. Museum methods based on age ratios in collections avoid these problems because sampling can be extensive across space and time, but they incur uncertainties with respect to age estimation, sampling bias, and population growth rate. In addition, they rarely allow hypothesis testing with respect to year, condition, and age-related survival, although such effects could be analyzed with suitable samples (cf., for example, Loison et al. 2002). Age ratio

analysis is amenable to likelihood approaches (e.g., Udevitz and Ballachey 1998). Indeed, the age ratio is an unbiased maximum likelihood estimator of adult survival rate, and its analysis can be adapted to test additional effects in a likelihood framework.

As CD&N point out, age ratios must be used with care to estimate survival rates. The same is true of mark–recapture data. The sophistication of mark–recapture models cannot reduce potential biases, uncertainties, and sampling limitations inherent in the data themselves. Nor could mark–recapture models be applied, for example, to a hemispheric analysis of survival in 30 populations of 19 species ranging from Alaska to Patagonia, as in the case of Ricklefs's (1997) study of *Turdus*, or to the kinds of questions regarding populations of hybridizing warblers throughout their ranges and over elevation gradients posed by Rohwer (2004). While CD&N argue that they could construct scenarios that would invalidate these comparisons, they could neither test these ad hoc scenarios statistically nor deny the close match between survival estimates from age ratios and band-return data for well-studied north temperate populations of *Turdus* and *Dendroica*. Any estimate of survival probability has associated uncertainty. Different approaches are suitable for different questions. We hope that students of population statistics will recognize the potential of using age ratios to estimate survival where this cannot be addressed by banding studies, and that they will work to evaluate potential sources of uncertainty and refine underlying models.

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