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EFFECTS OF SAMPLING DESIGN ON AGE RATIOS OF MIGRANTS CAPTURED AT STOPOVER SITES[1]

JEFFREY F. KELLY AND DEBORAH M. FINCH
USDA, Forest Service, Rocky Mountain Research Station, 2205 Columbia SE, Albuquerque, NM 87106, e-mail: jfkelly@fs.fed.us

Abstract. Age classes of migrant songbirds often differ in migration timing. This difference creates the potential for age-ratios recorded at stopover sites to vary with the amount and distribution of sampling effort used. To test for these biases, we sub-sampled migrant capture data from the Middle Rio Grande Valley of New Mexico. We created data sets that reflected the age ratios of migrants that would have been captured with stratified and concentrated designs at four levels of mist-netting effort. Analysis of these data indicate that age-ratios of Neotropical migrants varied significantly with sampling design, but not with sampling effort. More after-hatch-year Neotropical migrants were captured with stratified than with concentrated sampling designs. Age-ratio of temperate migrants did not vary with either amount of sampling effort or sampling design. Sampling design is an important consideration in the interpretation of age ratios among stopover sites, and standardization of sampling among sites could improve our understanding of differential migration of age classes.

Key words: age-ratio, Neotropical migrant, sampling design, stopover biology, temperate migrant.

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Recent studies of songbird migration have documented strong influences of age class on autumn stopover biology, particularly the tendency for age classes to differ in the timing of autumn migration (Woodrey and Chandler 1997, Woodrey and Moore 1997). Regardless of the mechanisms that generate differences in timing of passage of age classes, this difference creates the potential for age ratios recorded at banding stations to vary as a function of the amount and distribution of sampling effort.

Numerous authors have compared age ratios among stopover sites to better understand migration biology (Johnson 1973, Ralph 1981). Recently, Woodrey and Chandler (1997) used age ratios to demonstrate differential timing of the onset of autumn migration among age classes in two of five species examined (Red-eyed Vireo, *Vireo olivaceus* and Magnolia Warbler, *Dendroica magnolia*). However, for the other three species (Swainson's Thrush, *Catharus ustulatus*; American Redstart, *Setophaga ruticilla*; and Common Yellowthroat, *Geothlypis trichas*), among-site patterns were less clear (Woodrey and Chandler 1997). Some have also speculated that age ratios measured at stopover sites may be useful in understanding population fluctuation (Hussell and Ralph 1996). The utility of age ratios in such regards is predicated on their comparability among sites and through time.

We suspect that variation in sampling effort may create differential biases in the age ratios documented. To our knowledge, however, the relationship between sampling protocol and age ratio of migrants captured has not been quantified. Here we analyze the effects of some aspects of sampling design on age ratios of migrants captured during stopover. In particular, we ask (1) how does the distribution of netting effort through the migration period affect age ratios and (2) how does total amount of sampling effort expended affect age ratios?

METHODS

STUDY AREA

The Middle Rio Grande Valley is a 260-km long stretch of river between Cochiti Dam and Elephant Butte Reservoir in New Mexico. We netted at two sites in the Rio Grande Valley: the Rio Grande Nature Center (35°07′N, 106°41′W) and the Bosque del Apache National Wildlife Refuge (33°48′N, 106°52′W). The primary natural vegetation in these areas was dominated by native cottonwood (*Populus deltoides*), willow (*Salix exigua* and *S. gooddingi*), exotic Russian olive (*Elaeagnus angustifolia*), and saltcedar (*Tamarix* spp.; Yong et al. 1998, Kelly et al. 1999).

DATA COLLECTION

In 1994–1997, we used 35–40 mist nets (12 × 2.6 m, 30- or 36-mm mesh) to capture autumn migrants. Nets were operated 5 days week^{-1} from 7 August to 5 November. Owing to inclement weather, our actual effort averaged (± SD) 4.5 ± 0.6 days week^{-1} (n = 52 weeks). Nets were opened 15 min prior to sunrise and remained opened for 6 hr day^{-1}. Nets were checked at 20–30-min intervals. We used skull ossification, and various plumage and morphological characteristics to age birds (Pyle 1997). Each bird captured was marked with a uniquely numbered aluminum leg band, weighed, measured, and released. We divided the migrant passerines into Neotropical and temperate migrants. We define Neotropical migrants as those that winter primarily south of 25°N latitude, and temperate migrants as those that winter primarily north of that latitude (Hussell et al. 1992).

DATA ANALYSIS

We sub-sampled our capture data to create eight simulated datasets, which were divided equally between two sampling designs (stratified and concentrated). Stratified design types included birds captured on randomly selected days within each time stratum. For example, in the 1 day week^{-1} sampling design we included birds captured on one randomly drawn day from each week of the season. The four levels of effort used in the stratified design were 1, 2, 3, and 4 days week^{-1}. Our concentrated effort sampling designs consisted of all birds captured in a given number of days centered on the overall migration peak. The levels of effort used were 13, 26, 39, and 52 days. These effort levels matched those in the stratified designs (i.e., 1 day week^{-1} for 13 weeks is 13 days of effort). We identified the overall migration peak by averaging all initial capture dates of passerines (23 September). All analyses are based on initial captures.

We limited our analyses to species for which we identified the age class of at least 20 individuals in all sampling designs. The two age classes we used were hatch-year and after-hatch-year. There was the potential that birds classified as unknown age were biased toward a single age category (i.e., hatch-year females) and the degree of bias likely varied among species. There are two reasons why we do not think this bias diminishes the relevance of our results. First, we used an analysis that was paired within species. Thus, the age ratio of a species was only compared to another ratio from that same species. Second, because we used standard procedures for assigning birds to age classes (Pyle 1997), bias that occurs in our data is also likely to occur in data from other stopover sites. Therefore, we think our approach depicts a realistic analysis of the effects of distribution and amount of sampling effort on age ratio of birds captured.

Because in most species age can only be reliably distinguished in the autumn, we limited our analysis to this season. We calculated the percent of birds in the after-hatch-year age class and refer to these percentages as the age ratios. For each species at each level of effort, we calculated the difference in age ratios between design types.

We used the differences in age ratio between design types as the dependent variable in analyses of variance; the level of effort was the independent variable. Because we used the difference between design types as the dependent variable, the intercept of the ANOVA model should not have differed from zero if the design types (i.e., concentrated vs. stratified) did not differ. Alternatively, a significant difference between the model intercept and zero would indicate a significant difference in age ratio between design types. We ran separate ANOVAs for Neotropical and temperate migrants.

RESULTS

There were 16 species of Neotropical migrants and 11 species of temperate migrants for which we identified at least 20 individuals to age class in all sampling designs. For Neotropical migrants, significantly more after-hatch-year birds were captured with stratified than with concentrated designs ($F_{1,60}$ = 18.5, P < 0.001, Fig. 1, Table 1). The number of Neotropical migrants with age ratios that differed by greater than 10% between design types was eight, six, five, and one for effort of 13, 26, 39, and 52 days, respectively. In all but one of these cases, stratified designs resulted in

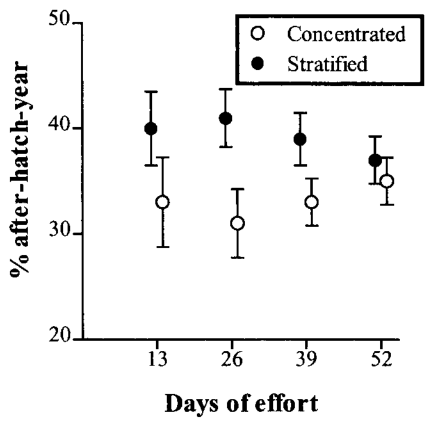

FIGURE 1. Percent of after-hatch-year Neotropical migrants captured with stratified and concentrated designs for four levels of sampling effort (n = 16 species). A higher percentage of after-hatch-year Neotropical migrants was captured with stratified than with concentrated designs at all effort levels.

capture of a greater percentage of after-hatch-year birds than concentrated designs.

There was no effect of sampling design on the percent of temperate migrants captured that was after-hatch-year birds ($F_{1,40}$ = 0.3, P = 0.6, Table 1). Only in two cases, both when 13 days of effort were used, did age ratios of stratified and concentrated designs differ by greater than 10%.

The amount of effort used had no effect on the age ratios of either Neotropical ($F_{3,60}$ = 1.3, $P > 0.2$) or temperate migrants ($F_{3,60}$ = 0.1, $P > 0.9$) . With minimal sampling effort, stratified designs resulted in age ratios that were similar to those based on our total effort (60 days); this pattern was not evident for concentrated designs. Specifically, based on 13 days of stratified effort, 19 of 27 species (12 Neotropical and 7 temperate migrants) had age ratios that were within 5% of the age ratios calculated from 60 days of effort; only 1 species had an age ratio that differed by greater than 10% from that calculated with 60 days of effort. In addition, with 26 days of stratified effort, 26 of 27 species had age ratios that differed by less than 5% from those based on 60 days of effort. Based on 13 days of concentrated effort, only 9 of 27 species (3 Neotropical and 6 temperate migrants) had age ratios that were within 5% of those calculated with 60 days of effort; 9 species had values that differed by greater than 10% from the age ratio based on 60 days of effort. With 26 days of concentrated effort, 15 of 27 species had age ratios that differed by less than 5% from those based on 60 days of effort.

DISCUSSION

Our results demonstrate that sampling methodology can strongly affect the age ratio of Neotropical migrants captured. The difference in age ratios is likely related to differences in the timing of passage of these age classes in most species. Various studies have documented earlier migration and shorter stopovers by after-hatch-year than hatch-year birds in autumn (Morris et al. 1996, Woodrey and Moore 1997, Yong et al. 1998). Of the designs we examined, early arriving after-hatch-year birds would only have been captured with stratified designs.

The lack of effect of sampling design on age ratios of temperate migrants probably reflects the later arrival, on average, of temperate migrants relative to Neotropical migrants (Finch, unpubl. data) and possibly significant migration of temperate species beyond the end of our netting season. These factors combined to make temperate migrants less sensitive to the design elements we manipulated. This insensitivity, however, does not mean that age ratios of temperate migrants are necessarily more robust to other differences in sampling design.

Although the effects of sampling design on age ratios of Neotropical migrants are large, it is clear that they can be overcome. The most rigorous approach is to compare sites that net daily throughout migration; Woodrey and Chandler (1997) clearly demonstrated the utility of this approach. With less than daily effort, it may also be possible to compare age ratios among sites, but this approach requires assumptions about the timing of passage of age classes at different sites.

Our results should not be used to argue that studies using greater that 52 days of effort are immune from the sampling effects we identified here. Although the age ratios of stratified and concentrated designs appear to converge at 52 days of effort (Fig. 1), this pattern is primarily an artifact of the total sampling effort used in our study. We used a maximum of 60 days of sampling effort in any given autumn, which means that at 52 days of effort our two simulated design types shared a minimum of 44 days (85%) in common. Thus, the convergence at 52 days of effort (Fig. 1) is likely exaggerated in our analysis.

It is clear from our analysis that if sampling effort is limited (e.g., 13 days), then a stratified approach is more likely to produce age-ratio estimates that approximate those obtained with greater effort. This level of

TABLE 1. Percent of captures ($\bar{x}$ ± SD) that was after-hatch year birds for 16 Neotropical and 11 temperate migrants captured in the Middle Rio Grande Valley, New Mexico. Percentages are reported for simulated sampling designs that used 13, 26, 39, or 52 days of sampling effort; effort was either concentrated at the migration peak or stratified across the migration period.

Migrant type	Days of effort	Percent after-hatch-year	
		Stratified	Concentrated
Neotropical	13	32.6 ± 16.7	40.3 ± 13.7
	26	30.7 ± 12.8	40.9 ± 11.1
	39	32.8 ± 9.0	38.8 ± 10.4
	52	35.4 ± 8.5	37.4 ± 9.1
Temperate	13	35.3 ± 15.2	34.0 ± 13.9
	26	35.4 ± 13.5	35.1 ± 13.0
	39	35.2 ± 12.8	34.3 ± 12.0
	52	34.9 ± 11.9	35.1 ± 11.8

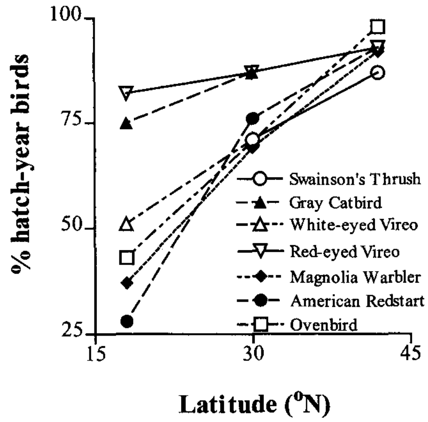

FIGURE 2. Percent of Swainson's Thrushes, Gray Catbirds (*Dumetella carolinensis*), White-eyed Vireos (*Vireo griseus*), Red-eyed Vireos, Magnolia Warblers, American Redstarts, and Ovenbirds (*Seiurus aurocapillus*) captured during autumn migration that was hatch-year birds. These percentages are plotted against latitude of the stopover sites. Data are from Appledore Island, Maine (Morris et al. 1994), Vera Cruz, Mexico (Winker 1995), and Fort Morgan, Alabama (Woodrey and Moore 1997).

effort is substantially less than that used in the published literature and is unlikely to produce good estimates for most migration parameters (Hussell and Ralph 1996), and thus we would not encourage such designs generally. A low-effort stratified approach could be useful, however, where coarse age-ratio data are needed over a broad geographic area or where available effort is limited.

The design factors we examined are not unique in their potential to create bias. The number of potential methodological difficulties is large and include vegetation structure surrounding nets, judgements about age-class identification, and climatic effects. Whereas it may be unrealistic to expect any study to overcome all of these difficulties, it would be useful to know more about the potential effects of these methodological issues when interpreting patterns in age ratios. These considerations are important because the literature indicates broad geographic patterns in age-ratio data, such as a latitudinal trend in age ratios (Fig. 2). Standardizing sampling designs among sites might allow further testing of potential mechanisms that create such patterns.

From our results it is clear that changing the distribution of sampling effort among years or sites and then comparing those age ratios to assess stopover biology or migration dynamics could result in erroneous conclusions. Specifically, relative to a site (or year) that employed a stratified sampling design, one that used a concentrated design would report a lower proportion of hatch-year birds. Even when substantial effort was used, consistent differences remained between concentrated and stratified designs. For this reason, we encourage (1) attention to sampling design when interpreting age ratios and (2) further investigation of the effects of sampling design on age ratios.

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