Introduction

The aim of this paper is to summarize background information on what migration monitoring is, what biases are present and how they can be addressed, evidence that resulting trends are biologically meaningful, and what the benefits and limitations of the method are. Some topics have been covered elsewhere in greater detail (Dunn and Hussell 1995, Dunn et al. 1997, Francis and Hussell 1998). However, an overview provides a useful introduction to this session, and here I discuss potential biases more fully than elsewhere.

For the purposes of this presentation, ‘migration monitoring’ refers to intensive (near daily) counting of migrants at specific sites, with the aim of tracking population change over time. Each daily count is a sample of the birds resting in, or passing through or over the specified count area within a 24-hr period. Counts can consist of many sample types, such as number of birds crossing the face of the moon, registrations on a radar screen, number of migrants recorded giving flight calls as they pass overhead, number of birds counted in diurnal migration or stopover, or number of resting birds captured in mist nets, to name a few. Here I concentrate on the latter two types; specifically, hawk watches and counts of nocturnal songbird migrants during stopover.

In total, there are more than 150 North American landbird species for which migration counts are potentially as good as, or better than, other sources of data currently available for trend analysis (Hussell 1997, Dunn unpubl. data). These include raptors (which are often too sparsely distributed and secretive to be well sampled by the Breeding Bird Survey), long-distance migrants which breed in the boreal forest and winter in the neotropics (escaping coverage both by Breeding Bird Surveys [BBS] and Christmas Bird Counts), and short-distance migrants that breed in arctic and boreal zones and winter in the US.

Sources of Variation in Migration Counts

Migration counts have been criticized as reflecting variation resulting from weather and other factors unrelated to population change, which could render trends unreliable. In order to answer this criticism, it is necessary to review the sources of variation in migration counts, and the ways in which they can be addressed.

The schematic in figure 1 indicates the sources of variation in daily counts. The ‘monitored population’ is the portion of the population contributing migrants to the flow of birds potentially countable at the monitoring site. Birds do not all pass in one day, of course, but rather come in pulses. The ‘migrating population’ (large chevron) represents the number of birds passing through or over the count site in a 24-hr period. The size and seasonal distribution of these pulses will vary with weather factors and lag effects (such as depletion in numbers due to high proportions of birds already having passed). Nonetheless, the total of all birds in all migrating populations over a given season should add up to the ‘monitored population.’ As long as migrating populations are well-sampled, seasonal variation in the frequency of migration pulses should not cause variation in annual indices derived from migration counts.

Figure 1— Schematic diagram of migration, indicating stages at which variability can affect daily bird counts (see text). (Redrawn from Dunn and Hussell 1995).

Of course, not all birds in a migrating population can be counted. Most observers counting diurnal migrants observe during a limited time period each day, and many birds will pass through before or after that...
period. In the case of nocturnal migrants, not all of the birds passing over during the night will actually stop to spend the day at the monitoring site. The ‘count population’ in figure 1 (inner chevron) represents the number of birds in the migrating population that are present during the count period and therefore ‘available’ to be included in the count. At some sites the count population may represent a very high proportion of the migrating population (as illustrated for site 2 in figure 1); for example, when diurnal migrants must pass through a narrow funnel due to local geography. Under average conditions, however, the count population may often represent a relatively small proportion of the migrating population.

Ideally, the count population would always represent a constant proportion of the migrating population. This is certain not to be true, however, due primarily to variable weather conditions, but also to other factors. For example, migrants running into poor weather may land en masse at a site, when they might otherwise have continued migrating. These ‘fall-outs’ represent a count population that is a much higher proportion of a given night’s migrating population than would normally be the case. Weather will also affect the proportionate size of the count population in more subtle ways. If winds are blowing in a particular direction, for example, a higher proportion of diurnally-migrating birds may be moved towards the observation post, where a greater number can be seen and identified than usual. Analyses can model the effects of weather and to some degree adjust for them (see next section).

Finally, not every bird in the count population will be detected and included in the daily migration sample. If the daily tally consists of netting totals, for example, many individuals that are present (i.e., part of the count population) will nonetheless escape becoming part of the actual sample. If visibility is poor at a hawk watch, a smaller proportion of the count population will be detected than when it is clear; and if leaves have emerged, fewer nocturnal migrants may be recorded in visual counts during their stopover than on days prior to leaf-out. Again, inclusion of weather and date factors in analyses can help reduce the effects of such variation.

Variation in daily effort will also cause variation in the proportion of the count population that is tallied, and it is for this reason that it is important to standardize daily count protocol to the extent possible. Visual counts should be taken over a standardized count period (taking place at the same time each day), mist-netting should be done with standardized effort, nets should be of the same type and be put in the same location from day-to-day and year-to-year, etc. (See Hussell and Ralph 1998 for detailed recommendations on operating procedures).

Habitat type and structure affects the numbers and kinds of birds present at a stopover site, and using standardized count locations is important for ensuring that sampling is the same each day. However, change in habitat over time will alter the proportions of birds present that are tallied in daily counts. For example, fewer birds may be visible, or captured in mist nets, as vegetation grows taller. Habitat change is the most serious potential bias for trend monitoring using migration counts. Whenever possible, sites should be selected where vegetation is unlikely to change over time (e.g., riparian shrub that is maintained by regular flooding). Habitat management plans should be developed and strictly adhered to (Hussell and Ralph 1998). Pooling data from several nearby stations (close enough to certainly be sampling the same ‘monitored population,’ as defined for figure 1) may help modulate effects of habitat change at individual sites.

Landscape-level habitat change could also alter the number of birds tallied at a stopover site, independently of population change. For example, birds in a landscape full of suitable stopover habitat will spread throughout the area, but if the landscape is cleared of all but a single grove of trees, then the number of birds in the isolated habitat patch will increase even if population size has not changed. Trends based on data from coastal sites, islands or oases, where birds tend to land regardless of habitat, should be less affected by changing landscapes. At other sites, landscape-scale changes can only be taken into account when interpreting the meaning of trends on a site-by-site basis. If there are multiple sites sampling the same population but experiencing different degrees of landscape change, these effects could potentially be modeled in pooled analysis. Detecting changes in migrants’ use of a particular stopover site because of habitat change (separate from changes in population size) is, of course, a valid study objective in itself, but will require careful survey design in order to allow teasing apart of the causal factors.

Habitat change has much less effect on counts of diurnal migrants such as hawks. Numbers seen should be little affected by condition of habitat on the ground, as long as vegetation growth does not alter the observers’ field of view over time.

**Detecting the Population Size Signal**

Migration count data are highly skewed (a few high daily counts in a season, and many low ones). Figure 2 illustrates the kind of patterns that can typically occur. In year 1, daily counts were close to the long-term average, but several days were missed at the peak of the season when counts would normally be high. Counts in year 2 were more variable, and there was a
fall-out early in the season that led to one extremely high count. Despite the high daily variation in counts, and the very high count during year 2, it is obvious from the figure that in general, the daily counts in year 1 were higher than in year 2.

The trend analysis method commonly used for migration counts (Dunn et al. 1997, Francis and Hussell 1998) is based on the assumption that each day’s count is an independent sample of the monitored population, and that the difference in mean log daily counts among years is the best signal that population size has changed between years. Weather effects may obscure the population size signal on some days (e.g., the fall-out day in year 2; fig. 2), but is unlikely to do so across the entire season. Because each day’s count is given equal weight for the season, it does not matter if a few days are missed, even at the height of migration. However, if daily counts contain many residents and lingering birds counted on previous days, the assumption that each day’s count is an independent sample of the population is violated. (See Hussell and Ralph [1998] for further discussion and ways to minimize repeat counts. The analysis method described below is not suited to species such as shorebirds which typically remain at a given stopover site for several days or weeks.)

Because the analysis method assumes independence of daily samples, good migration monitoring sites for nocturnal migrants are, somewhat paradoxically, the sites where birds least want to be, such as sites with poor stopover habitat where birds stop only because there are few alternatives (e.g., islands, coastlines). Birds leave as soon as possible, such that daily turnover is essentially complete. Many people assume that such sites are unsuited to migration counting, because daily number of birds present is often highly variable as a result of weather conditions. However, the assumptions of the analysis are most likely to be met at such a site, and weather-related variability can be reduced through analysis.

Analyses can model the variation in daily counts that is caused by environmental variables unrelated to population size (see details in Dunn et al. (1997) and Francis and Hussell 1998). In brief, a multivariate analysis is run in which the dependent variable is the log-transformed daily count (log transformed to reduce skew and to allow use of parametric statistics). Independent variables (including higher-order terms where necessary to model non-linear effects) describe date, moon phase (in analyses for nocturnal migrants, since moon phase has been shown to influence their numbers on stopover), and weather conditions (wind speed and direction, temperature, visibility, etc.). Finally, a dummy variable is entered for each year. In effect, the analysis determines whether a particular day’s count is higher or lower than expected for the date of the count, given the weather and moon phase conditions under which the count was taken (e.g., higher or lower than expected for that date given temperatures above normal and winds from the southeast). The coefficient estimated by the analysis for a given year variable represents the mean daily count of birds expected in that year, under average conditions of weather, date and moon phase. Note that, for the model to work well, there must be a large collection of daily samples of the number of birds expected under different conditions (near daily samples over 5-10 years) before appropriate adjustments can first be estimated. (Thereafter, however, additional years can be immediately compared with earlier years.) Results of analyses have been shown to reduce the variance of annual indices by as much as 5-fold over unadjusted annual indices (Hussell 1985).

Analyses that model date effects (omitting weather) are easy to do, and will give results that are more accurate and precise than simply summing all daily counts for use as an annual index. Step-by-step instructions for conducting such analyses using standard statistical software can be obtained from the author, either for nocturnal passerines (daily counts) or for diurnal raptors (hourly counts).

If sites are close enough together that it is certain they are sampling the same ‘monitored population’ (see text describing figure 1), then data can be pooled for common analysis as in Francis and Hussell (1998), who effectively weighted each site according to magnitude of daily counts. The population signal is assumed to be the same at each site, so the weighting method should not affect the result. However, if stations are far enough apart that they may be sampling different populations, which could be changing in different ways, then data should only be combined if the relative

Figure 2— Hypothetical daily migration counts in each of two years, adapted from real data. Curved line shows long-term average count; “0” indicates days in year 1 when no data were collected.
size of the sampled populations is known, so that each site can be given appropriate weighting. Unfortunately, precise population origin of migrating birds is almost never known. The magnitude of counts at each site is no guide to the size of the population being sampled (see text describing figure 1, in which site 2 has the higher count population but a smaller monitored population), so should not be used as a weighting factor when sampled populations are not identical. Currently, therefore, we can only detect regional patterns of population change from migration counts by looking for regional similarities in the separate results from each station. An important corollary is that each migration station is free to choose count methods best suited to conditions at the site, because magnitude of counts (which is affected by count method) will not be a factor in comparing trends among locations.

**Evaluation of Migration Count Trends**

Comparisons of ground counts and birds flying over (as assessed by radar, infrared and other detection methods) indicates weak to moderate correspondence between numbers of birds migrating and those on the ground on a night-to-night basis, but a more general correspondence over the course of a season (Williams et al. 2001, Zehnder et al. 2001), as suggested by discussion of figure 1. No such comparison has been made using ground counts adjusted for weather.

There is accumulating evidence that weather-adjusted migration counts produce population trends which correlate significantly with independent trends from the Breeding Bird Survey, although with maximum r² values of about 0.65, and correspond well in range of trend magnitudes (Hussell and Brown 1992, Hussell et al. 1992, Pyle et al. 1994, Dunn and Hussell 1995, Dunn et al. 1997, Francis and Hussell 1998). Strength of the relationships has been shown to depend on the degree to which the BBS trends represent the same population being sampled by the migration count (Hussell 1997, Francis and Hussell 1998). Migration counts sample birds from a broad geographic range (e.g., southern Ontario stations may sample birds from Alaska as well as from northern Ontario and western Quebec; Brewer et al. 2000), so migration count trends at certain sites may integrate data from portions of the range where populations could well be following separate trajectories. More comparative evaluation of migration count trends is needed, particularly for stations known to sample migrants only from a well-defined region that is also well-covered by BBS. Good candidates include sites in the southeastern United States which sample Neotropical migrants that breed only within the eastern United States.

**Strengths and Limitations of Migration Counts for Population Monitoring**

Overall, intensive, site-specific migration counts have the following strengths:

- For many North American species, migration counts offer the best (sometimes the only) source of information on population change, and for other species, migration counts can help confirm trends from independent monitoring programs.

- Migration counts sample birds from broad areas of breeding (e.g., Wassenaar and Hobson 2001), such that a trend from a single site represents conditions on a large portion of the breeding range.

- All individuals are sampled (juveniles and non-breeders as well as breeders), avoiding certain biases in surveys that primarily record singing birds.

- For certain migration counts (particularly diurnally-migrating raptors), habitat change at the count site should have little effect on results.

Limitations of migration counts for population monitoring purposes include the following:

- Daily counts are affected by weather, which requires sophisticated analysis to address. This is beyond the capabilities of many station operators, so analysis capabilities probably have to be developed on their behalf (e.g., centrally, as in the Canadian Migration Monitoring Network; see http://www.bsc-eoc.org/national/cmnn.html). Multivariate analysis methods have only recently been developed, and more work should be done to ensure that the most appropriate adjustments are being made.

- In most cases, the breeding and wintering locations of migrants counted at a particular site are unknown, such that further research or conservation action cannot be directed at the most appropriate breeding or wintering location, although advances are being made in defining linkages to breeding and wintering sites (e.g., Rubenstein et al. 2002).

- Trends from different sites cannot be pooled into regional or range-wide trends (see discussion above). Analysis of data from many more sites is needed, in order to determine how variable trends may be among nearby sites and across regions.

- Habitat change is potentially a serious cause of bias in migration count trends for species counted during stopover (see discussion above).
• Counting migrants for the purpose of detecting population trends requires sustained effort over many years, often requiring paid staff to ensure long-term continuity.

Other Types of Migration Counts

This paper has concentrated on intensive counts at specific sites, but much of the discussion is relevant as well to other types of migration counts. For example, analysis of daily bird lists contributed to a long-running checklist program in Quebec showed that trends in numbers of birds counted during migration corresponded poorly to BBS trends (Dunn et al. 1996, 2001). This result should not be surprising, given the needs described above for standardized effort and near-daily counts, and given the known biases of generalized birding (e.g., tendency for observers to go out on dates when many birds can be expected, and to cease visiting sites that become unproductive).

If migration counts are taken from radar images of nocturnal passage, the entire daily migrating population (fig. 1) can, in theory, be counted. This would circumvent the potential biases in ground counts that are caused by daily variation in the proportion of the migrating population that forms the count population, and the proportion of the count population that is actually detected by observers. However, radar images do not reliably distinguish between individual targets and flocks of small birds, detection rates vary with height of flight, and sensitivity of radar equipment is likely to improve over time. While all these issues can be addressed to some extent (e.g., through analysis or equipment calibration), there is one crucial limitation to radar counts: species-specific population trends cannot be derived, because species are indistinguishable on radar. (This is also a problem with counts of birds passing the disk of the moon; but that method has the added disadvantage that counts can only be made on nights – and at the hours of the night – when the moon is fully visible.)

Recording of migration flight calls is another means of taking a migration count. Not all species have distinctive calls, and for those that do, there is little known about the factors that might affect calling rate. If call rate varies—for example with conditions of visibility, motivation of the bird or its physical condition, elapsed time of flight, or number of conspecifics within hearing—then call counts will be subject to many biases, just as ground counts are. In addition, calls are likely to differ in detectability over the full range of altitudes at which birds migrate. If call counts are taken in combination with radar, then correction could be made for altitude, but only if it is assumed that all species are equally distributed among altitudinal levels.

Some combination of ground counts, radar and call recording may provide more accurate and precise estimates of population trend than ground counts alone. However, given the effort and expense of using all methods in combination, few stations are likely to try this, and most studies that combine methods will likely be focused on research rather than on population monitoring per se. This kind of research may not lead to development of new methods for population monitoring, but should help in evaluating the best methods for running traditional migration monitoring stations, and in improving our understanding of the sources of variation in daily counts.

Conclusions

Partners in Flight has recommended improvement of migration monitoring as a means of addressing important information gaps on the status of North American landbird species (Rich et al. 2004). Money should go first into developing centralized data analysis and liaison with existing stations in order to promote adoption of standardized protocols. Most existing stations were started for reasons other than population monitoring, and often, relatively little would be needed to convince operators to upgrade their efforts so that results will be suitable for trend analysis. Establishment of new stations by enthusiasts should also be encouraged (especially in areas with little coverage, such as the southeastern US). However, until we learn more about the number and distribution of stations required to generate trends for particular breeding populations, large amounts of money should probably not be directed towards establishing a lot of new, professionally-run monitoring stations, unless they are justified by collection of data that will be useful as well for other purposes (e.g., collection of data on age ratios, stopover ecology, habitat use, etc.).

Literature Cited


