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Extracting Long-Term Patterns of Population Changes from Sporadic Counts of Migrant Birds

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Declines of many North American birds are of conservation concern. Monitoring their population changes has largely depended on formally structured Breeding Bird Surveys, and Migration Monitoring Stations, although some use has been made of lists by birders. For almost 40 years, birders have kept daily counts of migrant landbirds during visits to Seal Island, off Nova Scotia’s south tip. Here we present results for several common migrants using day-counts made between August 15 and November 15. Most existing analyses have used linear models to extract trends and other variables from such long-term data sets. Instead we applied Generalized Additive Models (GAMs) to extract the continuous trend functions and patterns of influence of observer number, wind speed, wind direction on count nights and prior nights, and moon phase. The results suggest that GAMs are a powerful way of dealing with such “noisy” data of the sort collected by birders in their recreational pursuits. In addition, it is possible to analyse groups of species (related taxonomically or ecologically) simultaneously with the potential of determining overall more general trends.

Keywords: Seal Island, Generalized additive models, Count data, Overdispersion.
INTRODUCTION

Declines of many North American bird populations are of conservation concern. Effort-standardized Breeding Bird Surveys (BBS) are the most established method of monitoring these population trends, and are readily available at http://www.mbr-pwrc.usgs.gov/bbs/genintro.html. These are seasonally restricted, incorporate local population changes due to roadside habitat changes (in both ambient sound levels and vegetation), and they undersample remote regions, especially in northern Canada, where many migrant species predominately nest. Accordingly, a variety of methods have been used to estimate population trends from long-term counts made during migration seasons. These time series range in quality from counts of birds captured at specific banding stations by effort-standardized nets (Lloyd-Evans and Atwood, 2004) or on associated standardized census routes (Dunn et al., 2004), to combined daily counts from many localities and observers (Cyr and Larivée, 1993; Dunn et al., 2001), with all the attendant "noise". Some effort has been made to remove other possible effects in extracting long-term trends from such data. Hussel et al. (1992) were the first to formally include the effects of season (by expressing counts as deviations from average for that date), weather variables, and lunar phase (influencing nocturnal migration) as covariates with year. Others since have followed similar procedures (Dunn et al., 1997, for example). Link and Sauer (1998) later controlled for effort parametrically and more recently (Link and Sauer, 2002; Link et al., 2006) hierarchical models have been proposed to model data from multiple geographic scales. It has also been practice to transform counts (or daily deviations) as log(count + 1).

The statistical techniques proposed in this paper allow us to model population counts using smooth functions of explanatory variables with the smoothness of such functions being estimated as part of the model fitting. We note that Fewster et al. (2000) have also considered models with smooth terms. However, their models include only one smooth function and require that the smoothness of this term be chosen manually. It is not clear that such an approach is even feasible when considering models with multiple smooth functions. Our techniques are applied to analyzing long-term counts using a rich source of data from Seal Island (43 25 N, 66 00 W), about 24 km from the nearest mainland of southern Nova Scotia (Figure 1). The island attracts migrating landbirds from over a wide span of ocean, especially night migrants over the sea at daybreak. Among them are an unusually high proportion of stray birds from afar (McLaren, 1981), which are of course a major attraction for birders. Our intention is not primarily to supply alternative estimates of long-term rates of population change for the small numbers of species we consider, but rather to illustrate some powerful statistical techniques for considering other influences on such estimates.

DATA AND METHODS

The Island and The Counts

Seal Island is small, elongate (ca. 1 X 6 km) and largely covered by dense, often impenetrable, spruce forest, with open areas in the middle and around the periphery. Migrant birds generally concentrate (and are most readily seen and heard) in these open areas and along the edges of the forest, so that counts and estimates of their numbers are readily obtained. Forays on occasional paths into the dense forest generally add little. Visitors arrive on the island via a two-hour boat trip, and use various accommodations. Since 1967, numerous individuals and groups visiting the island have kept daily checklists (accumulated over the years by McLaren) that supply the data used here. Although the island has become seasonally more populous (less so in migration seasons) from addition of housing in a small area designated “Fishermen’s reserve”, the island habitats have not changed markedly over the years, and visiting landbirds presumably lack immediate alternative
destinations. It is thus unlikely that secular changes on the island have had any effect on bird counts over the years.

The field data are counts or estimated numbers of each species recorded during a day by one or more observers on the island during 439 days from August 16 to November 15 between 1971 and 2004 (Figure 2).

Selection of Species

To assess the statistical methodology we selected four common species, well-represented among island migrants (total counts in Table 1), from each of four broadly delineated winter ranges: the Ruby-Crowned Kinglet (*Regulus calendula*) is a short-distance migrant wintering largely in the southern United States; the Cape May Warbler (*Dendroica tigrina*) largely in the Caribbean; the American Redstart (*Setophaga ruticilla*) mostly in Central America; and the Red-eyed Vireo (*Vireo olivaceus*) wintering almost entirely in South America.

We also chose five abundant species (Table 1) that winter largely or entirely within South America to test the usefulness of combining groups of species for inference. These were, in addition to the Red-eyed Vireo, Eastern Kingbird (*Tyrannus tyrannus*), Bay-breasted (*Dendroica castanea*) and Blackpoll (*D. striata*) Warblers, and Bobolink (*Dolichonyx oryzivorus*).

Variables Influencing Counts

Year and Season

The primary aim of our analyses is to extract long-term population changes by using sample year as a variable. Species have different seasonal migration schedules, so count data (entered as days from August 15) must also be considered.

Count Effort

Only counts made during full days on the island were used, unless the observers had arrived very early or departed very late in the day. Weekend trips thus often supplied only one day’s count. Our only measure of daily effort is the number of observers in visiting parties that were competent at identification and enumeration of birds. Parties either stayed together or broke up to varying extents, determined in part by the abundances of birds. The effects on efficiency of coverage of the island are uncertain, but whether separate groups covered different or the same parts of the island, all counts and estimates are of numbers observed on the island as whole. Generally the paths around the perimeter and much of the open central areas (Figure 1) of the island were surveyed, but coverage was sometimes more desultory in poor weather and possibly less complete when there were large numbers of birds. No attempt is (or could be) made to devise more precise measures of daily effort. Thus, the daily numbers represent a large amount of rather "noisy" data.

Weather

The island is close enough to mainland Nova Scotia to reflect migration patterns in the region, but far enough out so that daytime migrants are less likely to use it as a stopover. Much experience by birders on the island indicates that almost all birds, even nominal daytime migrants (except some strong fliers like diurnal raptors) appear in numbers in early morning, and either stay on the island or move off (often from the north end in autumn) during the day. Nighttime wind directions are a known important influence on intensity of migration off Atlantic Canada (Richardson, 1972), and other weather variables, like cloud cover, rain and fog, are strongly associated
with winds (clearer skies with westerlies and northerlies, more fog and rain with easterlies through southerlies). Hourly weather records are available for Yarmouth, some 50 km north of the island, at: http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html. We use wind direction (listed to nearest 10 degrees) at midnight AST as an indication of weather conditions to which night migrants in the region might be subjected. We also use wind speeds from the same source. When wind speeds were registered as zero (thus a null value for wind direction), we entered the available wind directions for the nearest hour to midnight (direction averaged when times before and after midnight were tied). In addition we used a categorical variable to represent the other four states of weather listed in the above website as rain, fog, cloud and clear sky.

Birds arriving on the island may stay for a variable amount of time. This time may be less than the autumn average of about three days in coastal Maine (Morris et al., 1996), as birds caught offshore by day may take corrective movements soon after (Richardson, 1972), and as evident from observations of birds leaving the island by day. Individually identifiable birds, however, have shown that some may stay for days. There is no easy way to remove such “repeats”, but to gauge possible influences of winds on departures and arrivals during previous nights, we include midnight wind directions (but not speeds) at Yarmouth, NS, during the three previous nights.

Lunar Cycle

Moonlight has long been thought to affect arrivals and departures of migrant birds. Some species, e.g. American Woodcock (Scolopax minor) (Krementz et al., 1994), and Sky Lark (Alauda arvensis) (James et al., 2000), evidently migrate coincident with full or waxing moons. Pyle et al. (1993), however, showed that decreased moonlight was associated with higher departure levels at Southeast Farallon Island, off the coast of California, and presumably amplified migration more widely. We test the effect of lunar cycle using date-specific illuminated proportions of the moon obtainable from http://aa.usno.navy.mil/data/docs/MoonFraction.html.

Statistical Analyses

We would like to determine whether a significant trend exists in the number of birds visiting Seal Island over the last 35 years. From a statistical perspective, it is natural to define the response $Y$ as the number of birds (of a certain species) observed on a particular day and attempt to model $Y$ as a function of a collection of explanatory variables thought to influence $Y$. We note that the response $Y$ is nonnegative and as such naturally rules out some of the more standard statistical approaches (e.g. linear models). In addition, with count data of this sort there is often an abundance of zeros, known generally as zero inflation, which must be taken into account in order to make valid statistical inferences.

We start by considering the most common approaches to properly accounting for zero inflation. Barry and Welsh (2002) suggest modelling the data in two steps. First they model the association between the presence and absence of a bird and the covariates. Then, in the second step they model the relationship between abundance and the covariates, conditional on the bird being present. Alternatively, one could consider the zeros and positive counts together using a model that allowed for overdispersion. Preliminary results from both methods lead to similar conclusions. Hence for reasons of efficiency we chose to pursue the latter approach as it did not require the fitting of two separate models. Further details are provided below.
Model Definition

Generalized linear models (GLMs) are an extension of classical linear models. A linear model specifies the (linear) relationship between a response variable \( Y \), and a set of explanatory variables, the \( X \)'s, so that

\[
E(Y) = X\beta
\]

where \( \beta \) is the vector of regression coefficients computed from the data. However, there are many relationships that cannot adequately be summarized by a simple linear equation. For instance, in our situation the response variable \( Y \) is a count and as such is discrete rather than continuous. Furthermore, it may not be reasonable to assume that the effect of the explanatory variables on the response variable is linear. Desirably, the GLM differs from the linear model in two major respects: first, the distribution of the response variable can be (explicitly) non-normal, and does not have to be continuous; second, the response variable values are predicted from a linear combination of explanatory variables, which are connected to the response variable via a link function. To illustrate, in the GLM the expected value of the response variable, \( E(Y) = \mu \) is related to the explanatory variables in the following way

\[
g(\mu) = X\beta
\]

where \( g \) is called the link function. Various link functions (McCullagh and Nelder, 1989) can be chosen, depending on the assumed distribution of the \( Y \) variable. As we are dealing with counts, we assume a Poisson distribution with log link function.

GLMs are fully parametric models. While much flexibility is available through this formulation, with ecological data, responses are often complicated functions of the explanatory variables. Generalized Additive models (GAM) provide an alternative as they are a natural extension of the GLM in that they consider additive predictors of the form

\[
\eqref{gam_predictor} = s(X_1) + \cdots + s(X_k),
\]

where the \( s \) are smooth functions (not necessarily the same at each appearance) of the explanatory variables. These smooth terms give additional flexibility to the model. The use of a nonparametric additive predictor is the major difference between the GAM and the GLM.

GAM models are usually fitted by penalized likelihood maximization, in which the model (negative log) likelihood is modified by the addition of a penalty for each smooth function, penalizing its ‘wiggliness’. To control the tradeoff between penalizing wiggleness and penalizing badness of fit, each penalty is multiplied by an associated smoothing parameter. How to estimate these parameters, and how to practically represent the smooth functions are the main statistical questions introduced by moving from GLMs to GAMs.

Model Implementation

Wood (2004) recently proposed a method for fitting GAMs to data. His method differs from those that have come before it (e.g. Hastie and Tibshirani (1986)) in that the degree of smoothness of model terms is estimated as part of the fitting. Even with small numbers of smooth terms in the model, this approach offers substantial computational savings. Each smooth term is represented using penalized regression splines with smoothing parameters estimated using generalized cross validation (GCV). His method is implemented in the mgcv package for R, a language and environment for statistical computing and graphics available at http://www.r-project.org/.

GCV is a computationally efficient approach for estimating smoothing parameters. It is motivated by first considering ordinary cross validation where one proceeds by leaving one of the data
points out, fitting the model to the remainder and then calculating the squared differences between the left out datum and the fitted model. This procedure is repeated for each data point in the data set and then the average squared difference calculated. This quantity is the ordinary cross validation score. As it turns out, by writing this score as a weighted sum of the model residuals, one does not need to re-fit the model for each left out datum. The GCV score is obtained by replacing all of the individual weights in this summation by the average weight. The reader is referred to Wood and Augustin (2002) for further details. Low values for GCV indicate a good model, while high values suggest a poor model.

GCV is used to estimate the smoothness of model terms, given that the terms are included in the model. However we would also like to judge whether a term should be in the model at all, that is, to perform variable selection. The need to answer this question arises separately because GCV cannot reduce the degrees of freedom of a term all the way to zero. That is, once a term has zero wiggliness, it is not possible to simplify the model by further smoothing parameter changes. Hence, to perform variable selection we proceed by dropping each term from the model in turn, and seeing if this reduces the GCV score relative to the full model. In addition, it is also recommended (Wood and Augustin, 2002) that one examine the confidence bands for the smooth terms. Those whose confidence bands include zero everywhere are natural candidates for removal. What follows is an algorithmic description of our model fitting approach:

1. Fit an initial model including all potential explanatory variables and interactions. All explanatory variables are included nonparametrically with the exception of those which are factors.

2. Examine the estimated degrees of freedom of all nonparametric terms and then refit the model with those close to 1 entering into the model parametrically.

3. Examine the p-values (or the corresponding confidence intervals) of the explanatory variables. Begin by identifying the first potential candidate for removal as that for which the p-value is the largest, and bigger than 0.10, if such a candidate exists.

4. Compare the GCV score for the model with and without the variable identified in the previous step. If the GCV is smaller without the variable, make this model the current one.

5. Repeat the previous two steps until there are no further candidates for removal.

Note that to obtain the p-values required in Step 3 above, a chi-square test, based on an estimated covariance matrix, is used to assess the significance of nonparametric terms (Section 4.8.5 of Wood, 2006).

**Results**

Since our purpose is to test a statistical methodology, here we present the results and at the same time assess their plausibility using what is known of long-term population changes and other characteristics of the selected species. We first give results for four species with distinct wintering ranges (and therefore migration patterns) and then consider a group of five long-distance migrants to South America.
Population Changes of Four Species

To assess the plausibility of population changes, we use the interactive BBS web site (URL above), which permits assessment of long-term trends (Sauer et al., 2005), but not the patterns of population changes, for the period 1966 to 2004. Generally, we use the trends given for the Atlantic Flyway, which combines BBS results for routes in the northeastern U.S.A. and eastern Canada (Newfoundland to Ontario). The BBS results are obtained by fitting a generalized linear model with negative binomial errors. The results are conditional on the count totals for each individual leading to a product of Dirichlet compound multinomials, each with a different overdispersion parameter. Quasi-likelihood methods based on the first two moments are used for each individual Dirichlet compound multinomial to obtain parameter estimates as maximum likelihood is difficult for this model (see Link and Sauer (1997)). We also refer to some BBS trend maps (same URL). Particularly pertinent are recent analyses of captures of birds for banding at the Manomet Bird Observatory (hereafter Manomet), on the central Massachusetts coast. Lloyd-Evans and Atwood (2004), their Table 1, give percent changes (with p-values) of many species at Manomet between the periods 1970-1985 and 1986-2004. This paper provides details of the statistical analysis.

We propose the following model for the four species:

\[
g(\mu) = s(\text{year}) + s(\text{day}) + s(\text{no:obs}) + s(\text{wind}:0) + s(\text{wind}:1) \\
+ s(\text{wind}:2) + s(\text{wind}:3) + s(\text{windspd}) + s(\text{moon}) + \text{factor(\text{sky})}
\]

where \(\mu\) is the expected number of birds observed and the error distribution is assumed to be Poisson. Note that the assumed model is referred to as quasi-poisson as an additional parameter is also included to account for overdispersion. Estimates of this overdispersion parameter ranged from approximately 4 to 10 (such estimates would be expected to be close to 1 were there no overdispersion). The \(s\) terms are smooth functions (to be estimated) of the number of observers present (\text{no:obs}), the wind direction at midnight before the count (\text{wind}:0), the wind direction at midnight the night before (\text{wind}:1), the wind direction at midnight three nights before (\text{wind}:2), the wind speed (\text{windspd}) and the illumination of the moon (\text{moon}). Also included is the categorical factor \text{sky} that contains the levels clear, cloudy, fog and rain. The interpretation of the levels in the model are with respect to the reference: clear sky. All fitted models were found to account for reasonable proportions of variance (adjusted \(R^2\) ranging from .6 to .9), distributed among the (mostly highly significant) variables as reflected in the p-values (Table 2).

Ruby-Crowned Kinglet

The species is a non-migrant or partial migrant in some of its range, but it is very rare in Nova Scotia in winter. It is not known to nest on Seal Island. All smooth variables in the fitted model have highly significant effects, but none of the sky conditions are significant (Table 2). The negative trend on Seal Island agrees with both the BBS and Manomet results (Figure 3). In addition, there are large fluctuations, including evidence of a recent increase in counts. Note that the graph in Figure 3 displays the form of \(s(\text{year})\) as a function of time. Such plots are natural when fitting GAMs (with linear models such plots are redundant as they would simply be straight lines). The corresponding confidence bands are based on Bayesian intervals (Wood and Augustin, 2002).

Cape May Warbler

The species once summered in very small numbers on the island, but has not been found to do so in recent years. All smooth variables in the fitted model have significant effects, but among the sky
conditions, only fog has a significant negative influence (Table 2). The very strong negative trend on Seal Island since 1980 agrees with the non-significant trend at Manomet, but not with the Atlantic Flyway BBS (Figure 4). The dome-shaped pattern on Seal Island may reflect a more regional situation. The Cape May Warbler is well known to respond to outbreaks of Spruce Budworm (Patten and Burger, 1997, for example), and the Seal Island results seem to echo the huge amplitude of the late 1960s to mid-1980s outbreak in New Brunswick (Figure 4). The BBS trend maps indicate strong decreases in New Brunswick, much of Maine, southeastern Quebec, and southern Nova Scotia, with mixed increases and decreases elsewhere.

American Redstart

Of the smooth variables in the fitted model, the wind direction at midnight one day before, the wind speed and moon illumination are not significant effects, nor is rain. All other smooth variables are significant and sky conditions of both cloud and fog have strong negative effects (Table 2). The decline in island counts is matched by the strong trend at Manomet, but not by the non-significant trend in the Atlantic Flyway BBS (Figure 5). The BBS trend maps show declines throughout the Maritime Provinces and eastern Quebec, but mixes of declines and increases throughout the Atlantic Flyway.

Red-eyed Vireo

Rain was the only significant factor (and again positive) (Figure 6; note fine scale and wide confidence intervals) in the model, but all smooth terms were significant (Table 1). The very slight decline on the island may match the weakly significant decline at Manomet, but not the significant increase in the Atlantic Flyway BBS (Figure 6). The BBS trend maps reveal substantial increases throughout eastern Canada and moderate decreases in New England.

Influences of Other Variables

Effects of nighttime winds

Both wind direction and wind speed at midnight just before the counts were made typically have strong effects (Table 2). Distinct positive peaks suggest arrivals from east, northeast or west through northwest, but not from southeast through southwest (Figure 7) (although the pattern for Cape May Warbler is weak and irregular). This may reflect large arrivals of birds from either nearby Nova Scotia or much further from the west to northwest (cf. map of Figure 1). By contrast, only winds from the west to northwest have a strongly positive effect on the Ruby-Crowned Kinglet, suggesting that large arrivals originate from elsewhere than Nova Scotia. The significant effects (Table 2) of wind speed also differ greatly among species (Figure 7). Effects of wind speed on counts of the two warblers and the Red-eyed Vireo are generally weak, with unreliable (wide confidence limits) positive effects of higher speeds. Again in contrast with the other three species, strongly positive influence of high wind speeds on counts of the Kinglet suggests that this tiny species is more often wind-drifted to the island from the west through northwest (as above).

Winds on prior nights (also significant, Table 2) will influence both the arrival on and departure from the island with the result that complex effects are expected. Nevertheless, there are some suggestive patterns (Figure 8), particularly in comparisons with winds on the night immediately before counts (cf. Figure 7). Note, in addition to some peaks similar to those of the night immediately preceding the count day, some prominent peaks occur with southerly winds, perhaps reflecting failure to depart from the island during unfavorable conditions for migration.
Effects of Season

Seasonal effects (first row of Figure 9) are all highly significant (Table 2). Numbers of the early-migrating warblers and the Red-eyed Vireo are, as expected, most common (seasonal influence > 0) from mid-August to early to mid-September and confidence intervals are understandably wide late in the season. The closely fitted early-October peak in numbers of Ruby-Crowned Kinglets and wide confidence intervals earlier in the season are also as expected for this known late fall migrant.

Effects of Number of Observers

The generally positive effects of observer number are as expected, but differences among the four species are suggestive (second row of Figure 9). The Ruby-Crowned Kinglet and Cape May Warbler are boreal species that range over the densely spruce-clad interiors of Seal Island, and may be more efficiently encountered and counted by larger (and more often split) parties. By contrast, American Redstarts and Red-eyed Vireos are attracted to edge habitats with the island’s limited deciduous growth, and accordingly are probably encountered more completely by birders walking around the island’s edges, regardless of party size. This seems reflected in the weaker fits of observer number for these species compared with those for the kinglet and Cape May Warbler (Table 2), and the indications of leveling off with more observers (second row of Figure 9).

Effects of Moon Illumination

The effects of moonlight on the counts of the four species are all highly significant (Table 2), but the actual influences are widely different (third row of Figure 9). The Ruby-Crowned Kinglet differs from the other three in having the strongest positive response to new-moon conditions. The positive effects (although with wide confidence intervals) of moderate to high (but not full) illumination on the two warblers and the Red-eyed Vireo may reflect complex influences of the moon’s visibility on departure decisions by these longer-distance migrants. Unlike a large waning moon, a large waxing moon would not be fully evident until after sunset. Moon phase might be more effectively treated as a circular statistic.

Group Analyses

It is often quite insightful to combine information from several different sources, particularly where data are sparse or where there is interest in seeing whether a common pattern occurs across several species. The combination of data across species can provide more precise estimates if a covariate has a common effect across all the species.

The GAM framework makes combining counts from different bird species quite straightforward. One needs only to include a new factor variable representing bird species along with interactions of this factor with other covariates of interest. Then the significance of the interactions of the bird species with other variables, say year, can be tested. If the interactions are important in the model in terms of reducing the GCV score, then the year effect differs among at least some of the species, and they should not be combined. If the interactions can be dropped, then we have the same yearly pattern for all species differing only by a constant factor.

Although we have reasonable amounts of data for those species analyzed earlier, it is worth illustrating the effects of combining data. To do so, we grouped five species wintering in South America. The model with the “year bird” interaction has a GCV score of 6.68 while the model without the interactions has a GCV score of 7.59. This reduction in GCV score along with the individual plots (Figure 10) are strong evidence that these five species have different year effects.
The year effects from the individual plots and those from the grouped analysis with interactions show considerable similarity (Figure 10). We did further analysis, by grouping Bobolink and Red-Eyed Vireo. The plots of year effect from the individual analysis, grouped with “year bird” interactions and grouped without interactions are shown in Figure 11. For these two species the evidence is less strong that the interactions are significant, with the GCV score only being reduced from 4.64 to 4.60 with the interactions, and patterns for the individual and the grouped plot with no interaction are similar but with tighter confidence bounds for the latter.

**DISCUSSION**

The great virtues of GAMs in thinking about count data are the continuous patterns of biological and environmental influences that may be revealed. Trends in long-term census data for many birds have been widely discussed and attributed, and we have shown that trends in our few examples are in general agreement with what can be demonstrated from other long-term census results. Other factors that have been previously assessed based on coefficients from regressions may have more complex continuous characteristics. For example, the effects of effort on census results may, as in our examples, be non-linear. Such variables should be readily assessed for many other data sets. The results might not only improve our analyses of existing long-term population data, but also serve as a guide for optimizing the circumstances (weather, observer effort, etc.) for obtaining better data in future.

Of greatest interest may be the fluctuations in population trends, which cannot be revealed in standard regressions or GLMs. Our aim here has been to demonstrate a technique that can detect such short-term changes, like the significant ones in the Ruby-Crowned Kinglet (as indicated by confidence intervals in Figure 3). This may open up opportunities for comparisons among different times series and search for common biological and environmental causes. In addition, our framework enables one to combine data from several sources (when appropriate) which may also prove quite useful in this context.

Regardless of the method used to determine trends, there is great value in publishing trend statistics. However, there are different statistical and biological issues that need to be resolved if trends from separate migration counts are to be pooled into regional or national trends. This is certainly a direction of further research.

**ACKNOWLEDGEMENTS**

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**LITERATURE CITED**


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Table 1: Total yearly counts for eight common species visiting Seal Island, Nova Scotia.

<table>
<thead>
<tr>
<th>Year</th>
<th>Ruby-Crowned Kinglet</th>
<th>Cape May Warbler</th>
<th>American Redstart</th>
<th>Red-Eyed Vireo</th>
<th>Eastern Kingbird</th>
<th>Bay-Breasted Warbler</th>
<th>Blackpoll Warbler</th>
<th>Bobolink</th>
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Table 2: Estimates (for parametric components only) and p-values for GAM model fits.

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FIGURE CAPTIONS

Figure 1. Location and characteristics of Seal Island, Nova Scotia. Permanent ponds on the island are outlined and the stippled areas are densely forested.

Figure 2. Days during which counts were recorded on Seal Island by year and season.

Figure 3. Population changes of the Ruby-Crowned Kinglet from Seal Island data compared with other sources.

Figure 4. Population changes of the Cape May Warbler from Seal Island data compared with other sources. The inset portrays the outbreak of Spruce Budworm (Egg mass density) in the 1970s to mid 1980s.

Figure 5. Population changes of the American Redstart from Seal Island data compared with other sources.

Figure 6. Population changes of the Red-eyed Vireo from Seal Island data compared with other sources.

Figure 7. Effects of wind direction (top panels) and speed (bottom panels) at midnight (at Yarmouth, NS) immediately prior to count days on counts of four species on Seal Island. The large confidence bands for wind speed are due to a small number of observations of high wind speeds.

Figure 8. Effects of wind directions at midnight (at Yarmouth, NS) one (top panels), two (middle panels) and three (bottom panels) days prior to count days on counts of four species on Seal Island.

Figure 9. Effects of season (first row), efforts (second row), and moon phase (third row) on counts of four species of birds on Seal Island, NS.

Figure 10. Analysis of a group of five species wintering in South America. Year effects from the individual fits (first row) are shown along with those from the grouped analysis (second row). Following are the year effects from the individual fits (third row) and those from the grouped analysis (last row), both of these latter results are based on the presumption that there is no overdispersion.

Figure 11. Analysis of the Bobolink and Red-Eyed Vireo. Shown are results from the individual fits (top panels), grouped analysis with interactions (middle panels) and grouped analysis without interactions (bottom panels).
Fig. 1:
Fig. 2:
Atlantic Flyway BBS trend, 1966-2004, -1.62, p<.001

Atlantic Flyway BBS trend, 1963-2004, +.69, p=.640
Fig. 5:
Atlantic Flyway BBS trend, 1966-2004, -.69, 
p=.690
Manomet Bird Observatory trend, 1970-85
versus 1986-2001, -55%, p<.001

Fig. 6:
Atlantic Flyway BBS trend, 1966-2004, +1.48, 
p<0.001
Manomet Bird Observatory trend, 1970-85
versus 1986-2001, -34%, p<.05
Fig. 7:

Ruby-Crowned Kinglet  Cape May Warbler  American Redstart  Red-Eyed Vireo

Fig. 8:

Ruby-Crowned Kinglet  Cape May Warbler  American Redstart  Red-Eyed Vireo
Fig. 9:

Ruby-Crowned Kinglet  Cape May Warbler  American Redstart  Red-Eyed Vireo

Fig. 10:

Eastern Kingbird  Bay-br. Warbler  Blackpoll Warbler  Bobolink  Red-Eyed Vireo
Fig. 11:

Bobolink

Red-Eyed Vireo
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