Extracting long-term patterns of population changes from sporadic counts of migrant birds

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SUMMARY
Declines of many North American birds are of conservation concern. For almost 40 years, experienced birders have kept daily counts of migrant landbirds during visits to Seal and Brier Islands, both of which are off Nova Scotia’s southern tip. Here we assess the utility of Generalized Additive Models (GAMs) to extract patterns of population change of a common migrant to Seal Island, the Ruby-crowned Kinglet, while controlling for other influences including season, weather and effort. We also demonstrate, using counts of the Kinglet from Brier Island as well as counts of another common migrant, the Yellow-rumped Warbler, how our GAM methods can combine data from different geographic areas or distinct species. Most existing analyses of similar long-term data sets have used linear models to estimate trends. Our results and comparisons suggest that GAMs are a powerful way of extracting more information from such data. Copyright © 2009 John Wiley & Sons, Ltd.

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1. INTRODUCTION
Declines of many North American bird populations are of conservation concern. In this paper, we propose a technique for estimating long-term patterns of population change when there are many sources of variability present. Our technique is applied to the analysis of almost 40 years of data collected on Seal Island (43 25 N, 66 00 W), about 24 km from the nearest mainland of southern Nova Scotia and on Brier Island (44 16 N, 66 22 W). These islands are renowned as stopover sites for migrating landbirds (McLaren, 1981).

The traditional sources for obtaining population trends in North America are standardized Breeding Bird Surveys (BBS) (Sauer et al., 2007) and less formal Christmas Bird Counts of winter residents (http://www.audubon.org/bird/cbc/index.html). A variety of methods have also been used to estimate
linear trends in populations of birds from long-term counts made during migration seasons. These 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). Some efforts have been made to remove some sources of variability in such data in order to identify whether or not long term trends actually exist. Typically these sources of variability are referred to as explanatory variables and include such effects as season, wind direction, to name just a few. Hussel et al. (1992) were the first to attempt to formally model the effects of season, weather variables, and lunar phase (influencing nocturnal migration) along 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 locations. One of the limitations of these approaches has been the necessity to model the relationship between the response and the covariates by a simple parametric function, typically a straight line.

The statistical techniques proposed in this paper make available some new methodology for modelling population counts that allows for more complex relationships between the response and explanatory variables. Such smooth functions are estimated as part of the model fitting. We note that LOESS has been used to depict graphical output of BBS and to estimate trends (Peterjohn et al., 1997). We also note that Fewster et al. (2000) have considered models with smooth functions. However, their models include only one smooth function (for the bird censuses themselves) and choose the smoothness of this term manually. It is not clear that manual smoothing is even feasible for models that are comprised of multiple covariates requiring multiple smooth functions.

In this paper we first demonstrate our methodology by extracting patterns of long-term population change for the Ruby-crowned Kinglet (Regulus calendula) using counts from Seal Island. Our results show that Generalized Additive Models (GAMs) are a powerful way of using count data to reveal complex patterns of population change while controlling for other potentially nonlinear influences. Next we present two further examples, the first simultaneously analysing data on Ruby-crowned Kinglet from both Seal and Brier Islands and the second using data on another common migrant, the Yellow-rumped Warbler (Dendroica coronata). These latter analyses demonstrate how our methods can be used to simultaneously model data from different sources and illustrate the types of novel conclusions that may result.

2. DATA AND METHODS

2.1. The islands and the counts

Seal Island is small, elongate (ca. 1 km × 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 of their numbers are readily obtained. Since 1967, numerous individuals and groups visiting the island have kept daily counts of each species (accumulated since 1970 by McLaren) that supply the data used here. Although the island has become seasonally more populous (less so in migration seasons) following the addition of housing in a small area designated ‘Fishermen’s reserve’, the island habitats have not changed markedly over the years. It is thus unlikely that secular changes on the island have had any effect on bird counts over the years.

Brier Island, the westernmost point of Nova Scotia, is somewhat larger (ca. 3 km × 7 km) and permanently settled only along its northern shore. Much of it has remained unchanged and about one-third is a nature reserve.

The data from Seal Island are counts of each species recorded during a day by one observer or a party on the island during 439 days from 16 August to 15 November between 1971 and 2007 (Figure 1). The data from Brier Island are counts by a single observer on 141 days during the same season and span of years, again see Figure 1.
To assess the statistical methodology we initially selected the Ruby-crowned Kinglet, as an abundant short-distance migrant on the island that winters largely in the southern United States.

2.2. Variables of interest

To determine the pattern of population change in the Ruby Crowned Kinglet using counts from Seal Island, we have to remove the effects of other explanatory variables. These include effort, weather and lunar cycle.

Effort is measured by the number of competent observers in visiting parties that were identifying and enumerating birds. Only counts made during full days on the island, between 16 August and 15 November, were used. All counts are of numbers observed on the island as a whole. When multiple observers were present a consensus on counts was reached by the party.

Seal Island is close enough to mainland Nova Scotia to reflect migration patterns in the region, but far enough away that daytime migrants are not likely to use it as a stopover. Observations by birders on the islands indicate that almost all birds, including the Ruby-crowned Kinglet and Yellow-rumped Warbler appear in numbers in early morning, and either stay on the island or move off (often northward) during the day. Nighttime wind directions are a known important influence on intensity of full 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°) and wind speed at midnight AST as an indication of weather conditions to which night migrants in the region are subjected. 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 intervals before and after midnight were tied). In addition we used a categorical variable to represent the other four states of weather listed more completely in the above website as rain (rain, showers), fog, cloud (cloudy, mostly cloudy), and clear (clear, mostly clear) sky. We note that the wind effects may be less on Brier Island than Seal Island due to the close proximity of the mainland to the former.

The time that birds stay on the islands varies and appears to be less than the autumn average of about 3 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 islands by day. Individually identifiable rare birds have, however, been shown to stay one to many days. There is no easy way to remove such ‘repeats’ among common species, 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.

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.
3. STATISTICAL METHODOLOGY

In general, we would like to estimate patterns of population change while taking into account other important variables influencing one species at one location, one species at several locations or several species at a location. 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). A common approach would be to transform the response in the logarithmic scale, but more appropriate alternatives exist using generalized (linear or additive) models. In addition, with count data of this sort there is often an issue known generally as ‘excess of zeros’, 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 ‘excess of zeros’. Barry and Welsh (2002) suggest modelling the data in two steps (non parametrically). First they model the association between the presence and absence of a bird and the covariates. Then they model the relationship between abundance and the covariates, conditional on the bird being present. Alternatively, if ‘excess of zeros’ is mild, one could consider the zeros and positive counts together using a model that allows for overdispersion. For our dataset, preliminary results from both methods led 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.

3.1. Model definition

GAMs consider additive predictors of the form

\[
g(\mu) = s(X_1) + \cdots + s(X_k)
\]  

where the \( s \) are smooth functions (not necessarily the same at each appearance) of the explanatory variables, the \( X \)'s, and \( g \) is the logarithmic link function relating the expected value of \( Y \) and \( \mu \) to the \( X \)'s. Various link functions (McCullagh and Nelder, 1989) can be chosen, depending on the assumed distribution of the response variable, \( Y \). As we are dealing with counts, we assume a Poisson distribution with log link function. The smooth terms \( s \) give additional flexibility to the model. The use of a nonparametric additive predictor is the major difference between the GAM and the Generalized Linear Model (GLM).

GAMs 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 wiggliness 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. A fitted model is usually presented using a series of plots depicting the estimated functions \( s(X_i) \) (see e.g. Figure 2) and the corresponding pointwise confidence bands based on Bayesian intervals (Wood and Augustin, 2002). As such, the behaviour of these nonparametric functions cannot be adequately summarized by a single coefficient (a slope, for instance), as in a parametric analysis. In GLMs (or linear models) equivalent plots would represent straight lines and are almost never depicted. Also, if one wants to compare the effect on the estimated average \( \hat{\mu} \) of a particular change (let’s say \( x_i^L - x_i^U \)) in one covariate \( x_i \) while keeping the other variables fixed, this can be done by computing...
the multiplicative factor \( \exp(s_i(x^T_i)) / \exp(s_i(x^T_j)) \). Note, however, that the estimated functions are not restricted to be monotonic as in (generalized) linear modelling, and accordingly pointwise comparison just described has to be interpreted carefully. In summary, GAMs allow us to see entire patterns, which is particularly useful when the patterns are inherently complex.

3.2. Model implementation

Wood (2004) recently proposed a method for fitting GAMs to data. His method differs from earlier attempts (e.g. Hastie and Tibshirani, 1986) in that the degree of smoothness of model terms is estimated as a 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). The Wood (2004) method is implemented in the mgcv package for R: a language and environment for statistical computing available at http://www.r-project.org/. GCV is a computationally efficient approach to address problems where an estimate of prediction error to be minimized needs to be defined. It is based on cross-validation
where one mimics the existence of a construction and a validation sample by leaving one of the data points out, fitting the model and then looking at the error made in predicting the omitted point by calculating the squared difference between the left-out datum and the prediction from the fitted model. This procedure is repeated for each data point of the sample and then the average squared difference is calculated. This quantity is the ordinary cross validation score. It can be shown, by writing this score as a weighted sum of the model residuals, that the model does not need to be re-fit for each left-out datum. The GCV score is obtained by replacing all of the individual weights in this summation by the average weight; Wood and Augustin (2002) give further details. Low values for GCV indicate a small prediction error.

In our context, GCV is used for two different purposes: smoothness parameter choice and variable selection. For the first purpose, GCV is directly implemented in the fitted method (Wood, 2004) and minimized with respect to the smoothness parameters. For variable selection, that is to determine whether a term should be added to the model at all, we proceed by removing 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 should examine the confidence bands for the smooth terms. Those with confidence bands that include zero everywhere are natural candidates for removal. What follows is an algorithmic description of our model fitting approach inspired by Wood and Augustin:

1. Fit an initial model including all potential explanatory variables and interactions. All explanatory variables are included nonparametrically with the exception of those that are factors.
2. Examine the estimated degrees of freedom of all nonparametric terms and then re-fit the model with those close to 1 entered 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 for example 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 $\chi^2$-test, based on an estimated covariance matrix, is used to assess the significance of nonparametric terms (Section 4.8.5 of Wood, 2006). As a result the p-values are approximate and hence we use the GCV score to make a final decision.

4. RESULTS

Since our purpose is to propose a statistical methodology for dealing with sporadic counts of migrant birds, 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 Ruby-crowned Kinglet.

4.1. Pattern of population change

We propose the following model:

$$g(\mu) = s(\text{year}) + s(\text{day}) + s(\text{no.\,obs}) + s(\text{wind.}0) + s(\text{wind.}1) + s(\text{wind.}2) + s(\text{wind.}3) + s(\text{windspd}) + s(\text{moon}) + \text{factor(sky)}$$
where $\mu$ is the expected number of birds observed and the distribution of $Y$ is assumed to be Poisson. In addition, we allow for an additional parameter to account for overdispersion. With such a modification the model is referred to as quasi-Poisson. This overdispersion parameter was estimated to be 11.88 (such an estimate would be expected to be close to 1 when there is no overdispersion). The $s$ terms are smooth functions (to be estimated) of the year (year), the particular day of the fall migration period (day), the number of observers producing the counts (no.obs), wind direction at midnight before the count (wind.0), wind direction at midnight the night before the count (wind.1), wind direction at midnight two nights before (wind.2), wind direction at midnight three nights before (wind.3), the wind speed (windspd) and the illumination of the moon (moon). Also included is the categorical factor sky that contains the levels clear, cloudy, fog and rain. The interpretation of the levels in the model is with respect to the reference: clear sky. The fitted model was found to account for a reasonable proportion of variance (adjusted $R^2$ was 0.72), distributed among the most highly significant variables. All smooth variables in the fitted model have highly significant effects, but none of the sky conditions are significant (at the $\alpha = 0.05$ level).

As stated earlier, our primary interest is in determining whether there is significant evidence of change in the population of Ruby-crowned Kinglet visiting Seal Island as part of their fall migration. The top left-hand plot in Figure 2 suggests a generally decreasing number of counts with year. More importantly, though decreasing overall, the population level does appear to fluctuate in a somewhat cyclical manner as evidenced from the shape of the nonparametric curve and further substantiated by the corresponding confidence intervals. To conclude only that the population is decreasing would certainly present an oversimplification.

As one means of assessing the plausibility of our conclusion that there has been a generally decreasing population of Ruby-crowned Kinglet visiting Seal Island, we use the interactive BBS web site (http://www.mbr-pwrc.usgs.gov/bbs), which permits assessment of long-term linear trends (Sauer et al., 2007), and depicts patterns of population changes graphically, for the period 1966–2004. We find that the slope estimate ($-1.2, p$-value $= 0.00$) for the Atlantic Northern Forest, which combines BBS results for survey routes in the northeastern U.S.A. and eastern Canada (Newfoundland to Ontario) supports our conclusion. See Link and Sauer (1997) for further details of how this estimate was obtained.

4.2. Influences of other variables

Figure 2 indicates that both wind direction and wind speed at midnight before the counts were made have strong effects. Winds from the west to northwest have a strongly positive effect on the counts of the Ruby-crowned Kinglet, suggesting that large arrivals originated from elsewhere than Nova Scotia. In addition, the 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.

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

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.
The generally positive effects of number of observers are as expected. The Ruby-crowned Kinglet is a boreal species that ranges over the densely spruce-clad interiors of Seal Island, and may be more efficiently encountered and counted by larger (and more often split) parties.

The effects of moonlight is highly significant and the Ruby-crowned Kinglet has an extremely positive response to new-moon conditions.

4.3. Combining count data from other sources

The GAM framework has the desirable flexibility for simultaneously modelling data from multiple sources. To illustrate, we now include in our model counts of the Ruby-crowned Kinglet obtained from Brier Island by introducing both a factor (for island) as well as interaction terms (year by island). This makes it possible to see if there are differences in behaviours on the two islands. The final models discussed below were again selected on the basis of the algorithm described earlier.

As before smooth functions of day, effort, wind direction, windspeed and lunar cycle all have highly significant effects. The categorical factor sky is again not significant. In Figure 3 we present the 2 year by island interaction terms, both of which are highly significant. One can see a similar decreasing pattern in the population of Ruby-crowned Kinglet returning to both islands over the years with that of Brier Island noticeably less cyclical in nature.

Again, for sake of illustration we now combine data on another species (rather than data from another location as above). Specifically we wish to determine whether the Yellow Rumped Warbler population behaves similarly to that of the Ruby-crowned Kinglet. Here we find the year by bird interactions significant with the resulting smooth functions as shown in Figure 4. Again, there appears to be a generally decreasing trend in the two bird populations over time but that of Ruby-crowned Kinglet (left) seems to fluctuate more extremely. Interestingly, both species show similar patterns of peaks and troughs, much more extreme in the Ruby-crowned Kinglet.
5. DISCUSSION

The great virtue of the GAM approach to count data is the potential to reveal complex patterns of biological and environmental influences. 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 more completely described by smooth functions, with their slopes being in general agreement with what has been demonstrated from other long-term census results. Other factors that have been previously assessed from regression coefficients may have more complex continuous characteristics. For example, the effects of effort on census results may, as in our examples, be nonlinear. 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 patterns which cannot be revealed in standard regressions or GLMs. One 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 2). This may open up opportunities for comparisons among different time series and search for common biological and environmental causes. In addition, the GAM framework permits combining appropriate data from several sources, which may also prove quite useful for seeking common causes.

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

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