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Estimating Relative Abundance From Count Data

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Abstract: Much of the available information on large-scale patterns of animal abundance is based on count surveys. The data provided by such surveys are often influenced by nuisance factors affecting the numbers of animals counted, but unrelated to population size. Temporal and spatial patterns in nuisance factors may exist, causing simple summaries of counts to give a misleading view of patterns in population size. We develop models for count data that allows the incorporation of such factors, and describe methods for estimating spatial patterns of relative abundance from counts. We carry out spatial analyses of North American Breeding Bird Survey data, in which observer ability is a nuisance parameter nested within sites. In light of evidence that new observers tend to count more birds than the observers they replace, we model observer ability as a random effect with mean depending on observer initiation year.

Keywords: Animal Abundance, Counts, North American Breeding Bird Survey.

1 Introduction

Many large-scale surveys of animal populations provide counts of individuals observed, rather than complete enumerations (censuses) of population sizes at sample locations. Count data thus obtained are imperfect representations of population sizes: it is almost always the case that some of the variation in counts reflects the effect of variables not related to population size. Examples of such "nuisance variables" are effort expended in counting, observer ability, and method of observation; changes in any of these can have qualitatively predictable results. Since most analyses of count data are carried out with the goal of examining temporal or spatial patterns in population size, it is important to examine the possibility that patterns in nuisance variables create (or mask) patterns of change in the populations under consideration.

The North American Breeding Bird Survey (BBS, see Robbins et al., 1986, Peterjohn, 1994, or Peterjohn et al., 1995) provides an excellent example of pattern in nuisance variables. BBS counts are collected annually along roadside routes by highly skilled observers; observer changes and missing values are prominent features of the data. Evidence has been found of trend in the basic competence of the pool of observers (see Sauer et al., 1994, or Link and Sauer, 1997). This feature of the BBS has profound implications for analyses of temporal patterns of population change from its data: patterns of change in raw counts may provide a biased view of patterns of change in population size. Link and Sauer (1994, 1997) and James et al. (1996) provided analytical methods of controlling for differences among observers in analyses of temporal patterns.

In this paper our focus is on the analysis of spatial, rather than temporal, patterns in count data. Analysis of spatial pattern is of considerable importance in landscape ecology (see Maurer, 1994); increasing use of Geographic Information Systems in ecology and conservation has created a need for spatial information on species abundance at a variety of scales. Many investigators have used count-based surveys such as the BBS to meet this need. Controlling for nuisance variables in these analyses is a considerably more challenging task than in analyses of temporal change, requiring a careful statement of model and assumptions. We describe models relating counts to population size, and discuss design and analysis considerations for count survey data. The use of these models is illustrated in an applications to BBS data.

2 Parametric Description of Count Data

2.1 Parameters Describing Population Patterns

Surveys producing counts at a collection of fixed sites implicitly assume the existence of local populations, or, alternatively, of locally homogeneous population densities that the counts are intended to reflect. Neither formulation may be wholly satisfactory when examined closely, since typically it cannot be assumed that a closed population exists at a survey site, or that population density is homogeneous. One way or another, however, the analyst of count data needs to distinguish effects on counts that are of biological relevance from effects relating simply to the collection of data. To this end, we formally posit the existence of a local population associated with each count; the population associated with site *i* on the *j*th sampling occasion, t_j, is of size N_{ij}. Note that temporal change in population must be included in models for spatial change when considering series of counts through time: geographic pattern in temporal population change must be properly accounted for in spatial analyses.

We treat each site's collections of population sizes as a single realization of a stochastic process, with parameters defined in terms of the expectations

$$\log\{E(N_{ij})\} = \theta_i + f_i(t_j) \quad ; \tag{1}$$

the only restriction placed on the model at this point is that $f_i(t_1) = 0$. We describe the *population trajectory*, $\exp\{f_i(t)\}$, and the *baseline abundance*, $\exp(\theta_i)$, and their relations to counts in the remainder of this section.

The trajectory can be thought of as a scaled and (possibly) smoothed version of the collection of population sizes through time. The trajectory is scaled in that $f_i(t_1) = 0$, whence θ_i is the logarithm of the expected population size at time t_1, and from which also it follows that $\exp\{f_i(t)\}$ denotes the proportional change in population size over the interval $[t_1, t)$.

The smoothing referred to relates to the stochastic nature of population sizes; even if population sizes generally follow a specific pattern of change (such as a straight line on the log scale), there is residual variation in population sizes that is not accounted for by the specification. (This component of variation is frequently overlooked in trend analyses, with serious consequences in analyses requiring estimates of variances, such as power calculations.) Here, we do not explicitly discuss the degree of smoothing, leaving this as an unspecified component of the variance-covariance structure of the stochastic process N_{ij}. However, we note that the definition of trajectory is flexible enough to allow for "year-effects" models in which for each i and each $t_j \quad t_1$, the value of $f_i(t_j)$ is a distinct, unrestricted parameter; in this case, no smoothing is incorporated in the model. Our emphasis in this paper is on estimation of indices to θ_i, supposing a specific form for the trajectory has been selected; this specification is typically determined by the amount of replication available in count data, the number of observations, and on assumptions of what are biologically reasonable patterns of population change (see Link and Sauer, 1997).

2.2 Parameters for the Relation Between Counts and Population Sizes

Analyses of count data require assumptions relating expected values of counts, Y_{ij}, to the expected values of the population sizes, N_{ij}. Such assumptions can be expressed in terms of the *count-proportion*, which we define as the ratio of expected values of count and population size; we use the symbol λ to denote the logarithm of the count-proportion, viz.,

$$\lambda_{ij} = \log\left\{ E(Y_{ij}) \,/\, E(N_{ij}) \right\} \; . \tag{2}$$

From (1) and (2) it follows that a loglinear model can be written for the counts, namely

$$\log(\mu_{ij}) = \theta_i + \lambda_{ij} + f_i(t_j) \; , \tag{3}$$

where $\mu_{ij} = E(Y_{ij})$.

To this point we have imposed no model constraints, except that $f_i(t_1) = 0$. Thus equation (3) allows a distinct count-proportion for each observation, and there are more parameters than observations. For count data to be useful, we must be able to impose reasonable model assumptions reducing the number of parameters relating to count rate. Without these, the log-trajectories $f_i(t)$ and log-abundances θ_i are not estimable. The natural place to look to impose constraints on the parameterization is at the model specification governing count-proportion; indeed, standardization of count survey protocols is intended to make this possible.

We begin with a general class of models for the count-proportion, given by the specification

$$\lambda_{ij} = \delta_{j(i)} + h\left(\xi_{ij}\right) . \tag{4}$$

Here, $\delta_{j(i)}$ is a "site-specific classification variable" (a factor, nested within sites), and $h(\xi)$ is a "count adjustment" (a parametric function describing the effect of observable covariables ξ_{ij} on expected count rates). Parameters governing the count adjustment are assumed to be constant across sites. Substituting (4) in (3) yields a loglinear model,

$$\log(\mu_{ij}) = \theta_i + \delta_{j(i)} + h\left(\xi_{ij}\right) + f_i(t_j) , \tag{5}$$

which will serve as the basis of our subsequent discussion.

2.3 Models with Constant Count-proportions

The most simple model for count data supposes that $\lambda_{ij} \equiv \lambda$ is a constant across sites, and through time. Thus the count-proportion is constant; no pattern is to be found in the count-proportion either through time or space. This assumption is clearly unreasonable, and is rarely explicitly stated, though it is implicit to many analyses (including any analysis in which unadjusted average counts are used as surrogates for local abundance).

Despite its limited usefulness in practice, this particular model assumption is interesting as a starting point for discussion of the use of count data. Substituting $\lambda_{ij} \equiv \lambda$ in (3) yields the model

$$\log(\mu_{ij}) = \theta_i + \lambda + f_i(t_j)$$

which is indistinguishable from

$$\log(\mu_{ij}) = \theta_i^* + \lambda^* + f_i(t_j) ,$$

where $\lambda^* = \lambda + c$, $\theta_i^* = \theta_i - c$, and c is some constant. Simply put, count data alone provide no information about the count-proportion, and hence virtually no information about the actual abundances; a count of 5 birds may represent a population of 20 birds and a 25% count rate, or it may represent a population of 50 birds, and a 10% count rate.

Given sufficient data, we *can* estimate $q_i = \theta_i + \lambda$. Since it is assumed that λ is constant across sites, the q's for sites *i* and *k* can be combined as

$$\exp(q_i - q_k) = \exp(\theta_i - \theta_k) = \frac{\exp(\theta_i)}{\exp(\theta_k)}$$

to obtain indices of relative population size. Without reliable estimates of the count-proportion, or unless it is reasonable to make even more stringent model assumptions (such as $\lambda_{ij} \equiv 0$), actual abundances are not estimable. Instead, our goal must be to define and estimate indices of the form $q_i = \theta_i + \mu$, where μ is a constant across sites; these indices can be used to estimate relative abundances, as we have here. We illustrate this in the following examples.

2.4 Count Adjustments

In another large-scale survey, the Christmas Bird Count (CBC, see Bock and Root, 1981), the number of observers and duration of count vary among sites and through time. Associated with each count is an effort covariable, ξ_{ij}; it is usually assumed that this is the only source of variation in the count-proportion. Thus equation (5) becomes

$$\log(\mu_{ij}) = \theta_i + h(\xi_{ij}) + f_i(t_j) \ . \tag{6}$$

Typically, it is supposed that $h(\xi)$ is a member of some specific parametric family of functions; one might assume, for instance, that

$$h(\xi) = \alpha - \beta/\xi \ , \tag{7}$$

or perhaps that

$$h(\xi) = \gamma + \theta\xi \ , \tag{8}$$

where α, β, γ, and θ are parameters, and ξ is the effort level [Butcher and McCulloch 1990 use a third alternative, $h(\xi) = \chi + \psi \log(\xi)$]. In any case, the constant term is not estimable, but as noted above must be absorbed into the constant term of an index $q_i = \mu + \theta_i$, where μ is some constant. In the case of assumption (7), for instance, the loglinear model is written as

$$\log(\mu_{ij}) = q_i - \beta/\xi_{ij} + f_i(t_j) \ , \tag{9}$$

where $q_i = \alpha + \theta_i$.

Ideally, the design of count surveys should make effort adjustments unnecessary. The problem is that the selection of a specific parametric form for the adjustments can have substantial effects on the estimates of trajectories and relative abundances. Furthermore, it may be difficult to decide which of several candidate forms for the adjustment is most appropriate.

For example, choosing between (7) and (8) may be difficult or impossible, as illustrated by Figure 1; if most of the "efforts" ξ_{ij} are in the range where the two curves agree, the choice will require enormous data resources. The effect of the choice can, however, be substantial for those few observations with extreme values of ξ_{ij}. Thus the reliability of the estimated trajectory and relative abundances may depend heavily on a fairly arbitrary model selection.

Some types of count adjustment are more easily specified. For example, BBS coordinators postulated that observers count fewer birds and species in their first year of service in consequence of a need to familiarize themselves with their survey routes and with survey protocols. Evidence of such an effect has been found in several studies (see Kendall et al., 1996, or Link and Sauer, 1997), suggesting BBS data be analyzed with the inclusion of a count adjustment

$$h(\xi_{ij}) = \Delta\xi_{ij} \ ; \tag{10}$$

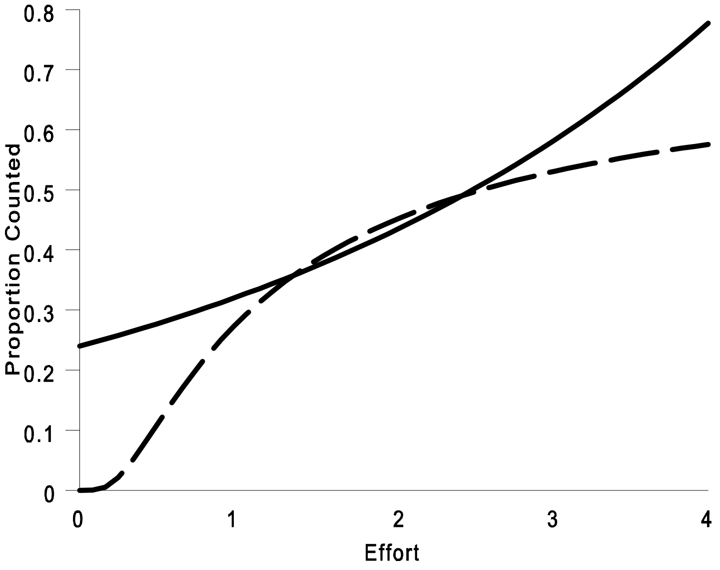

Figure 1: Graphs of candidate parametric functions representing the effect of effort on counts. Dashed curve is $f(\xi) = \exp(-0.30 - 1/\xi)$; solid curve is $f(\xi) = \exp(-1.44 + 0.30\xi)$.

here ξ_{ij} is a binary variable, equal to 1 if the *j*th count at site *i* was made by a new observer and zero otherwise, and $100(1-\Delta)\%$ is the percentage undercount associated with an observer's first year of service.

The difference between the two count adjustments here presented can be best described in the language of linear models: the first example involved a parametric function of a continuous variable (effort), the second consisted of a discrete variable or factor (first year of observation). The common feature of these covariables is that parameters describing their effects are assumed constant across sites. We recommend that surveys to produce count data be designed so as to minimize the need for count adjustments, especially those described by continuous variables, which can require fairly arbitrary selection of model components.

2.5 Site-specific Classification Variables

The model (4) for the count-proportion allows for the possibility of "site-specific classification variables"; in the language of linear models, these relate to factors that are nested within sites. For example, BBS data are naturally classified by observer, and since relatively few observers provide counts on two or more routes, these observer effects must be modeled as site-specific. Another example of site-specific classification variables is to be found in aerial surveys: aerial surveys that switch between using fixed-wing aircraft and helicopters can be anticipated to produce data at two distinct levels of count-proportion; if the effect of the change in protocol varies among sites, these effects must be modeled as site-specific classification variables.

In these cases the count-proportion can be modeled by $\lambda_{ij} = \delta_{j(i)}$; the subscript $j(i)$ denotes the classification corresponding to the jth count at site i. For the BBS, $j(i)$ denotes the observer that produced the jth count at site i.

Site-specific classification variables are less problematic than covariables requiring a continuous count adjustment, at least with regard to analyses of temporal change. A discrete classification can be thought of as a "blocking" variable for the analysis of trajectories: counts with the same classification are homogeneous with respect to an irrelevant source of variation, but parameters governing the trajectory are shared among classification groups. Trajectories can be estimated using the pattern of change within classification groups, with the specification that the parameters governing the pattern of change are the same among classification groups. Examples of this approach include the NSRR analysis of James et al. (1996) and the overdispersed multinomial analysis of Link and Sauer (1997). Thus the potential problem of model misspecification that arises in analyses with continuous covariates can be avoided in dealing with discrete covariables.

However, in analyses of spatial pattern, site-specific classification variables produce a new set of difficulties. Suppose that the count-proportion is modeled as $\lambda_{ij} = \delta_{j(i)}$, so that the mean counts are modeled by

$$\log(\mu_{ij}) = q_{j(i)} + f_i(t_j) \quad , \tag{11}$$

where $q_{j(i)} = \theta_i + \delta_{j(i)}$. As before, we are unable to estimate θ_i; we can estimate $q_{j(i)}$, but it is not immediately clear how these estimates can be used to extract information about the relative size of populations at distinct sites i and k . Differences $q_{j(i)} - q_{k(l)}$ reflect not only differences between routes $(\theta_i - \theta_k)$, but also differences between observers $(\delta_{j(i)} - \delta_{k(l)})$.

In the BBS, the $q_{j(i)}$'s are mean counts by observers, adjusted for temporal patterns of change in the population. Further modeling is required in order to define estimable parameters of the form $q_i = \theta_i + \mu$, which can be used as indices to examine spatial patterns of change. We address this issue in the next section.

3 Random Effects Models for Site-specific Classification Variables

Given that site-specific classification variables are needed to describe the count-proportion, and given that estimates of $q_{j(i)} = \theta_i + \delta_{j(i)}$ are available, estimation of relative population size at distinct sites requires a modeling of relations among the parameters $\delta_{j(i)}$ across sites. The simplest case is when the $\delta_{j(i)}$ can be assumed to be identically distributed random variables, with common mean μ. Then, an estimate of $q_i = \theta_i + \mu$ could be obtained by averaging estimates $\hat{q}_{j(i)}$ within sites. In the case of the BBS, this approach would lead to averaging of adjusted mean counts for observers within routes (the adjustment being for change in population size) to obtain a route specific index to population size.

Unfortunately, the site-specification classification parameters $\delta_{j(i)}$ are likely not to be spatially or temporally homogeneous. In the BBS, for instance, considerable evidence exists of trend in the ability of the pool of observers B the expected value of $\delta_{j(i)}$ can be thought of as an increasing function of $\zeta_{j(i)}$, the observer's initial year of service. It is necessary to adjust out the effects of the covariate $\zeta_{j(i)}$ before averaging estimates of the $q_{j(i)}$'s.

Thus while retaining the important feature that the $\delta_{j(i)}$ of model (11) are site-specific, our analysis of BBS data moderates the assumption somewhat by supposing that these effects can be thought of as random variables, with distributions having features in common across sites. Our model is similar to that of Morton (1987), except that we do not require identical distributions for the random effects; we allow the possibility that the random effects have expected values depending on observed covariates, $\zeta_{j(i)}$. We suppose that

$$\delta_{j(i)} = g\left(\zeta_{j(i)}\right) + \varepsilon_{j(i)} \,, \tag{12}$$

whence

$$q_{j(i)} = \theta_i + g\left(\zeta_{j(i)}\right) + \varepsilon_{j(i)} \,, \tag{13}$$

where $g(\zeta)$ describes the effect of covariate ζ, and the $\varepsilon_{j(i)}$ are identically distributed random variables with mean zero.

It would be possible to substitute (12) in the model specification (11), and to simultaneously estimate trajectory and factors influencing the count-proportion. Instead, we first obtain estimates $\hat{q}_{j(i)}$ and then analyze these according to the specification (13).

There are two reasons for this approach. First, as a practical matter, it may be that the model for the count-proportion can be applied at a much larger scale than it is convenient to analyze trajectories; spatial heterogeneity of trajectory may require numerous parameters and carry with it the attendant costs of high-dimensional optimization. A second consideration in favor of our two-stage approach is that misspecification of the model for the count-proportion can result in biased estimation of the trajectories. Since, as we have argued elsewhere (see Link and Sauer, 1997), the primary use of count data is in estimating patterns of temporal change, we believe that estimation of relative abundance should be maintained as a separate and distinct analysis to be carried out after having estimated trajectories with controls for differences in the count-proportion. Our two-stage approach to the analysis of trajectories and relative abundances thus not only has the advantage of conceptual simplicity, but also places priority on estimation of temporal pattern of population change while allowing for analysis of relative abundance at a large geographic scale. We illustrate this approach in the following example.

4 Example: Estimation of Spatial Patterns Using BBS Data

We consider the application of the means model (11) to a spatial analysis of Loggerhead shrike (*Lanius ludovicianus*) populations, using data from the BBS. Our analysis is structured by the intersections of states (provinces) with physiographic strata, as described by Robbins et al. (1986) and modified by Droege and Sauer (1989). These state-stratum units form convenient groupings of BBS routes for analysis; species tend to have similar relative abundances and temporal patterns of change within state-stratum units. Sampling intensity tends to be constant within state-stratum units, but to vary among units (see Peterjohn et al., 1995).

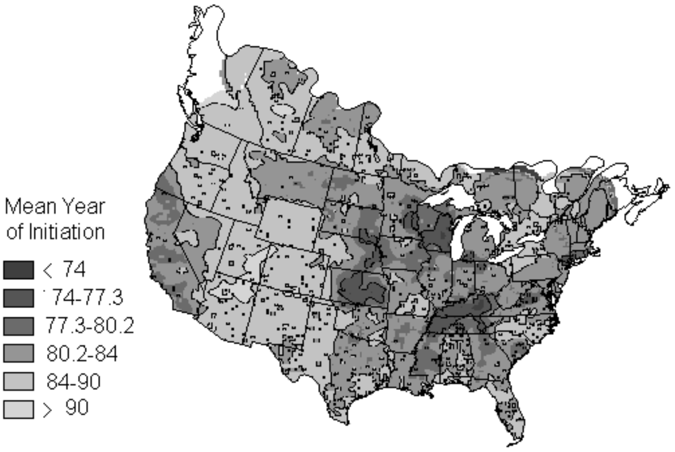

Figure 2: Smoothed map of average initiation year for BBS routes. Darkest regions correspond to regions with earliest average initiation year.

Some BBS routes have higher turnover rates for observers than others; some routes were initiated in 1966, and others later. We computed mean year of observer initiation for each BBS route, as a measure of these differences. A distance weighted smoothed map of average initiation year is given in Figure 2. Clear geographic patterns emerge, suggesting that maps of relative abundance from BBS data should be constructed having controlled for observer initiation year.

All told, there are 252 state-stratum units in the area surveyed by the BBS; Loggerhead shrikes were observed in 156 of them. The data set we consider comprises 35,496 records of counts provided by 7312 observers on 2506 routes in the 156 state-strata where shrikes were observed. 60% of the counts are zeros; 24.6% are one, two or three; and 15.4% are 4 or greater, including 18 counts [0.05%] of more than 40 shrikes. 28 to 31 years of data are available for 149 of the 156 state-strata.

To analyze these data, we assumed that the trajectories are spatially homogeneous within state-strata. Estimation and model selection were carried out using the quasilikelihood approximations to the Dirichlet compound multinomial distribution described by Link and Sauer (1997). For 74 state-strata, we fit year-effects models of the form

$$\log(\mu_{ij}) = q_{j(i)} + \phi_{t_j} \,, \tag{14}$$

where $q_{j(i)} = \theta_i + \delta_{j(i)}$; as before, i indexes BBS route within site, j indexes sampling occasions and $j(i)$ denotes the observer that produced the j^{th} count at site i. Parameters ϕ_t describe population change relative to a baseline year (1993, for which $\phi_t = 0$); parameters $q_{j(i)}$ reflect route-specific abundance, θ_i, and observer effects $\delta_{j(i)}$. For the remaining 82 state-strata, we fit reduced parameter models of the form

$$\log(\mu_{ij}) = q_{j(i)} + \beta(t_j - 1993) \;; \tag{15}$$

in 59 of these cases the slope parameter β was set equal to zero. The decision to fit reduced parameter models was made, in 58 of 82 cases, on the basis of likelihood ratio tests (p-value > .05 in test of linear model against year effects model). In the remaining 24 cases, year effects models were not estimable because of missing years or otherwise insufficient data. In 19 of these 24 cases, and 40 of the 58 cases where a linear model was selected, a likelihood ratio test of $H_0: \beta = 0$ was not rejected at significance level $\alpha = 0.05$, allowing a further simplification of the model.

We conditioned on observer totals, treating each observer=s data as an overdispersed multinomial random variable, and estimated year effects using techniques described by Link and Sauer (1997). The parameters $q_{j(i)}$ were then estimated by

$$\hat{q}_{j(i)} = \log\left\{ \frac{\sum_{k(i)=j(i)} Y_{ik}}{\sum_{k(i)=j(i)} \exp(\hat{\phi}_{t_k})} \right\} \;;$$

in words, the quantity in braces is the ratio of total counts to total of fitted trajectory values for observer $j(i)$. We thus obtained 7312 estimates $\hat{q}_{j(i)}$ corresponding to the 2506 routes.

The estimates $\hat{q}_{j(i)}$ were used to obtain estimates of relative abundance. Note from (13) that if there is temporal change in the pool of observers (i.e., $g(\zeta)$ is not a constant function of initiation year ζ), we cannot simply average these estimates within routes to obtain indices of abundance; we must control for such changes, or risk confounding spatial patterns of abundance with spatial pattern of initiation years for the pool of observers. We did so by fitting a model similar to (13), with $\hat{q}$'s substituted for q's, and supposing that the $\varepsilon_{j(i)}$'s have normal distributions. The effect of observer initiation year, ζ_{ij}, was modeled as a factor having one level for each of the possible initiation years. That is, we set $g(\zeta_{ij}) = \Gamma_{\zeta_{ij}}$ for parameters $\Gamma_1, \Gamma_2, \ldots, \Gamma_{31}$ corresponding to years 1966-1996; $\Gamma_1 = 0$ is required for identifiability. We used estimates of variances of $\hat{q}$'s from the original analysis as precision weights.

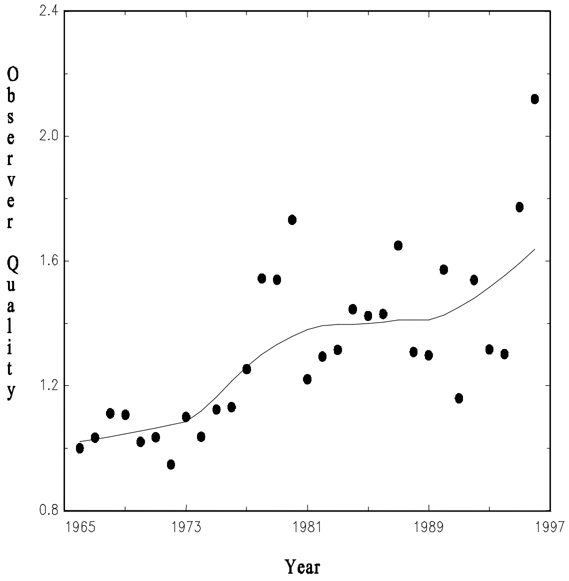

Figure 3: BBS average observer quality indices plotted against initiation year, based on Loggerhead shrike data. Baseline 1966 = 1.00. Smooth is Loess curve, tension parameter $f = 0.5$.

A practical consideration in modeling relative abundance from the $\hat{q}_{j(i)}$'s is that there are prohibitively many parameters to be estimated B 2537 in total. We dealt with this difficulty as follows: First, we estimated the 31 Γ_t's (initiation year effects) having conditioned on sufficient statistics for the 2506 parameters corresponding to route effects (i.e., the θ_i's). We then used the estimated Γ_t's to adjust $\hat{q}$'s for the effect of observer initiation year, obtaining

$$q\sim_{j(i)} = \hat{q}_{j(i)} - \hat{\Gamma}_{\zeta_{j(i)}} \quad ;$$

each $q\sim_{j(i)}$ is an abundance index for route i in 1993, corresponding to observer $j(i)$. For routes with more than one observer, a composite abundance index $\hat{q}_i$ was defined by taking a precision weighted average of the abundance indices $q\sim_{j(i)}$ for observers on the route.

Exponentiating the estimates $\hat{\Gamma}_t$, $t = 2, 3, ..., 31$, yields indices to the average ability of the pool of observers, scaled to the first year of the survey (1966). Figure 3 plots estimates of $\exp(\Gamma_t)$ against time; a Loess curve (tension parameter $f = 0.5$) has been added to produce a smooth of the indices against time. We note a clear pattern of increasing observer ability; the newest recruits to the BBS count 50-60% more Loggerhead shrikes than those that initiated the survey in the 1960's, even having controlled for differences among sites (including differences in the collections of sites surveyed) and for differences in shrike population sizes.

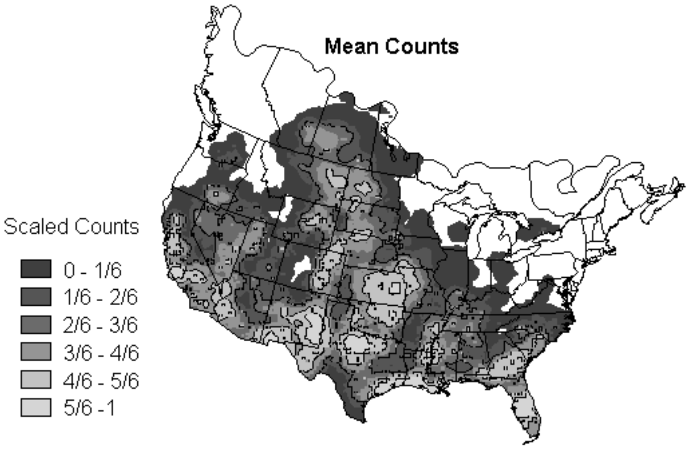

Figure 4: Smoothed map of patterns of relative abundance for Loggerhead shrike, having controlled for initiation year differences in the pool of observers. Grayscale partitions range according to sextiles of relative abundance, with darkest areas representing regions of greatest abundance.

Figure 4 is a smoothed map of patterns of relative abundance for Loggerhead shrike, having controlled for initiation year differences in the pool of observers. This map can be compared with Figure 5, produced by taking average counts on routes over the period 1990-1996, and using the same smoothing techniques as for Figure 4, but without controls for differences among observers. Patterns of difference between Figures 4 and 5 are most clearly identified by calculating a difference in the relative abundances, standardized by the square root of the modeled abundance. A map of such standardized differences is given in Figure 6. We note in particular that modeled relative abundances are greater in the central U.S. and mountains, and smaller in the Great Basin. These differences are explained in part by patterns of observer initiation year (cf. Figure 1) and in part by differences in the level of control for temporal patterns of change in the data.

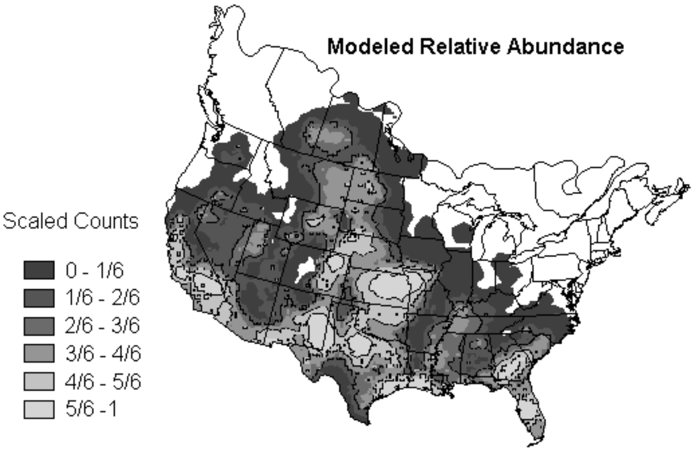

Figure 5: Smoothed map of average counts on routes over the period 1990-1996, without controls for temporal change in population or observer pool. Grayscale partitions range according to sextiles of relative abundance, with darkest areas representing regions of greatest abundance.

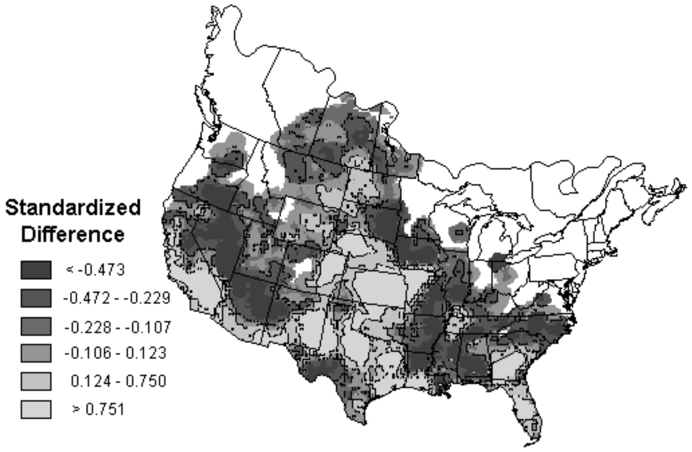

Figure 6: Differences in relative abundance estimates (Figures 4 and 5), standardized by the square root of the modeled abundance. Darkest (lightest) areas represent regions where modeled relative abundance is greater than (less than) unadjusted mean count for 1990-1996.

5 Discussion

Many investigators fail to recognize that counts are an imperfect mirror of population sizes. In our view, count data are only useful if 1) the count-proportion is estimated (such as in capture-recapture models), 2) the count-proportion can safely be assumed to be constant, or 3) factors affecting variation in the count-proportion can be first identified and then accommodated through parametric modeling. The approaches outlined in this paper are intended for application in the third of these cases. It should be noted that in the second and third cases described, *actual* abundances cannot be estimated; the methods we have outlined provide indices that can be used to estimate *relative* abundances.

In our example, we have provided clear evidence that count-proportions in the BBS are influenced by observer differences. This factor is confounded with temporal and spatial patterns of population change; estimates of spatial and temporal patterns in relative abundances are likely to be biased if these are not controlled for. This example, and many other published analyses of BBS data (see Sauer et al., 1994), indicate that change in the observer pool should be evaluated in any analysis of spatial pattern of BBS counts.

The pattern of change in BBS observer ability we estimated from Loggerhead shrike data is not peculiar to that particular species. In similar (unpublished) analyses for 76 other bird species, all with AOU numbers in the range 6100-6970, the patterns of change in observer quality indices Γ_t for these species were generally similar to that seen in the Loggerhead shrike analysis. In Figure 7, a composite observer quality index (variance-weighted averages, across 77 species) is plotted against time, summarizing these analyses; the pattern is quite similar to that seen in Figure 3. The apparent increase in quality of the observer pool is consistent with other published works on the topic (see Sauer et al., 1994). Note that this relationship is determined controlling for route effects; spatial patterns in year of route initiation do not affect this pattern.

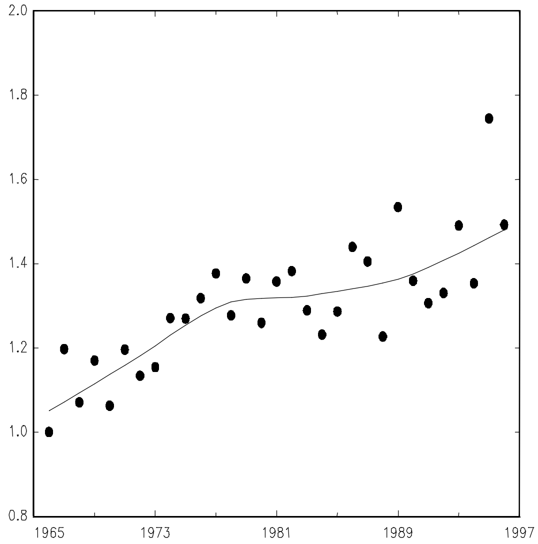

Figure 7: BBS average observer quality index plotted against year of initiation (composite index, a variance-weighted average for 77 species); the pattern is quite similar to that seen in Figure 3.

The reliability of estimates of relative abundance depends, of course, on the adequacy of the model for factors influencing the count-proportion. It should be noted that additional factors may influence count-proportions; as such factors are identified, they should be added to the model. Designers of count surveys should consider occasionally estimating count-proportions, with the goal of identifying such factors.

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